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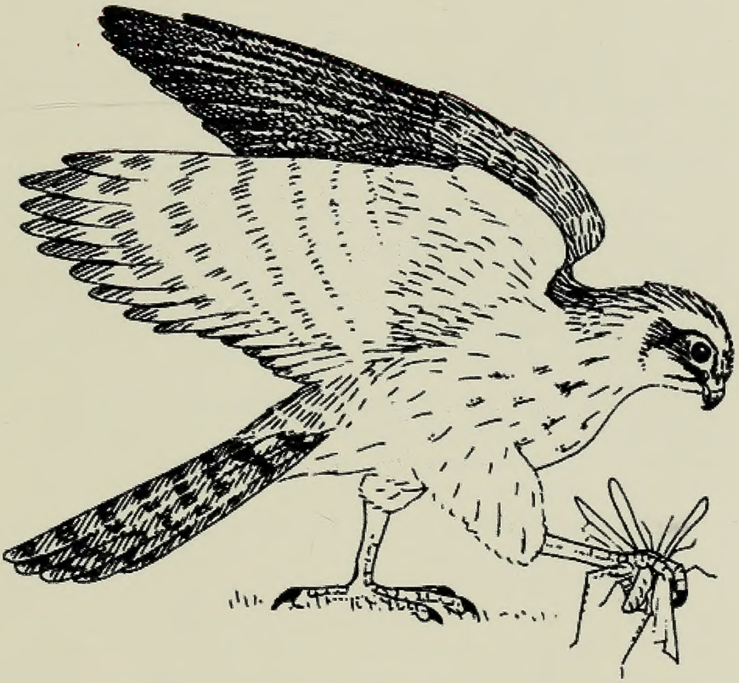

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A new species of three-toed sloth (Mammalia: Xenarthra) from Panamá, with a review of the genus *Bradypus*

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Abstract.—Morphological and morphometric analyses of three-toed sloths (*Bradypus*) from the islands of Bocas del Toro reveal rapid differentiation of several populations during the Holocene. These islands, lying off the Caribbean coast of western Panamá, were separated from the adjacent mainland by rising sea levels during the past 10,000 years. The sequence of island formation and the approximate ages of the islands are known. In at least four independent events, sloths on five of the islands evolved smaller size following insularization. Sloths on the younger islands remain conspecific with mainland populations of *Bradypus variegatus.* On Isla Escudo de Veraguas—the oldest and most remote island of the archipelago—however, the three-toed sloth has differentiated to the species level, and we here describe it as *Bradypus pygmaeus.* We provide updated diagnoses and distributions for the species of *Bradypus,* including a key to the genus.

Resumen.—Se realizaron análisis morfológicos y morfométricos de los perezosos de tres dedos (*Bradypus*) de las islas de Bocas del Toro, que mostraron una diferenciación rápida de varias de las poblaciones durante el Holoceno. Estas islas, que se ubican en la costa caribeña del occidente de Panamá, se separaron de tierra firme debido a aumentos en los niveles del mar durante los últimos 10.000 años. Se conoce la secuencia de formación de las islas y sus edades aproximadas. Los perezosos de cinco de las islas evolucionaron hacia un tamaño corporal menor en por lo menos cuatro eventos independientes, siguiendo el proceso de insularización. Consideramos que tanto los perezosos de tierra firme como los de las islas jóvenes son representantes de la especie *Bradypus variegatus*; sin embargo en la Isla Escudo de Veraguas, la más vieja y más remota del archipiélago, el perezoso de tres dedos ha logrado el nivel de especie y lo describimos acá como una especie nueva, *Bradypus pygmaeus.* Presentamos caracteres diagnósticos y distribuciones para las especies de *Bradypus,* incluyendo una clave de las especies del género.

Together with armadillos and anteaters, sloths make up the Neotropical order Xenarthra (Gardner 1993, or magnorder Xenarthra sensu McKenna & Bell 1997). Two distantly related genera of sloths, *Choloepus* (two-toed sloths) and *Bradypus* (three-toed sloths) are extant. Over much of their ranges, one species of *Choloepus* and one species of *Bradypus* occur together in the same habitat, exhibiting biotic sympatry (= syntopy; Sunquist & Montgomery 1973, Wetzel 1985, Taube et al. 1999). The two genera are easily distinguished by the number of clawed digits on their forelimbs (two for *Choloepus*; three in *Bradypus*), by the blunter muzzle of *Bradypus,* and by dentition—stronger and more complex in *Choloepus,* while simple and peg-like in *Bradypus* (Naples 1982, Wetzel 1985). Here we consider only the three-toed sloths, *Bradypus.*

The three nominal species of *Bradypus* can be distinguished both externally and cranially (Wetzel & Avila-Pires 1980, Wetzel 1985). The maned sloth (*Bradypus torquatus*) of southeastern Brazil has a distinctive plume or mane of long, jet-black hair from its nape to the middle of its back, and its skull is characterized by inflated pterygoid sinuses (illustrated by Wetzel 1985:10). Both the pale-throated sloth, *Bradypus tridactylus* (Guianas, eastcentral Venezuela, and northcentral Brazil), and the brown-throated sloth, *B. variegatus* (Honduras to Argentina), lack the mane and inflated pterygoids. Adult males of these two species also have a large orange patch (speculum) on the dorsum. They may be distinguished from each other by the bright golden-yellow throat and face in *B. tridactylus,* whereas the throat is brownish, at least at the base of the hairs, in *B. variegatus.* Most *B. variegatus* also possess a facial stripe not present in *B. tridactylus.* A single pair of large foramina in the anterodorsal nasopharynx in *B. tridactylus* are lacking in *B. variegatus* (illustrated in Wetzel 1985:10). Emmons & Feer (1997) provided external color illustrations of these sloths.

Three-toed sloths are arboreal folivores. They eat leaves of a variety of trees, including, but by no means limited to, *Cecropia* spp., which is a common early successional tree in Neotropical rainforests (Carvalho 1960, Montgomery & Sunquist 1975, Chiarello 1998b). Concomitant with their energy-poor diet, they have low metabolic rates and are not fully homeothermic (Britton & Atkinson 1938). Interestingly, temperature regulation is more effective in pregnant females (Morrison 1945). The percent of body weight made up of muscle in *Bradypus* is about half that of most mammals (Britton & Kline 1939); its muscle mass to surface area ratio may not be enough to create sufficient heat to maintain a constant body temperature. Clearly, the low level of energy expenditure by three-toed sloths for both movement and thermoregulation directly relates to their diet of leaves.

The natural history of *Bradypus* indicates a low potential for dispersal. Sloths avoid predation largely by avoiding detection, moving very slowly in trees (Brattstrom 1966). Their small home ranges average 1.6 ha (Montgomery & Sunquist 1975, see also Chiarello 1998a). Furthermore, their outer fur harbors an alga, which grows in grooves in the surface of the hair (Alston 1879:183, Aiello 1985), giving the pelage a green tint and providing camouflage. Sloths move even more slowly on the ground than in trees, traveling on average 0.4 km per hour (Britton & Kline 1939). Surprisingly, they are known to swim well in rivers (Beebe 1926:7–9, Carvalho 1960), but we have found no reference to their swimming in salt water. Perhaps they have a behavioral aversion to salt water or to rough water and wave action. Their relatively large size, restricted diet, and low dispersal potential make sloths a model system for investigating the evolution of body size in large insular mammals.

The islands of Bocas del Toro.—The province of Bocas del Toro is located on the Caribbean coast of northwestern Panamá adjacent to Costa Rica (Fig. 1). Just off the coast lies a group of continental islands that were formed during the Holocene as a result of postglacial events, including rising sea level and continental submergence due to meltwater loading and redistribution of the Earth's magma. Rising sea levels isolated hilltops and ridges, first as peninsulae, and then eventually completely separated them as islands. The islands of Bocas del Toro have low elevations and occupy a Tropical Moist Forest life zone, *bosque húmedo tropical* (OEA 1959). They vary in age, size, distance from the mainland, and depth of surrounding water. Mangrove swamps (primarily red mangroves, *Rhizophora mangle*) fringe parts of the shoreline of Bocas del Toro and the coasts of some of the islands, possibly acting as added barriers to the dispersal of some species.

Combining ocean floor topography with studies of pollen and coral cores from the western Caribbean allowed Handley and M. Varn (in litt.) to determine the sequence of island formation and to estimate the dates of separation events for the various islands of Bocas del Toro. We present their general conclusions as an introduction to this island system and to interpret the evolution of three-toed sloths in Bocas del Toro. Assuming that the present-day submarine topography of Bocas del Toro is not very different from that of the terrestrial topography 10,000 years ago (before flooding), then the depths of water at which land bridges to various present-day islands disappeared should be apparent from current sea-floor maps. Thus, given estimates of sea level at various time intervals in the past, it is possible to estimate the approximate date of isolation of each island. Handley and Varn obtained sea-floor data from maps of Bocas del Toro produced by the U.S. Army Map Service. Using geographic information systems (GIS) software, they digitized data points from isobars below present sea level. With a program produced by the Morphometrics Laboratory of the National Museum of Natural History, they converted the data points to a database transferable to Surfer 4 and then connected them to produce maps of bathymetric contours of Bocas del Toro for various depths below present sea level.

To estimate sea levels over the past 10,000 years, Handley and Varn utilized three models based on coral and pollen cores taken in the western Caribbean. Radioisotope dating of *Acropora palmata,* a coral restricted to the upper 5 m of water, formed the bases of the curves of depth-below-current-sea level vs. time produced by Lighty et al. (1982) and Fairbanks (1989). Bartlett & Barghoorn (1973) used the pollen of *Rhizophora mangle* in deep-sea cores from the Gatún Basin in Panamá to produce a similar curve. *Rhizophora mangle* is an obligate saltwater species and represents the major component of Neotropical coastal mangrove swamps. Handley and Varn then created a composite curve with years-before-present and depth-below-current-sea-level as axes. Using this curve, they roughly dated each of the bathymetric maps and thus estimated island ages from dates of disappearance of land bridges between islands and the mainland. Even if their absolute dates err in one direction or the other, relative dates of island formation will be correct to the extent that sea-floor contours in this region have remained constant through the Holocene.

Isla Escudo de Veraguas (= Isla Escudo) occupies a position well outside the Laguna de Chiriquí (Fig. 1a), and was the first of the islands to be separated from the mainland of Bocas del Toro (ca. 8900 years B.P.). It fragmented from the eastern shore of the Península Valiente and is not directly related to the other islands (Fig. 1b). To the northwest of the Península Valiente and Isla Escudo, the islands of the Laguna de Chiriquí are much younger (Fig. 1a). They fragmented sequentially from the Península Tierra Oscura, which was once a long, *J*-shaped peninsula jutting out from the southwestern shore of the Laguna de Chiriquí. The peninsula was formed by the opening of the Boca del Drago Pass at the western end of the Laguna (Fig. 1b). These islands are related to each other, but not to Isla Escudo. The outermost, facing the ocean, are about 5000 years old: Isla Colón, which was the first to split off of the Península Tierra Oscura (ca. 5200 years B.P.), and Isla Bastimentos, which separated from the peninsula along with what now is Cayo Nancy (ca. 4700 years B.P.). Cayo Agua became isolated from the adjacent mainland (now part of Isla Popa) about 3400 years B.P. Cayo Nancy recently split from Isla Bastimentos proper (<1000 years B.P.), and

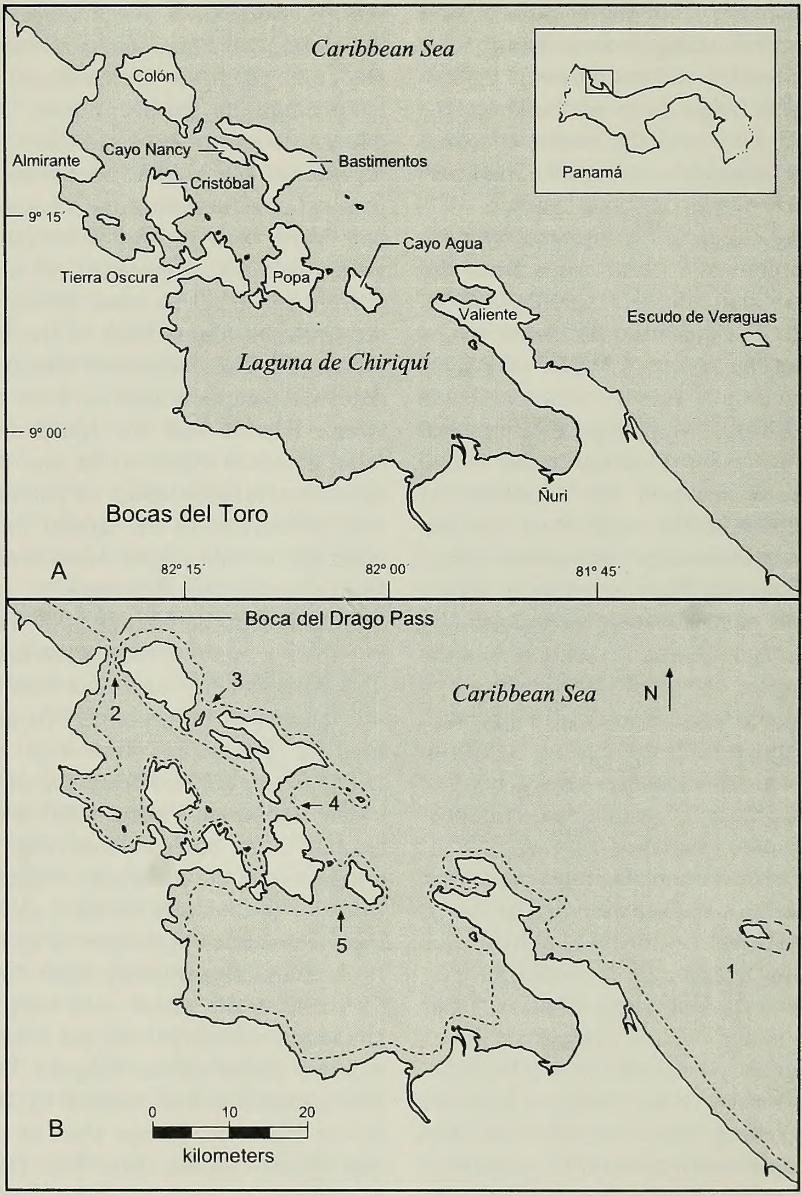

Fig. 1. Maps of Bocas del Toro showing major islands and place names on the mainland (A, upper) and reconstruction of the sequence of island formation (B, lower). In B, the dashed line approximates sea level at 10 m below present. Major events in the formation of the islands (Handley & Varn, in litt.) are as follows: 1) Isla Escudo separated from the southern coast of the province, ca. 8900 years B.P.; 2) the Boca del Drago pass opened, creating a *J*-shaped peninsula in the Laguna de Chiriquí, ca. 6300 years B.P.; 3) Isla Colón became isolated from the peninsula, ca. 5200 years B.P.; 4) the superisland Isla Bastimentos-Cayo Nancy became separated from what remained of the peninsula, ca. 4700 years B.P.; and 5) Cayo Agua was formed, ca. 3400 years B.P. More recently (in the past 1000 years), Isla Cristóbal and Isla Popa separated from the mainland, and Cayo Nancy split from Isla Bastimentos.

mangroves fringe the shallow channel between it and Isla Bastimentos. Isla Popa and Isla Cristóbal each separated from the mainland in the past 1000 years. They are isolated from the mainland only by narrow, shallow channels through mangroves. Island area and distance from the mainland follow, for each of the major islands: Cayo Agua—14.5 km^2, 6.6 km; Cayo Nancy—6.8 km^2, 9.5 km; Isla Bastimentos—51.5 km^2, 6.3 km; Isla Colón—59.0 km^2, 1.5 km; Isla Cristóbal—36.8 km^2, 0.3 km; Isla Escudo—4.3 km^2, 17.6 km; Isla Popa—53.0 km^2, 1.8 km. Further discussion of the history of Bocas del Toro and surrounding regions can be found in Jackson et al. (1996).

Biological interest in the islands of Bocas del Toro emerged recently (summarized in Handley 1959, Olson 1993, Kalko & Handley 1994). Early collecting took place from 1958 to 1967 and intensified from 1987 to 1993, when scientists from the Smithsonian Institution sampled the biota on all of the islands and at several sites on the adjacent mainland. The major mainland collecting sites of sloths were Almirante and Tierra Oscura in the west, and Ñuri and the Península Valiente in the east (Fig. 1a). Smaller collections of *Bradypus* were made at Sibube and Changuinola in western Bocas del Toro. We assume that the fauna of the coastal plain of Bocas del Toro was relatively uniform as the islands sequentially became isolated from the mainland (Handley 1959, Olson 1993, Kalko & Handley 1994). Colinvaux (1997) has shown that despite significant climatological fluctuations, the vegetation of lowland tropical forests in Panamá remained intact during glacial times, lending support to this premise. Subsequent to their isolation, numerous species—including bats, rodents, cats, and weasels present on the nearby mainland—have been extirpated from some or all of the islands. Conversely, a few apparently relict species no longer found on the adjacent mainland are present on the islands. Many of the species that have survived on the islands exhibit marked morphological differentiation from their mainland relatives. For example, a fruit-eating bat, *Artibeus incomitatus,* underwent rapid differentiation on Isla Escudo (Kalko & Handley 1994).

Collectors found three-toed sloths (*Bradypus*) on all of the major islands, as well as at the mainland sites. The *Bradypus* on several of the islands were notably small, and some lived in the red mangroves rather than in upland forest trees as elsewhere. On Isla Escudo, *Bradypus* was found only in mangroves. Except for one purchased at Tierra Oscura from a local boy who claimed to have caught it in a mangrove, no three-toed sloths were found in mangroves on the mainland of Bocas del Toro. The 1993 expedition searched in vain for sloths in extensive areas of mangroves near Ñuri. This ecological separation, coupled with the observed size differences, spawned the current study.

Materials and Methods

Museum specimens.—We examined a total of 531 specimens of the genus *Bradypus* in 13 natural history collections (see Specimens examined) identified as follows: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BM, now Natural History Museum of London); Field Museum, Chicago (FMNH); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN); Instituto del Desarrollo de Recursos Naturales Renovables, INDERENA, Bogotá (IND-M; specimens now part of the collection of the Instituto Alexander von Humboldt, Villa de Leiva); Michigan State University Museum, East Lansing (MSU); Museo del Instituto La Salle, Bogotá (MLS); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); United States National Museum of Natural History, Washington, DC (USNM; * denotes specimens returned to Panamá-INRENARE); Universidad del Cauca, Popayán (UC); Universidad del Valle, Cali

(UV), University of Kansas Natural History Museum, Lawrence (KU); and University of Michigan Museum of Zoology, Ann Arbor (UMMZ). Information provided by any source other than the collector is placed in [brackets]. Numbers in (parentheses) after the country name indicate the total number of specimens examined for that country.

In the Specimens examined sections, latitude and longitude are given after the place name to which the coordinates belong. Coordinates provided by the collector appear in parentheses. We provide latitude and longitude in brackets for localities that appear in the following standard references: Brazil—Paynter & Traylor (1991); Bolivia—Paynter et al. (1975); Colombia—Paynter (1997), except where more exact coordinates are given by Hershkovitz (1947) or in original sources cited in Anderson (1999), as noted; Costa Rica—McPherson (1985); Ecuador—Paynter (1993); French Guiana, Guyana, and Suriname—Stephens & Traylor (1985); Nicaragua—USBGN (1956), except where more exact coordinates appear in Genoways (1973); Panamá—Fairchild & Handley (1966); Peru—Stephens & Traylor (1983); and Venezuela—Paynter (1982); additional coordinates for localities in several countries were taken from Hershkovitz (1977), and are so noted.

Pelage analyses.—We analyzed geographic variation in pelage characters in the *Bradypus* from Bocas del Toro and in *B. variegatus* from other regions, principally from Nicaragua, central Panamá, and Colombia. Pelage analyses were based on specimens in the ICN, IND-M, KU, MLS, USNM, UC, and UV collections. Because different methods of field preparation or tanning can affect the color of fur, we did not consider subtle color differences. We focused on striking differences in color and color pattern. We eliminated juvenal and immature animals from the pelage analyses by including only individuals whose skulls indicated them as adult (see Cranial analyses) if skull was available, or that had clearly reached adult size if only a skin was present, based on the total length of specimens in that population verified as adult by their cranial characters.

We found seven pelage characters that varied among populations. Overall facial color is either tan (off-white to pale brown) or yellow (golden). Orange around the eyes is present to various degrees, or absent. Brow-color categories are: dark brow (a terminal band of 2–3 cm of dark brown or black hair), some dark hair on brow (a narrow terminal band of only about 1 cm of dark brown hair), or dark hair not present (in which case the brow is generally pale brown, with no dark terminal band). A distinct boundary line on the brow between the dark hair of the brow and the longer, paler hair of the crown is visible in some specimens, but in others the color of the brow hair blends in with that of the crown. Some individuals have a stripe down the midsagittal plane of the back. Dorsal underfur always appears blotchy, with pale and dark patches, but the surface coloration varies. Overall dorsal appearance is blotchy with brown and beige patches when the outer fur color corresponds to the color of the underfur in that particular area of the dorsum. In other animals, the surface color is uniformly pale, regardless of the color of the underfur. The color of the underfur can be observed by pushing aside the outer fur and examining the shorter underfur. In some specimens, the fur of the crown and the sides of the head is extremely long, overhanging the forehead and sides of the face and creating the aspect of a hood. In other specimens, the fur of the crown and sides of the head is shorter and not noticeably overhanging the face.

Cranial analyses.—For cranial analyses, we included only sloths that had reached adult size (Age classes 2 and 3, as defined below). Because no explicit standards exist for aging *Bradypus* skulls (but see Naples 1982:6–7), we developed the following system of age categories.

Age class 0, newborn and juvenile: all sutures open; size small; anterior skull elements small and poorly developed; masseter-temporal fossa smooth; postmastoid fossa not indicated; frontal sinuses little, if at all, swollen; lambdoidal crest not formed.

Age class 1, immature: all sutures open; size intermediate; anterior skull elements nearing adult proportions; masseter-temporal fossa usually smooth; postmastoid fossa may be indicated; frontal sinuses somewhat swollen; lambdoidal crest present (immatures may retain some juvenal characters).

Age class 2, young adult: all sutures open; size large; anterior skull elements at adult proportions. Young adults must also have some of the following: masseter-temporal fossa rugose to the touch; postmastoid fossa prominent; frontal sinuses swollen; lambdoidal crest sharp-edged.

Age class 3, full adult: some or all sutures closed; size large; anterior skull elements fully developed. Fully adult sloths have most or all of the following: masseter-temporal fossa visibly rugose; postmastoid fossa prominent; frontal sinuses swollen; lambdoidal crest sharp-edged.

Individuals reach adult size by Age class 2 in *Bradypus*. Skulls with all cranial sutures closed clearly represent adults, but closure of even one suture signifies full-adult status. The nasal (internasal) and interparietal sutures are usually the last to close. Closure of the basioccipital-basisphenoid suture represents a good indicator of maturity in bats and rodents, but this suture closes late in *Bradypus* after adult size is attained. Its lack of closure should not be used alone to judge adulthood.

Measurements.—We recorded external measurements—total length (TOTAL); tail length (TAIL); hind foot length (HF); and ear length (EAR)—in mm and body mass in kg from museum labels. Using dial calipers to the nearest 0.1 mm, we took 14 measurements on all adult-sized skulls of *Bradypus* (Age classes 2 and 3) from Bocas del Toro (Fig. 2). To examine geographic variation in size in *B. variegatus* from other parts of its range, we measured only greatest length of skull (GLS) on series of *B. variegatus* of Age classes 2 and 3, using either dial or digital calipers to the nearest 0.1 mm. We chose GLS because preliminary morphometric analyses indicated that it was most highly correlated with general size in *Bradypus*. Specimens from the American Museum of Natural History were not included in the quantitative analyses, but we report them as additional confirmed distributional records. Cranial nomenclature follows Naples (1982). We here define and illustrate (Fig. 2) our measurements for *Bradypus*.

Greatest length of skull (GLS): Distance between the anteriormost point of the nasals and a line connecting the posteriormost surfaces of the occipital condyles.

Anterior zygomatic breadth (AZB): Greatest breadth across the jugal (anterior) zygomata.

Posterior zygomatic breadth (PZB): Greatest breadth across the squamosal (posterior) zygomata.

Postorbital breadth (POB): Least breadth across the constriction of the frontals, posterior to the postorbital processes.

Squamosal process length (SPL): Distance between anteriormost point of the squamosal process of temporal (posterior zygomata), and the notch formed by the junction of the posterior border of the bulla and the mastoid process.

Maxillary toothrow length (MTRL): Greatest alveolar length from the anteriormost edge of the anterior chisel-shaped tooth to the posteriormost edge of the last molariform tooth in a maxillary toothrow.

Postpalatal length (PPL): Distance between the anteriormost margin of the mesopterygoid fossa and the anteriormost margin of the foramen magnum.

Palatal breadth (PB): Greatest alveolar breadth across the lateral margins of the first molariform teeth.

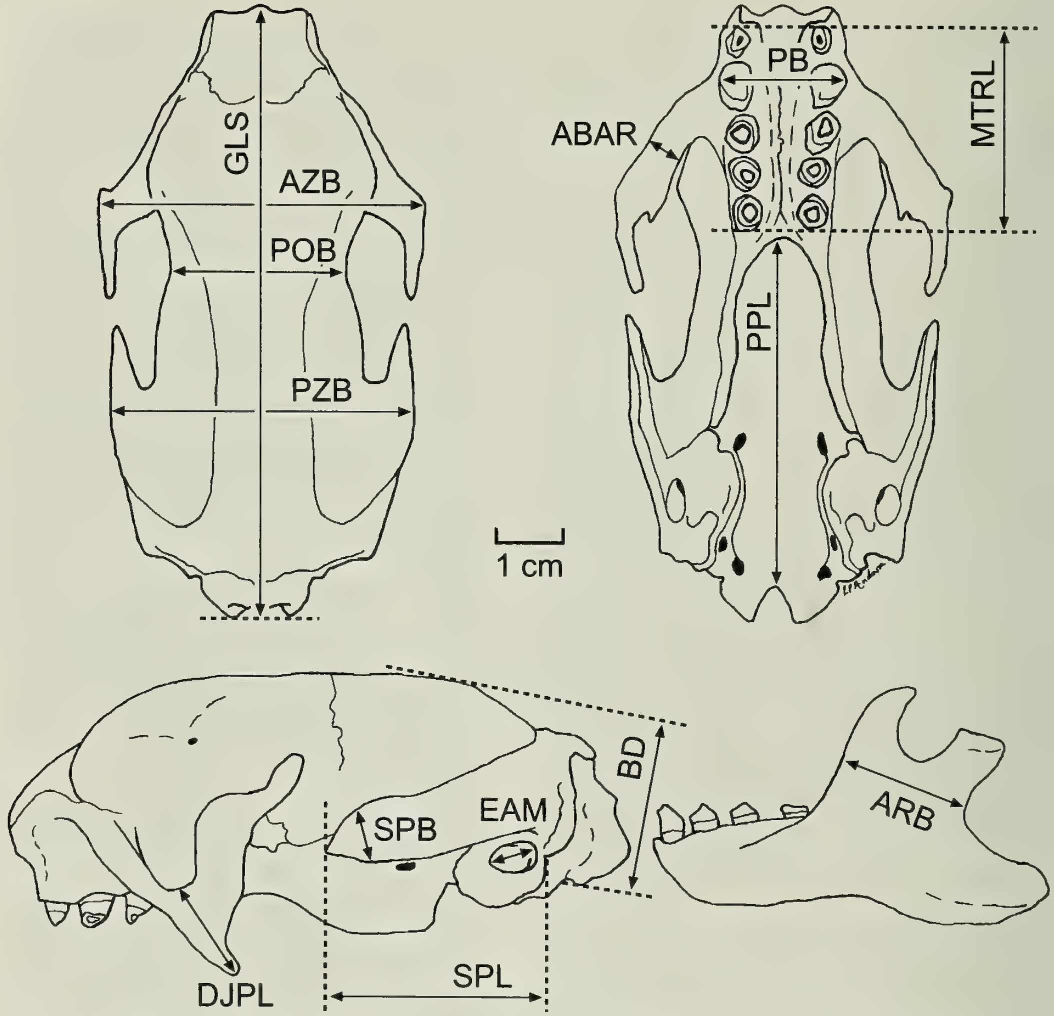

Fig. 2. Dorsal, ventral, and lateral views of a cranium and lateral view of a mandible of *Bradypus variegatus,* illustrating method of taking cranial measurements. Abbreviations and measurements are defined in the text.

Braincase depth (BD): Greatest distance between the medioventral surface of the basioccipital and the dorsalmost point of the braincase.

Antorbital bar breadth (ABAR): Least breadth across the flattened antorbital bar (jugal process of zygomata) anterior to its division into the ascending and descending jugal processes, taken in ventral view.

Descending jugal process length (DJPL): Distance between the ventralmost point of the descending jugal process and the nearest point on the dorsal border of the jugal process.

Greatest external auditory meatus diameter (EAM): greatest internal diameter of the external auditory meatus.

Squamosal process breadth (SPB): Breadth of the squamosal process, taken 5 mm posterior to the anterior tip of the process.

Ascending mandibular ramus breadth (ARB): Least distance between the anteriormost point of the angular notch of the mandible, between the condylar and angular processes, and the nearest point on the anterior margin of the ascending ramus below the coronoid process.

Statistics.—We calculated descriptive statistics and performed analyses of variance (ANOVAs) using MINITAB 11.12 software for personal computers (MINITAB 1996) and used SAS 6.12 for UNIX (SAS 1990) to examine the data using multivariate statistics. We used a Type-I error rate of $\alpha = 0.05$ for all tests. The probability levels that we report should be considered approximate, however, because our sample sizes were too small to test adequately for departures from multivariate normality.

We conducted a multiple-group discriminant function analysis (DFA) on the *Bradypus* of Bocas del Toro using $\log_{10}$-transformed measurements. Collection locality denoted group membership. Ear length and body mass were excluded from the DFA because few individuals carried those measurements. We tested for multivariate differences among localities by *F*-statistics for Mahalanobis distances between pairs of group centroids using Holm's (1979) modification of the Bonferroni correction for multiple comparisons. We then conducted multiple unplanned comparisons between all pairs of localities for scores on the first two canonical axes, using Tukey's test with a family-wide error rate of $\alpha = 0.05$.

Additionally, we performed a principal components analysis on the same data matrix without regard to collection locality. The first principal component (PC I) of the covariance matrix of $\log_{10}$-transformed measurements was used as the best measure of overall sloth size in further analyses. For the two populations with several individuals of both Age classes 2 and 3 (Cayo Nancy and Isla Escudo), we tested for a difference in mean PC I scores between age classes while controlling for locality, using a general linear model. Likewise, for those localities with multiple individuals of each sex—Cayo Agua, Cayo Nancy, Isla Popa, Península Valiente, and Tierra Oscura—we tested for a difference in mean PC I scores between sexes, again controlling for locality in a general linear model. Finally, we tested for differences between all pairs of localities on PC I, with the same protocols as in the comparisons of scores on the first two canonical axes.

We used measurements of greatest length of skull (GLS) to compare the small sloths from Bocas del Toro with *Bradypus variegatus* from mainland localities outside Bocas del Toro, as preliminary analyses indicated that GLS correlated highly with PC I, and thus represented a good measure of overall size. Series from Bonanza, El Recreo, and Tepeyac (Nicaragua); Bajo Calima-Río Raposo and Tumaco (Colombia); and Mojui dos Campos (Brazil) were our six mainland localities outside of Bocas del Toro, as few specimens were available from other sites. We conducted an ANOVA on GLS measurements of the six mainland samples outside Bocas del Toro and our samples from the five islands with small sloths in Bocas del Toro (Cayo Agua, Cayo Nancy, Isla Bastimentos, Isla Colón, and Isla Escudo), using a Tukey's test with a family-wide error rate of $\alpha = 0.05$.

Results

Pelage.—Externally, the *Bradypus* of Bocas del Toro resemble specimens from central Panamá more closely than they do those of Nicaragua or South America (Table 1). All Central American specimens have tan faces, whereas faces of most South American sloths have a yellowish cast. In addition, while the sloths of Bocas del Toro, central Panamá, and many localities in Colombia have at least some orange coloring around their eyes, Nicaraguan specimens lack this trait. Most individuals from Bocas del Toro have either some (~1 cm) or much (2–3 cm) black or dark brown brow hair. Specimens from central Panamá and extreme NW Colombia match those from Bocas del Toro in this trait, but Nicaraguan and most other South American sloths lack a dark brown brow. A distinct brow line is found in specimens from central Panamá, extreme NW Colombia, and in some localities in Bocas del Toro, but not in specimens from Nicaragua or elsewhere in Central America or western Colombia. Thus, the *Bradypus* from Bocas del Toro group with other Central American and western Colombian three-toed sloths, with closer affinity to those from central Panamá and extreme NW Colombia to the east rather than with sloths from Nicaragua to the northwest.

Within Bocas del Toro, geographically proximate populations share discrete pelage characters, often linking island populations with nearby populations on the mainland (Table 1; Fig. 1). For example, the only populations in Bocas del Toro with individuals lacking a dorsal stripe are found at Tierra Oscura and on the adjacent islands of Cristóbal, Popa, and Cayo Nancy. For dorsal appearance, there is a west-to-east cline from uniform to blotchy. The populations with the highest frequencies of individuals with a distinct brow line are two proximate localities in the west (Isla Colón and the adjacent mainland at Almirante) and two in the east (Isla Escudo and Ñuri, the nearest site on the mainland). Finally, while sloths from most localities in Bocas del Toro have orange eye patches, those of four central localities (Almirante, Isla Cristóbal, Isla Popa, and Península Valiente) have little if any orange. Overall, pelage of specimens from Isla Escudo closely matches pelage characters found at Ñuri. However, characters variable in the Ñuri population appear to be fixed on Isla Escudo. Sloths from Isla Escudo were unique in possessing long hair on the crown and sides of the head, giving the impression of a hood.

Quantitative measurements.—Both univariate and multivariate statistics documented the smaller overall size of *Bradypus* on the five outer islands (the older islands) of the archipelago of Bocas del Toro—Cayo Agua, Cayo Nancy, Isla Bastimentos, Isla

Table 1.—Discrete pelage characters for *Bradypus* from Bocas del Toro as well as from other selected regions throughout the range of *Bradypus variegatus.* Character abbreviations are as follows: face color, tan (T) or yellow (Y); orange on face, yes (Y), slight (slt), or no (N); dark on brow, yes (Y), some (S), or no (N); line on brow, yes (Y) or no (N); dorsal stripe, yes (Y) or no (N); dorsal appearance, uniform (U) or blotchy (B); and hood, yes (Y) or no (N). If samples are mixed for a character, both states are given with the most common state before the slash. Geographic groupings are arranged from NW to SE, with abbreviations as follows: NIC, Nicaragua; A, Almirante; CO, Isla Colón; N, Cayo Nancy; B, Isla Bastimentos; CR, Isla Cristóbal; TO, Tierra Oscura; P, Isla Popa; CA, Cayo Agua; V, Península Valiente; NU, Ñuri; E, Isla Escudo; CP, Central Panamá; SAW, South America west of the Andes; SAE, South America east of the Andes. Refer to Fig. 1 for geographic locations within Bocas del Toro.

Character	Locality														
	NIC	A	CO	N	B	CR	TO	P	CA	V	NU	E	CP	SAW	SAE
Face color	T	T	T	T	T	T	T	T	T	T	T	T	T	Y/T	Y/T
Orange on face	N	Y	Y	Y	Y	Y/slt	Y	Y/slt	Y	slt/N	Y	Y	Y	Y/N	N/Y
Dark on brow	N	S/Y	Y/S	S/N	S	S	S	N	S/Y	S	S/Y	Y	Y	N/Y	N/Y
Line on brow	N	N/Y	Y	N	N	N	N	N	N/Y	N	N/Y	Y	Y/N	N/Y	N/Y
Dorsal stripe	Y	Y	Y	N/Y	Y	N	N	Y/N	Y	Y	Y	Y	Y	Y	Y
Dorsal appearance	B	U/B	U	U/B	U	U	U/B	B/U	U/B	B/U	B/U	B/U	U/B	B	B
Hood	N	N	N	N	N	N	N	N	N	N	N	Y	N	N	N

Table 2.—Descriptive statistics for external and cranial measurements (mm), mass (kg), and scores on multivariate axes of *Bradypus* of Age classes 2 and 3 from Bocas del Toro, Panamá, showing small body size of several insular populations. Each measurement or score is given as the mean ± 2 standard errors, minimum–maximum, and sample size. See text and Fig. 2 for methods of taking cranial measurements, Hall (1962) for external measurements, and Materials and Methods for details of the multivariate analyses (C 1 & PC I). Islands are arranged from outermost to innermost; mainland localities from west to east.

Locality	Total length	Tail length	Hind foot length	Ear length	Mass	Greatest length of skull	Anterior zygomatic breadth	Posterior zygomatic breadth
Isla Escudo	505.4 ± 11.42	49.7 ± 4.26	102.4 ± 3.92	10.0 ± —	2.9 ± 0.37	69.0 ± 1.34	41.5 ± 2.30	39.5 ± 2.04
	485–530	45–60	94–110	10–10	2.5–3.5	67.5–72.2	38.3–45.7	36.5–42.9
	(7)	(7)	(7)	(1)	(7)	(6)	(6)	(6)
Isla Bastimentos	513.2 ± 18.04	42.8 ± 4.72	114.0 ± 2.76	12.2 ± 0.95	3.2 ± 0.20	70.4 ± 1.53	42.6 ± 1.93	39.1 ± 1.23
	485–540	37–50	110–118	11–14	3.1–3.3	68.3–73.4	40.4–45.2	37.0–41.6
	(6)	(6)	(5)	(6)	(2)	(6)	(5)	(6)
Cayo Agua	547.8 ± 11.26	45.1 ± 1.25	114.5 ± 3.52	12.5 ± 0.58	3.8 ± 0.19	72.5 ± 1.18	45.3 ± 0.75	44.0 ± 0.68
	520–575	40–47	105–127	11–14	3.3–4.2	68.7–74.9	43.5–47.8	42.1–45.9
	(12)	(11)	(12)	(12)	(10)	(12)	(12)	(12)
Isla Colón	547.7 ± 14.44	49.7 ± 8.36	121.3 ± 8.52	11.0 ± 1.15	3.7 ± 0.48	73.4 ± 2.96	45.5 ± 2.42	42.8 ± 1.88
	535–560	45–58	113–127	10–12	3.2–4.0	70.5–76.6	42.6–48.5	40.2–44.6
	(3)	(3)	(3)	(3)	(3)	(4)	(4)	(4)
Cayo Nancy	565.4 ± 15.84	55.2 ± 3.76	117.4 ± 7.14	13.0 ± 2.60	3.6 ± 0.37	76.0 ± 2.60	44.2 ± 1.90	42.5 ± 2.26
	542–585	49–60	106–128	11–18	3.1–4.2	73.2–80.0	42.1–47.1	39.3–45.2
	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Isla Cristóbal	582.4 ± 16.28	56.6 ± 2.42	124.5 ± 4.80	10.6 ± 1.96	4.1 ± 0.47	79.3 ± 2.00	47.6 ± 1.81	44.8 ± 1.93
	555–605	53–60	120–131	8–14	3.4–4.8	76.5–82.1	44.4–49.8	41.3–47.0
	(5)	(5)	(4)	(5)	(5)	(5)	(5)	(5)
Isla Popa	591.5 ± 18.28	57.7 ± 2.90	128.0 ± 6.04	11.5 ± 1.00	4.4 ± 0.31	80.0 ± 1.29	48.9 ± 1.76	45.6 ± 1.13
	562–618	52–61	116–138	10–13	3.9–5.0	77.7–82.5	46.3–52.3	43.8–47.4
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Almirante	581.5 ± 57.80	67.3 ± 5.46	135.0 ± 12.56	14.5 ± 1.00	— ± —	79.7 ± 2.88	48.6 ± 1.74	45.6 ± 1.41
	531–657	62–71	118–148	14–16	—	75.9–82.5	46.8–50.5	44.2–47.4
	(4)	(3)	(4)	(4)	(0)	(4)	(4)	(4)
Tierra Oscura	591.4 ± 28.20	48.7 ± 3.60	134.4 ± 4.40	13.3 ± 1.36	5.2 ± 0.56	80.5 ± 2.50	50.0 ± 1.60	47.2 ± 1.57
	538–645	42–55	126–140	10–15	4.5–6.3	76.1–86.0	47.5–53.7	45.5–51.4
	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)
Valiente	585.7 ± 23.60	51.5 ± 4.70	128.7 ± 4.78	15.0 ± 0.89	4.6 ± 0.23	80.3 ± 1.99	49.9 ± 1.98	46.6 ± 1.28
	545–634	47–62	120–137	13–16	4.5–5.2	77.7–83.5	47.3–53.4	44.9–49.1
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Ñuri	608.4 ± 16.44	54.6 ± 4.54	130.4 ± 4.32	12.0 ± 1.31	4.7 ± 0.53	78.4 ± 1.13	48.3 ± 1.27	45.3 ± 1.19
	572–632	45–64	122–136	10–14	3.7–5.5	77.0–80.6	46.1–50.6	43.8–47.9
	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)

Table 2.—Extended.

Locality	Postorbital breadth	Squamosal process length	Maxillary toothrow length	Postpalatal length	Palatal breadth	Braincase depth	Antorbital bar breadth	Descending jugal process length	External auditory meatus diameter
Isla Escudo	21.2 ± 0.79	21.5 ± 0.81	23.3 ± 0.76	34.8 ± 1.20	16.3 ± 0.49	24.5 ± 0.39	3.2 ± 0.27	16.2 ± 0.92	5.9 ± 0.45
	20.2–22.4	20.3–22.9	22.3–24.7	33.3–37.0	15.5–17.2	23.7–25.0	2.8–3.7	14.7–18.0	5.3–6.7
	(6)	(7)	(6)	(6)	(7)	(6)	(7)	(7)	(7)
Isla Bastimentos	21.9 ± 0.90	24.3 ± 1.25	23.9 ± 0.82	35.4 ± 0.99	16.6 ± 0.56	24.8 ± 0.48	3.1 ± 0.28	13.2 ± 1.83	5.2 ± 0.29
	20.4–22.9	22.4–27.0	22.5–25.0	34.0–36.9	15.7–17.4	23.8–25.6	2.6–3.5	10.3–17.1	4.6–5.5
	(5)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Cayo Agua	22.3 ± 0.66	26.4 ± 0.75	23.9 ± 0.71	36.0 ± 0.81	16.6 ± 0.41	26.1 ± 0.27	3.9 ± 0.24	16.0 ± 0.96	5.2 ± 0.20
	19.8–24.2	23.2–28.0	22.0–26.8	33.2–38.0	15.6–18.0	25.0–26.8	3.2–4.6	13.4–18.4	4.7–5.8
	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)
Isla Colón	23.0 ± 1.17	25.3 ± 1.55	25.3 ± 1.33	36.4 ± 2.96	17.0 ± 0.74	25.2 ± 1.15	3.9 ± 0.57	15.7 ± 1.25	5.7 ± 0.34
	21.7–24.2	23.2–26.6	23.5–26.7	33.7–39.8	16.2–17.9	23.8–26.6	3.2–4.6	14.2–16.9	5.3–6.1
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
Cayo Nancy	24.2 ± 0.60	26.2 ± 1.13	25.2 ± 0.91	38.0 ± 2.08	17.2 ± 0.82	26.0 ± 0.85	3.4 ± 0.22	15.3 ± 1.46	5.7 ± 0.43
	23.6–25.3	24.3–27.8	24.0–26.5	35.1–40.3	16.6–18.8	24.9–26.8	3.2–3.8	13.1–17.4	4.9–6.1
	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Isla Cristóbal	24.9 ± 1.01	27.2 ± 1.41	25.5 ± 0.92	40.0 ± 0.93	18.3 ± 0.59	27.3 ± 0.89	4.0 ± 0.45	15.9 ± 0.94	5.1 ± 0.19
	23.8–26.5	25.2–29.5	23.7–26.2	38.9–41.7	17.6–19.1	26.2–28.7	3.2–4.4	14.1–16.9	4.9–5.4
	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Isla Popa	23.8 ± 1.09	28.4 ± 1.05	24.6 ± 0.35	41.0 ± 1.79	17.4 ± 0.48	27.6 ± 0.59	4.5 ± 0.35	16.3 ± 1.58	5.1 ± 0.36
	21.3–25.1	26.4–30.0	23.9–25.1	37.1–42.7	16.6–17.9	26.4–28.2	4.0–5.2	14.1–19.9	4.5–5.5
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(5)
Almirante	24.6 ± 1.12	28.1 ± 1.66	25.5 ± 1.41	40.7 ± 1.62	18.3 ± 0.54	27.0 ± 0.46	4.4 ± 0.21	17.1 ± 2.22	5.6 ± 0.26
	23.2–25.8	26.7–30.5	23.8–26.8	39.3–43.0	17.8–19.0	26.7–27.7	4.2–4.6	14.3–19.4	5.3–5.8
	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
Tierra Oscura	25.0 ± 1.20	28.6 ± 1.15	25.1 ± 0.86	41.4 ± 1.33	18.7 ± 0.77	27.9 ± 0.72	4.8 ± 0.35	16.5 ± 1.11	5.6 ± 0.28
	22.0–26.4	26.7–30.6	23.9–27.4	38.9–43.9	17.7–20.7	26.3–28.7	4.0–5.3	14.6–19.0	5.1–6.1
	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)	(7)
Valiente	25.0 ± 1.02	27.7 ± 0.64	25.1 ± 0.77	41.9 ± 1.77	18.3 ± 0.81	28.5 ± 0.33	4.6 ± 0.36	16.3 ± 1.35	5.5 ± 0.27
	23.9–26.6	27.0–28.8	23.7–26.0	39.8–45.3	16.8–19.6	28.0–29.0	4.1–5.3	13.2–17.9	5.1–6.0
	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Ñuri	25.1 ± 0.44	27.4 ± 1.02	25.3 ± 0.69	40.1 ± 0.86	18.4 ± 0.71	28.2 ± 0.55	4.3 ± 0.29	15.4 ± 1.79	5.6 ± 0.16
	24.4–26.0	25.6–29.1	24.3–26.7	38.9–41.8	16.5–19.3	27.3–29.3	3.8–4.7	12.3–18.8	5.2–5.8
	(6)	(7)	(6)	(7)	(7)	(7)	(7)	(7)	(7)

Table 2.—Extended.

Locality	Squamosal process breadth	Ascending mandibular ramus breadth	First canonical axis (C 1)	First principal component (PC I)
Isla Escudo	4.3 ± 0.47	13.2 ± 0.92	−7.32 ± 0.71	−0.28 ± 0.05
	3.5–5.0	11.9–14.9	−8.03–−6.34	−0.35–−0.22
	(7)	(7)	(5)	(5)
Isla Bastimentos	5.4 ± 0.64	16.4 ± 0.62	−4.70 ± 0.63	−0.14 ± 0.07
	4.9–7.0	15.3–17.4	−5.33–−4.36	−0.18–−0.07
	(6)	(6)	(3)	(3)
Cayo Agua	6.3 ± 0.39	15.9 ± 0.60	−2.41 ± 0.72	−0.04 ± 0.03
	5.5–7.5	14.0–17.5	−4.46–−0.43	−0.14–0.02
	(12)	(12)	(11)	(11)
Isla Colón	5.3 ± 0.60	15.8 ± 1.22	−4.34 ± 1.79	−0.08 ± 0.12
	4.5–5.9	14.7–16.8	−6.14–−3.39	0.20–0.00
	(4)	(3)	(3)	(3)
Cayo Nancy	6.0 ± 1.02	16.0 ± 1.50	−2.05 ± 0.46	−0.05 ± 0.07
	4.9–7.9	13.4–17.7	−2.78–−1.39	−0.15–0.05
	(5)	(5)	(5)	(5)
Isla Cristóbal	6.4 ± 0.73	17.2 ± 1.39	3.38 ± 0.75	0.06 ± 0.08
	5.0–7.0	15.5–18.8	2.66–4.18	−0.06–0.13
	(5)	(5)	(4)	(4)
Isla Popa	6.6 ± 0.23	16.8 ± 0.65	4.26 ± 0.37	0.11 ± 0.03
	6.3–6.9	15.6–17.5	3.67–4.68	0.09–0.16
	(5)	(5)	(5)	(5)
Almirante	6.0 ± 0.76	16.9 ± 0.26	3.16 ± 1.01	0.09 ± 0.07
	4.9–6.7	16.6–17.2	2.57–4.17	0.04–0.15
	(4)	(4)	(3)	(3)
Tierra Oscura	5.9 ± 0.39	17.6 ± 0.83	3.06 ± 0.91	0.12 ± 0.05
	5.0–6.5	16.3–19.5	1.41–4.76	0.02–0.19
	(7)	(7)	(7)	(7)
Valiente	5.7 ± 0.64	16.7 ± 0.87	3.36 ± 1.09	0.09 ± 0.04
	5.0–7.1	15.7–18.0	1.49–5.55	0.04–0.17
	(6)	(6)	(6)	(6)
Ñuri	5.8 ± 0.47	16.1 ± 0.49	2.91 ± 0.49	0.06 ± 0.03
	5.0–6.9	15.1–17.0	2.27–3.76	0.01–0.10
	(7)	(7)	(5)	(5)

Table 3.—Approximate statistics for morphometric separation among populations of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá. *F*-statistics with 17 and 30 degrees of freedom are given for Mahalanobis distances between pairs of group centroids, with an asterisk (*) signifying significant differences, using Holm's (1979) correction for multiple tests. Below the *F*-statistic, pairs are marked by PC I (Principal component I), C 1 (Canonical axis 1), or C 2 (Canonical axis 2) if their mean scores on those respective axes were significantly different by Tukey's tests of multiple comparisons with family-wide error rates of $\alpha = 0.05$. Note that the sloth of Isla Escudo is morphometrically distinct from all other samples in Bocas del Toro, and that the samples from Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón are significantly smaller than most or all mainland localities (*F*-statistics, PC I, and C 1). Significance levels attached to all tests must be regarded as approximate due to small sample sizes. Locality abbreviations are given in Table 1.

	E	B	CA	CO	N	CR	P	TO	V	A
B	5.18* C 1, 2									
CA	7.65* PC I, C 1, 2	3.22 C 1								
CO	3.49* PC I, C 1, 2	2.00	1.96							
N	4.41* PC I, C 1, 2	3.00 C 1, 2	2.15 C 2	1.54						
CR	11.55* PC I, C 1, 2	6.74* PC I, C 1, 2	5.37* C 1, 2	5.41* C 1	3.32* C 1					
P	14.68* PC I, C 1, 2	8.46* PC I, C 1, 2	7.44* PC I, C 1, 2	7.19* PC I, C 1	5.29* PC 1, C 1	0.84				
TO	14.94* PC I, C 1, 2	6.92* PC I, C 1, 2	6.55* PC I, C 1	5.39* PC I, C 1	4.46* PC I, C 1	2.12	2.69			
V	13.23* PC I, C 1, 2	7.17* PC I, C 1, 2	7.19* PC I, C 1, 2	6.04* PC I, C 1	4.19* PC I, C 1	1.51	1.72	0.70		
A	9.08* PC I, C 1	6.13* PC I, C 1, 2	4.90* PC I, C 1, 2	4.39* PC I, C 1, 2	2.62 C 1	1.05	1.30	1.74 C 2	1.41	
NU	11.67* PC I, C 1, 2	6.67* PC I, C 1, 2	5.99* C 1, 2	5.00* C 1	3.03 C 1	1.67	2.29	1.09	0.91	0.80

Colón, and Isla Escudo—in comparisons with those from the younger islands (Isla Popa and Isla Cristóbal) and sites on the adjacent mainland (Tables 2 and 3). The discriminant function analysis showed differences in both size and shape. In the DFA, 32 of 55 comparisons between pairs of group centroids were significantly different and followed a clear pattern (Table 3, Fig. 3). The sloths on Isla Escudo were morphometrically distinct from all other populations. Furthermore, sloths on the outer islands were generally distinct from those of Isla Popa and Isla Cristóbal as well as from those from all mainland sites in Bocas del Toro. The first canonical axis accounted for most (63%) of the variation among groups, and the first and second together encompassed 76% of the variation (Table 4). The first canonical axis may be interpreted as general size, with smaller sloths having lower scores. Most measurements loaded strongly and positively on this axis; external auditory meatus diameter (EAM) had a negative loading, but its magnitude was small enough to be negligible, indicating that EAM diameter did not correlate with general size. The second canonical axis contrasted tail length and EAM diameter to squamosal process breadth and ascending mandibular ramus breadth (Table 4). Sloths with relatively long tails, large EAMs, narrow squamosal processes, and narrow rami scored high on this axis.

In the principal components analysis of overall variation in the sloths of Bocas del Toro, the first component (PC I) accounted for 51% of the variation among individuals, without regard to locality (Table 5). Specimens from Isla Escudo again plotted far from all other specimens from Bocas del Toro (Fig. 4). The loadings on PC I indicate that it represents overall size, with EAM loading so slightly as to be immaterial. No difference between Age classes 2 and 3 or age-locality interaction was detected for PC I scores in a general linear model ($F_{age\ 1,6} = 0.23$, $P = 0.650$; $F_{age*locality\ 1,6} = 0.00$, $P = 0.981$). Similarly, the difference between the sexes and the sex-locality interaction also were nonsignificant ($F_{sex\ 1,23} = 1.32$, $P = 0.262$; $F_{sex*locality\ 4,23} = 1.04$, $P = 0.408$). These tests suggest that our pooling of the sexes and Age classes 2 and 3 was justified. Scores on PC I, however, were significantly different among localities in a one-way ANOVA ($F_{10,46} = 21.79$, $P < 0.001$). Patterns of localities differing significantly on PC I paralleled the results for the first canonical axis (Table 3). PC II and PC III represent shape differences, but given the multiple groups involved they probably do not represent the most appropriate way to examine shape.

In comparing the small sloths from Bocas del Toro with six series of *Bradypus variegatus* from its range outside Bocas del Toro, only the population on Isla Escudo is significantly smaller than all mainland samples (Table 6) in the greatest length of skull. Sloths from the other differentiating populations in Bocas del Toro—Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón—fall within the size variation in *B. variegatus* from Colombia and Brazil.

Discussion

The three-toed sloths of the outer islands of Bocas del Toro—Isla Colón, Isla Bastimentos, Cayo Nancy, Cayo Agua, and Isla Escudo—are significantly smaller than the *Bradypus* of the adjacent mainland of Bocas del Toro, as evidenced by Canonical axis 1, Principal component I, and univariate statistics. Furthermore, sloths on those five islands themselves vary in mean size, with those from Isla Escudo being the smallest (Tables 2 and 3). The samples from Isla Popa and Isla Cristóbal, which are young islands close to shore, are not significantly different in size from sloths on the mainland of Bocas del Toro (Table 3).

Sloths on Isla Escudo display differences in cranial shape when compared with other populations of *Bradypus* from Bocas del Toro. The position of specimens from Isla Escudo on the second canonical axis (Fig.

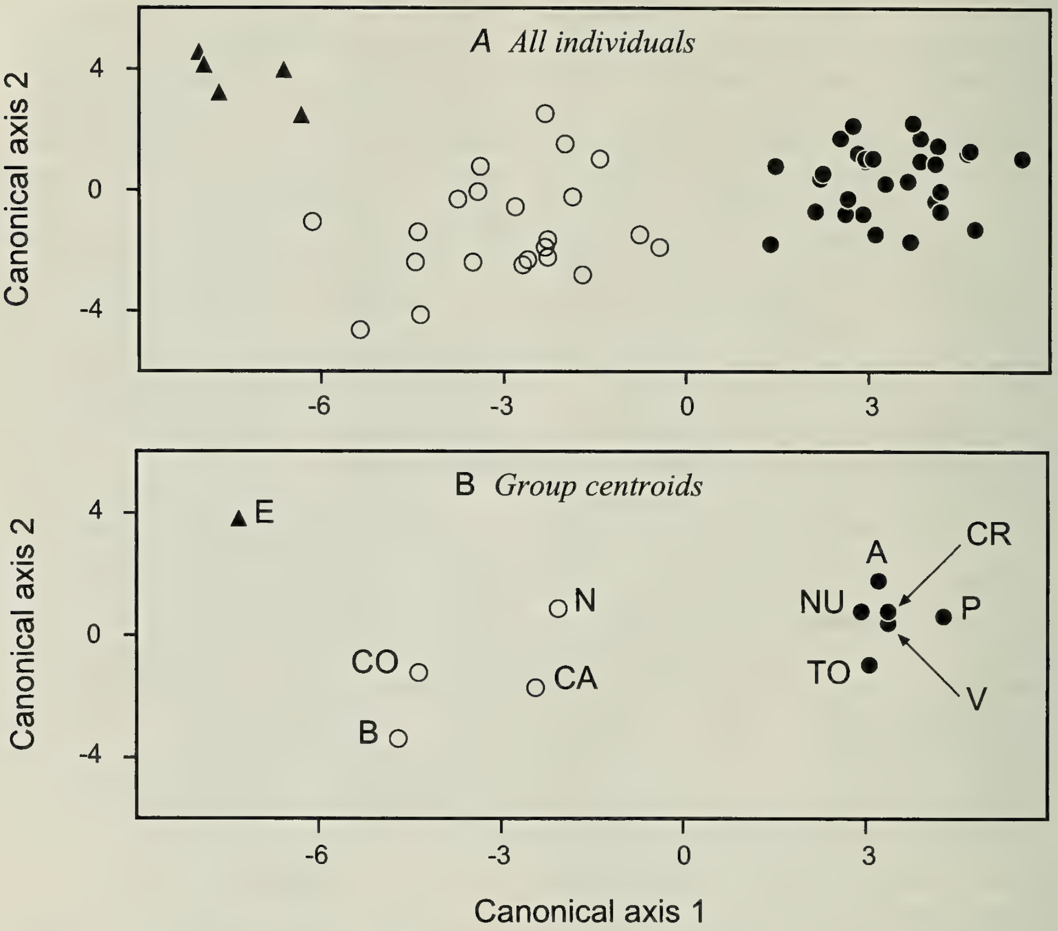

Fig. 3. Plot of specimen scores (A, upper) and locality centroids (B, lower) on the first two canonical axes from a multiple-group discriminant function analysis of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, showing morphometric distinctiveness of sloths of Isla Escudo and moderate dwarfing on four other islands. In A, specimens from Isla Escudo are marked with solid triangles; specimens from the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles; and specimens from the mainland and from the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. Abbreviations for locality centroids in B follow, with symbols following the same scheme as in A: A, Almirante; B, Isla Bastimentos; CA, Cayo Agua; CR, Isla Cristóbal; CO, Isla Colón; E, Isla Escudo; N, Cayo Nancy; NU, Ñuri; P, Isla Popa; TO, Tierra Oscura; V, Península Valiente.

3) is due primarily to their large external auditory meatus, narrow squamosal process, and narrow ascending mandibular ramus (Table 2, Table 4). For the other island and mainland populations in Bocas del Toro, variation in shape is minimal as compared with differences in size.

Although the sloths from the outer islands share small size, our examinations of pelage show similarities between island and mainland populations that were once contiguous (Table 1, Fig. 1). These analyses show that the small sloths on the outer islands share no discrete pelage characters. The pelage traits are independent of body size, which is notably predisposed to convergence (Roth 1992). The few cranial characters common to the small sloths on various islands are all gracile traits associated with size reduction and ontogenetic

Table 4.—Loadings (correlation coefficients) of three external and 14 cranial measurements ($\log_{10}$-transformed) on the first three canonical axes of a multiple-group discriminant function analysis of three-toed sloths (*Bradypus*) from 11 localities in Bocas del Toro, Panamá. Eigenvalues and the corresponding cumulative percent of total dispersion explained are given for each axis. For the analysis, specimens were grouped by collection locality. See Materials and Methods for variable abbreviations. The first canonical axis represents a measure of general size.

	C 1	C 2	C 3
TOTAL	0.804	0.026	0.081
TAIL	0.423	0.620	−0.136
HF	0.822	−0.158	0.252
GLS	0.895	0.046	0.132
AZB	0.856	−0.141	0.096
PZB	0.797	−0.178	−0.004
POB	0.742	0.027	0.268
SPL	0.795	−0.324	−0.058
MTRL	0.452	0.009	0.202
PPL	0.862	0.124	0.202
PB	0.716	0.027	0.398
BD	0.885	−0.027	0.136
ABAR	0.760	−0.258	0.107
DJPL	0.236	0.160	−0.199
EAM	−0.152	0.437	0.515
SPB	0.477	−0.467	−0.355
ARB	0.681	−0.481	0.070
Eigenvalue & (cumulative % of total dispersion)	17.7800 (63.3%)	3.6367 (76.3%)	2.2703 (84.4%)

truncation (e.g., thin zygomatic arches, weakly developed temporal crests). The geographic distribution of the pelage traits apparently represents the relictual manifestation of previously continuous geographic variation that was subdivided into isolated populations when the islands formed. Movement of sloths between islands or to or from the mainland probably has been insignificant. We propose that those populations independently underwent selection for smaller size when separated from the mainland, under a vicariant model consistent with the patterns of island formation elucidated by Handley & Varn (see Introduction). This hypothesis of strict vicariance is currently being tested by Anderson and L. Olson by comparing a population-level phylogeny produced from DNA sequence data, with an area cladogram based on the sequence of island formation derived from sea level mapping (Brooks & McLennan 1991:197–198, Avise 1994).

Thus, we suggest that the evolution of smaller body sizes occurred at least four times in Bocas del Toro: independently on Isla Escudo, Isla Colón, and Cayo Agua—each of which formed separately—and once on Cayo Nancy and Isla Bastimentos together (they became isolated from the mainland as a unit and only recently have become separated from each other). The sloths from the outer islands are not linked by a common ancestry as might be presumed because of their small size, but rather they adapted separately as isolated populations while experiencing similar environmental changes following insularization, in an instance of parallel evolution. The sloth of Isla Escudo has clearly reached the species level, but we consider that the populations on Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón remain conspecific with *Bradypus variegatus*. Future work will evaluate the factors that may have led to these instances of dwarfism.

We have documented the extremely small size of the three-toed sloth on Isla Escudo, as well as its unique cranial and pelage characters relative to other known species of the genus. For these reasons, we here formally describe this endemic insular population as:

Bradypus pygmaeus, new species
Fig. 5

Holotype.—USNM 579179, adult female, skin and skull (Fig. 5), collected on 27 Mar 1991 by Charles Handley and Penny Nelson, from Panamá: Bocas del Toro: Isla Escudo de Veraguas, West Point. Original number EPN 166. Also examined: nine paratypes from Isla Escudo: USNM 578413, 579171–579175, 579176 (returned to Panamá-INRENARE), 579177–579178.

Etymology.—From the Latin *pygmaeus*,

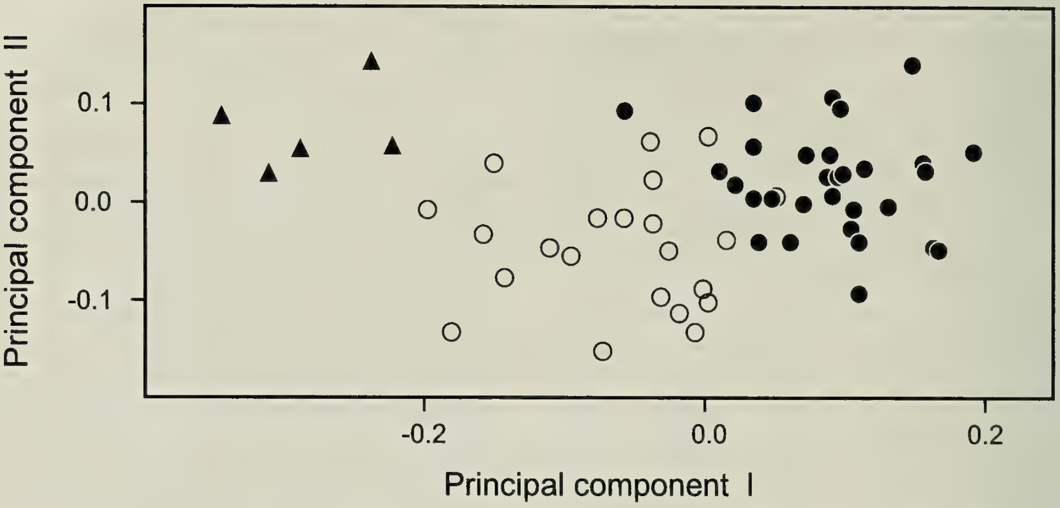

Fig. 4. Plot of specimen scores on the first two axes of a principal components analysis of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, showing dwarfing of sloths on Isla Escudo and four other islands. Specimens from Isla Escudo are marked with solid triangles; specimens from the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles; and specimens from the mainland and from the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. The first principal component represents general size.

meaning dwarf or pygmy. Suitable vernacular name is pygmy three-toed sloth.

Distribution.—Known only from Isla Escudo de Veraguas, Province of Bocas del Toro, Republic of Panamá, where it is found exclusively in red mangroves at sea level (Fig. 6).

Diagnosis.—A species of *Bradypus* characterized by the following combination of characters: size small (Table 2); orange speculum on dorsum of adult males; nape without black mane; face tan with distinctive dark band across forehead; long hair of forehead hanging over face, giving the impression of a hood; pterygoids not inflated; no foramina in anterodorsal nasopharynx; frontal sinuses swollen; stylomastoid foramen miniscule, external carotid foramen usually absent or minuscule; external auditory meatus large; ventral surface of hyoid (stylohyal) smoothly concave; descending process of jugal long and thin; coronoid process of mandible thin and strongly falcate.

Description.—Size small (*n* = 7 adults: total length, $\bar{X}$ = 505.4 mm, range 485–530 mm; tail, $\bar{X}$ = 49.7 mm, range 45–60 mm; hind foot, $\bar{X}$ = 102.4 mm, range 94–110 mm; mass, $\bar{X}$ = 2.9 kg, range 2.5–3.5 kg); dorsal coloration usually blotchy and always with a midsagittal stripe; adult males with orange speculum, woolly around anterior margin; fur of crown long and shaggy, hanging over short hair of face to give a hooded appearance; brow very dark with abrupt posterior termination (line on brow present); face buff with orange wash around dark eye stripe; throat grizzled gray-brown.

Skull small (*n* = 6 adults: greatest length, $\bar{X}$ = 69.1 mm, range 67.5–72.2 mm; anterior zygomatic breadth, $\bar{X}$ = 41.5 mm, range 38.3–45.7 mm; maxillary toothrow length, $\bar{X}$ = 23.3 mm, range 22.3–24.7 mm; see also Table 2) and gracile (Fig. 5); parietal ridges weak and usually convex (hourglass-shaped when viewed dorsally); masseter-temporal fossa rather smooth; pterygoids thin, not inflated; no foramina present in anterodorsal nasopharynx; premaxillae minute, barely if at all articulated with maxillary; zygomatic arch incomplete, anterior and posterior roots slender; descending process of jugal long and thin; lambdoidal crest continuous across posterior margin of occiput, lateral margins of crest straight in lateral view; occipital region barely projecting posterior to lambdoidal crest; hyoid (stylohyal) smoothly arched on ventral surface to point of articulation with epihyal on anterior limb; posterior limb of hyoid usually wider than anterior limb; external auditory meatus large; stylomastoid foramen minute; external carotid foramen usually closed or miniscule; ventral mandibular surface strongly concave; coronoid process of mandible thin and strongly falcate.

Tooth formula: (anterior chisel-shaped teeth 1/1, molariform teeth 4/3) × 2 = 18 (terminology of Naples 1982). Upper anterior chisel-shaped tooth tiny or absent; lower anterior chisel-shaped tooth anteroposteriorly compressed.

Measurements of the holotype.—Total length, 510 mm; tail length, 54 mm; hind foot length, 94 mm; mass, 3.5 kg. Cranial measurements (in mm): GLS, 68.8; AZB, 43.6; PZB, 40.7; POB, 20.5; SPL, 21.3; MTRL, 22.8; PPL, 33.3; PB, 16.3; BD, 24.7; ABAR, 3.2; DJPL, 16.2; EAM, 6.7; SPB, 5.0; ARB, 12.8.

Table 5.—Loadings, eigenvalues, and cumulative percent of variance explained for the first three axes of a principal components analysis undertaken on three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, using the covariance matrix of $\log_{10}$-transformed values of 14 cranial measurements and three external measurements for each of 57 individuals. See Materials and Methods for abbreviations. The first principal component represents general size, which is uncorrelated with external auditory meatus diameter (EAM).

	PC I	PC II	PC III
TOTAL	0.786	0.302	0.103
TAIL	0.331	0.788	0.456
HF	0.801	0.141	−0.057
GLS	0.878	0.221	0.075
AZB	0.905	0.049	−0.218
PZB	0.895	−0.010	−0.214
POB	0.682	0.129	0.044
SPL	0.874	−0.062	0.073
MTRL	0.610	0.164	0.214
PPL	0.839	0.269	0.017
PB	0.712	0.236	−0.042
BD	0.794	0.054	−0.187
ABAR	0.866	−0.092	−0.419
DJPL	0.354	0.348	−0.251
EAM	−0.044	0.481	−0.252
SPB	0.689	−0.477	0.455
ARB	0.842	−0.191	0.200
Eigenvalue & (cumulative % variance explained)	0.0164 (51.2%)	0.0046 (65.5%)	0.0033 (75.9%)

Table 6.—Results of ANOVA of greatest length of skull (GLS) measurements. All possible pairwise comparisons were made among samples of *Bradypus* from the five outer islands of Bocas del Toro, Panamá and six samples of *B. variegatus* from mainland localities outside Bocas del Toro using Tukey's procedure with a family-wide error rate of α = 0.05. Results for comparisons of island populations vs. mainland populations outside Bocas del Toro are presented here. Significant comparisons are marked with an asterisk (*), whereas nonsignificant ones are denoted "*n.s.*" Bonanza, El Recreo, and Tepeyak are localities in Nicaragua; Bajo Calima-Río Raposo and Tumaco lie along the southern Pacific coast of Colombia; and Mojui dos Campos is located in the lower Amazon of Brazil. Note that sloths from Isla Escudo are significantly smaller than those of all mainland localities outside Bocas del Toro, whereas the *Bradypus* from the four other outer islands of Bocas del Toro fall within the range of variation of *B. variegatus* in South America. Descriptive statistics (mean ± 2 standard errors, minimum–maximum, and sample size) are given here in mm for mainland localities outside Bocas del Toro; see Table 2 for descriptive statistics of localities in Bocas del Toro.

	Bonanza 78.9 ± 1.12 75.3–82.3 (12)	El Recreo 78.5 ± 1.15 76.1–80.7 (7)	Tepeyak 83.2 ± 3.08 80.0–86.5 (4)	Bajo Calima-Río Raposo 73.7 ± 2.18 68.9–76.8 (6)	Tumaco 76.9 ± 4.18 70.6–79.3 (4)	Mojui dos Campos 72.8 ± 1.15 67.0–78.3 (21)
Isla Colón	*	*	*	*n.s.*	*n.s.*	*n.s.*
Isla Bastimentos	*	*	*	*n.s.*	*	*n.s.*
Cayo Nancy	*n.s.*	*n.s.*	*	*n.s.*	*n.s.*	*n.s.*
Cayo Agua	*	*	*	*n.s.*	*n.s.*	*n.s.*
Isla Escudo	*	*	*	*	*	*

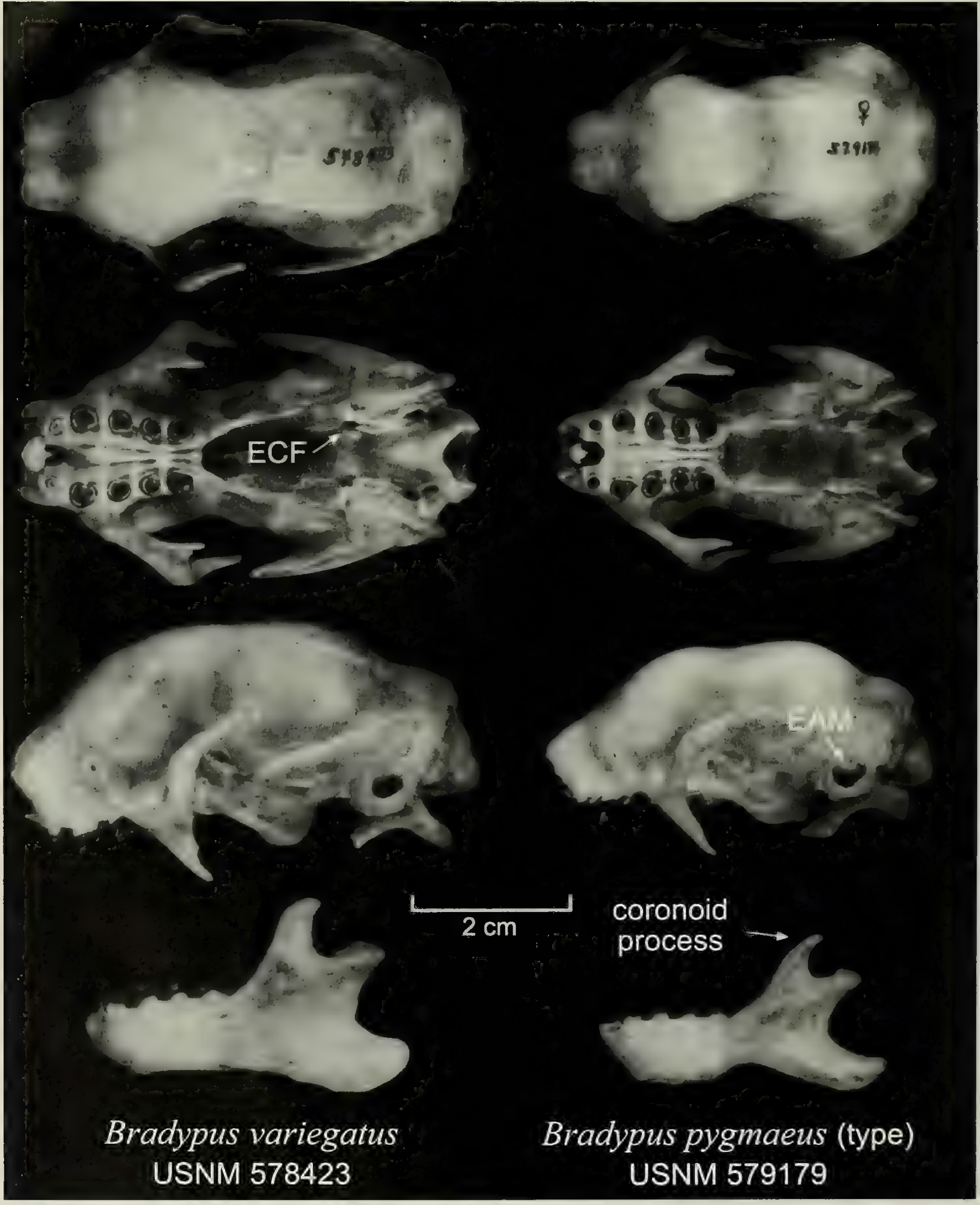

Fig. 5. Dorsal, ventral, and lateral views of the crania and lateral view of the mandibles of the holotype of *Bradypus pygmaeus* (USNM 579179, right) from Isla Escudo and a specimen of *B. variegatus* from the adjacent mainland on the Península Valiente (USNM 578423, left). Note the diminutive size and gracile qualities of *B. pygmaeus* and the open external carotid foramen (ECF) of USNM 578423, which is closed in USNM 579179. Also note the strongly falcate coronoid process on the mandible of *B. pygmaeus* and the large external auditory meatus (EAM) characteristic of that species, despite its overall small size.

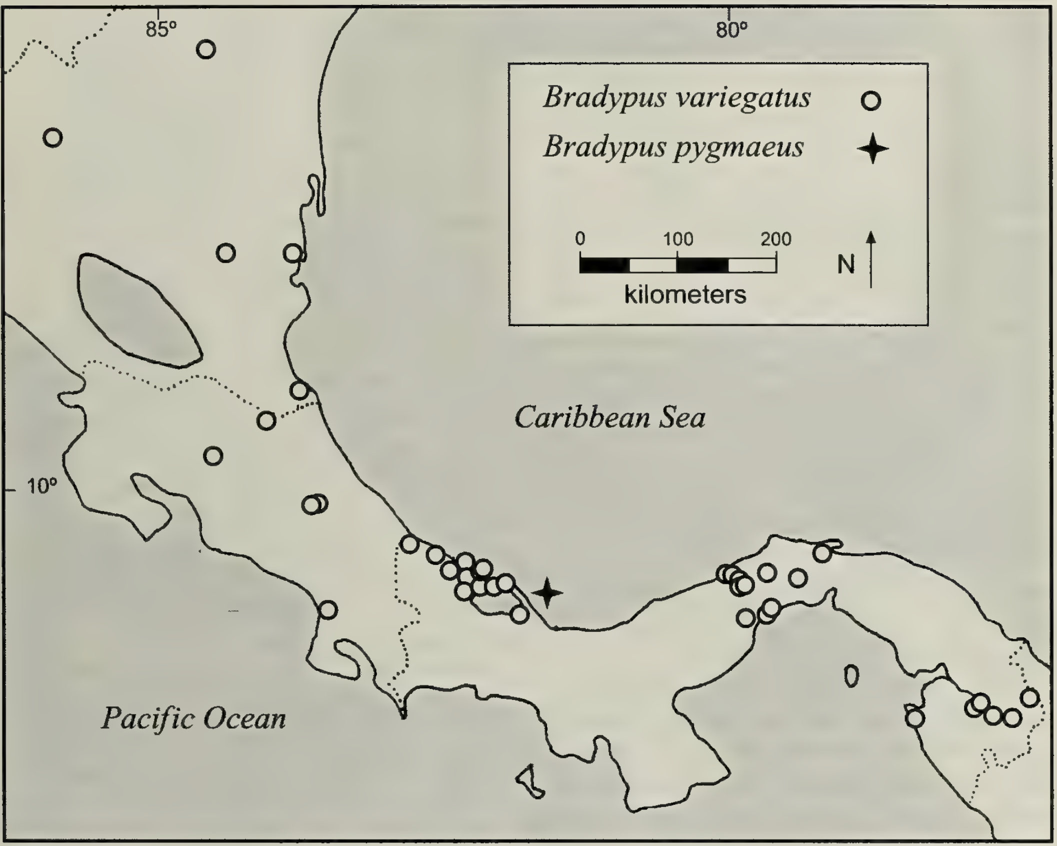

Fig. 6. Verified Central American distribution of *Bradypus*. Georeferenced collection localities reported here are plotted for *B. variegatus* (open circles) and *B. pygmaeus* (star). The distribution of *Bradypus variegatus* continues northward into Honduras (voucher specimens from the Río Patuca region [see Specimens examined] and additional sight records reported in Marineros & Martínez-Gallegos 1998) and south into South America (see Fig. 7). *Bradypus pygmaeus* is endemic to Isla Escudo de Veraguas in western Panamá. See Specimens examined sections for full provenience and museum catalogue numbers.

Comparisons.—Compared with populations of *Bradypus variegatus* on the adjacent mainland, *B. pygmaeus* averages approximately 40% smaller in mass, 15% smaller in total length, and 12–16% smaller in most cranial dimensions. It is smaller than any studied population of *Bradypus variegatus* in Central or South America (Tables 2, 3, and 6). Additionally, its external auditory meatus is conspicuously large for a sloth of overall small size. The diameter of the EAM decreases as the bulla ossifies; the development of this region of the skull is especially truncated in *B. pygmaeus* (Fig. 5).

Discrete cranial characters separate *Bradypus pygmaeus* from all other species of the genus. It lacks the distinctly inflated pterygoid sinuses and the two or three roughly circular foramina in each side of the anterodorsal nasopharynx of *B. torquatus* (Wetzel & Avila-Pires 1980, Wetzel 1985). It lacks the pair of oblong foramina present in the medial roof of the anterodorsal nasopharynx of *B. tridactylus* (Wetzel 1985). From populations of the closely related *B. variegatus*—including both mainland sloths and the moderately dwarfed sloths of other islands in Bocas del Toro—the pygmy sloth differs in having (Fig. 5):

external carotid foramen, through which the carotid artery normally passes, absent or minute in most specimens (the homologous foramen is markedly larger in *B. variegatus,* suggesting a different pattern of cranial circulation); stylomastoid foramen at the posterior external base of the auditory bulla tiny (the facial nerve exits this foramen in *B. variegatus,* in which the foramen is markedly larger and almost always visible to the naked eye); external auditory meatus large (usually smaller in *B. variegatus* and all other three-toed sloths); ventral edge of stylohyoid usually smoothly concave (angular or undulating in *B. variegatus*); coronoid process of the mandible slender and strongly falcate (usually thick and straight-edged or only moderately curved in *B. variegatus*). No other insular population of three-toed sloth in Bocas del Toro shows autapomorphic cranial characters.

Externally, *Bradypus pygmaeus* may be separated from *B. torquatus* of both sexes by the lack of a black dorsal mane originating at the nape and by the presence of short, tan facial pelage with a black stripe lateral to the eye; and in adult males by possessing a dorsal speculum. From *B. tridactylus,* the pygmy sloth is distinguished by its tan facial and gular pelage and dark stripe lateral to the eye. In contrast, *B. tridactylus* has brilliant golden hair on the brow, face, and throat. The pygmy sloth differs externally from *B. variegatus* by long hair projecting over the brow, creating the aspect of a hood (Table 1). This character provoked Handley to refer to this sloth in the field as the "monk sloth." No other sloth of the Bocas islands is hooded, and the "ruff" on the brow (hair projecting over the forehead) mentioned for other Central American *Bradypus* by Goldman (1920:57), Goodwin (1946:352), Hall (1981:279), and others is not so long and distinctive.

Specimens examined.—Bradypus pygmaeus, total 10. Panamá (10). Bocas del Toro: Isla Escudo de Veraguas (9°06′N, 81°33′W), 1 (USNM 578413); Isla Escudo de Veraguas (9°06′N, 81°33′W), West Point, 9 (USNM 579171–579175, 579176*, 579177–579179).

Bradypus torquatus Illiger, 1811

Distribution.—Restricted to the Atlantic forests of southeastern Brazil (Fig. 7; Wetzel & Avila-Pires 1980).

Diagnosis.—Size large; no speculum on dorsum (contra Eisenberg & Redford 1999: 94); nape with distinct black plume or mane; facial and body pelage grizzled; hair of forehead short; pterygoids distinctly inflated; two or three small, circular foramina present on each side of anterodorsal nasopharynx.

Comparisons.—This species is easily separated from all other species of the genus by its black dorsal mane and inflated pterygoids.

Comments.—Extremely rare in museum collections. Endangered due to deforestation in its restricted range (Emmons & Feer 1997). Considered the most basal species of *Bradypus* (Wetzel & Avila-Pires 1980) and placed in its own subgenus, *Scaeopus.*

Specimens examined.—Bradypus torquatus, total 4. Brazil (4). Bahia. Itabuna, near Ilhéus [14°48′S, 39°16′W], 1 (USNM 259473); Tres Bracos, Fazenda Piabanha (13°32′S, 39°45′W), 37 km N, 34 km E Jequie, 2 (USNM uncatalogued, field numbers MTB 1706–1707). State unknown: no specific locality, 1 (MCZ 1024).

Bradypus tridactylus Linnaeus, 1758

Distribution.—The Guianas and adjacent regions of eastcentral Venezuela (Estado Bolívar) and northcentral Brazil, principally north of the Amazon (Fig. 7). Distribution probably does not extend southwest of the Rio Negro or as far south of the Amazon as indicated in Eisenberg & Redford (1999), where it is replaced by *Bradypus variegatus.*

Diagnosis.—Size average for genus; orange speculum present on dorsum of adult males; nape without black mane; face and

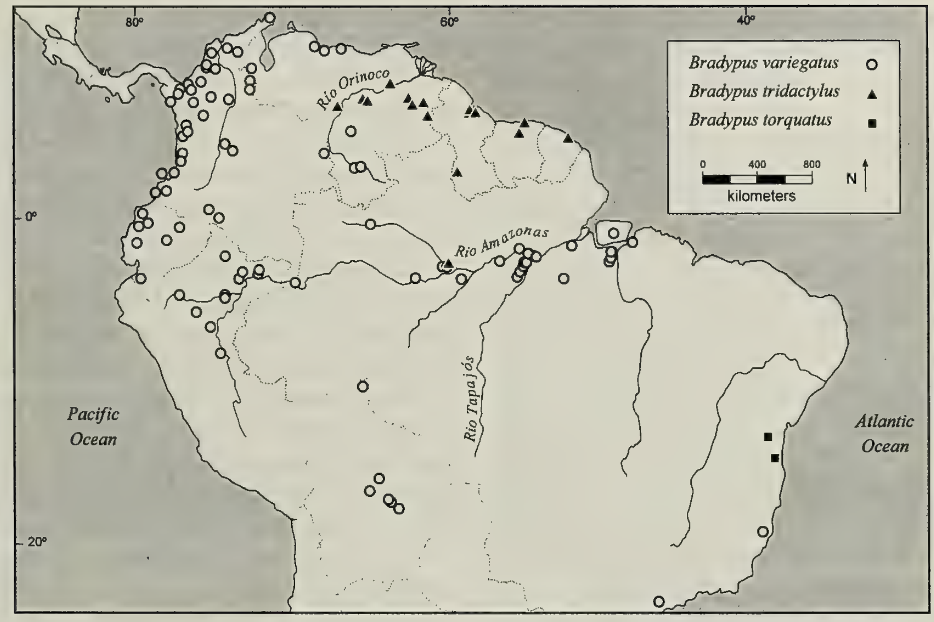

Fig. 7. Verified South American distribution of *Bradypus*. Georeferenced collection localities are mapped for *B. variegatus* (open circles), *B. tridactylus* (solid triangles), and *B. torquatus* (solid squares). The distribution of *Bradypus variegatus* continues northwest into Central America (see Fig. 6) and south to Argentina (voucher specimen from Jujuy province, see Specimens examined). Wetzel and Avila-Pires (1980) reported additional distributional records for *B. torquatus,* which ranges southward from the localities of that species confirmed and plotted here. See Specimens examined sections for full provenience and museum catalogue numbers.

forehead golden with no dark stripe at level of eyes (contra Emmons & Feer 1997:43); throat golden to the base of the hairs, or predominantly golden with bases of hairs smoky gray; hair of forehead short and stiff; pterygoids not inflated; a single pair of oblong foramina present in the anterodorsal nasopharynx; frontal sinuses seldom swollen.

Comparisons.—Bradypus tridactylus may be easily separated from *B. torquatus* by the lack of a black dorsal mane or inflated pterygoid sinuses. It is most similar to *B. variegatus,* whose range it probably contacts in Venezuela and Brazil. It differs from that species by possessing a pair of oblong foramina in the anterodorsal nasopharynx, and by its golden throat. All *B. tridactylus* have golden faces and throats, either golden to the base of the hair or with a slight smoky gray color at the base of the hairs. In contrast, most *B. variegatus* have tan faces. Many specimens of *B. variegatus* in South America possess golden faces, however, and a few Brazilian populations even have throats frosted with golden-tipped fur (e.g., localities on the lower Rio Tapajós), but the base of the gular hairs is characteristically brown for most of the length of the hair in those populations. The golden facial and gular hair of *B. tridactylus* is generally shorter and stiffer than in *B. variegatus.* See Comments in *B. variegatus.* No *B. pygmaeus* have golden throats or faces. The dorsum of *B. tridactylus* is often speckled or blotchy, but this character does not serve to distinguish it from *B. variegatus* (contra Eisenberg 1989, Eisenberg & Redford 1999), which often displays this trait as well.

Comments.—In the older literature, individuals of *Bradypus variegatus* were often incorrectly reported as *B. tridactylus.*

Specimens examined.—Bradypus tridactylus, total 50. Brazil (6). Amazonas: Manaus [3°08′S, 60°01′W], 1 (AMNH 143012);

Rio Amazonas, bought in Manaus [3°08′S, 60°01′W], 4 (FMNH 165441–165444); Rio Amazonas, Manaus [3°08′S, 60°01′W], Hacienda Rio Negro, 1 (AMNH 78968). French Guiana (1). Cayenne [4°56′N, 52°20′W], 1 (AMNH 77891). Guyana (20). Cuyuni-Mazaruni: Essequibo, Kartabo Point [6°23′N, 58°41′W], 12 (AMNH 42454, 42871–42872, 42888, 48369, 74134–74137, 142932, 142934, 142992); Kalacoon [= Kalakun, 6°24′N, 58°39′W], 2 (AMNH 48103, 269846); Kartabo [6°23′N, 58°41′W], 1 (AMNH 48180); Kartabo River, 1 (AMNH 74131); Kyk-over-al [island in Mazaruni River facing Karatabu Point (= Kartabo Point), AMS 1944], 1 (AMNH 48104). Demerara-Mahaica: Dunoon [6°25′N, 58°18′W, Hershkovitz 1977], 1 (UMMZ 46410). Upper Takutu-Upper Essequibo: Dadanawa [2°50′N, 59°30′W], 20 mi E, 1 (USNM 362241); no specific locality [in former Rupununi], 1 (USNM 395070). Suriname (7). Brokopondo: Saramacca Rivier, Loksie Hattie [5°10′N, 55°28′W, Hershkovitz 1977], 1 (FMNH 95443). Paramaribo: near Paramaribo [5°50′N, 55°10′W], 1 (MCZ 19570); Paramaribo [5°50′N, 55°10′W], 900 ft, 2 (FMNH 93297, 95446); Paramaribo [5°50′N, 55°10′W], brush land, 900 ft, 1 (FMNH 93296). Saramacca: La Poule, 2 (FMNH 95444–95455). Venezuela (16). Bolívar: Camarata Valley, 450 m, 1 (AMNH 135474); Ciudad Bolívar [8°08′N, 63°33′W], 3 (AMNH 16134–16136); El Manaco (6°17′N, 61°19′W), 59 km SE El Dorado, 150 m, 1 (USNM 374821); La Bomba [7°02′N, 61°33′W], 1 (AMNH 30738); Los Patos (7°11′N, 62°22′W), 25 km SE El Manteco, 350 m, 2 (USNM 374822, 387803); Maripa [7°26′N, 65°09′W], 2 (AMNH 21305–21306); Río Suapure [6°48′N, 67°01′W], 4 (AMNH 16932–16934, 17560); Río Supamo (7°00′N, 62°15′W), 50 km SE El Manteco, 150 m, 1 (USNM 374818); Ríos Mato [7°09′N, 65°07′W] and Caura, 1 (AMNH 30201).

Bradypus variegatus Schinz, 1825

Distribution.—From eastern Honduras to northern Argentina (Wetzel & Avila-Pires 1980, McCarthy et al. 1999). Widespread in forested areas at low-to-middle elevations of eastern Central America (Fig. 6); South America west of the Andes to southern Ecuador; east of the Andes in South America throughout Amazonian forests (but not in the Guianan region, where replaced by *B. tridactylus*); and in some areas of southeastern Brazil and northern Argentina (Fig. 7). Absent from the open *llanos* of Colombia and Venezuela, the Brazilian *cerrado,* and other savanna habitats—contrary to distributional maps provided by Emmons & Feer (1997) and Eisenberg & Redford (1999).

Diagnosis.—Size variable but most populations averaging at least 72 mm in GLS; orange speculum present on dorsum of adult males; nape without black mane; face tan or golden—if golden, hairs usually with dark brown bases; face usually with dark band lateral to eye; throat brown or occasionally brown frosted with golden; hair of forehead variable in length but never hanging over face giving the appearance of a hood; pterygoids not inflated; no foramina present in anterodorsal nasopharynx; frontal sinuses often but not always well-swollen; stylomastoid foramen large; external carotid foramen large; external auditory meatus medium in size; ventral surface of hyoid (stylohyal) distinctly bent or undulating, not smoothly concave; descending process of jugal variable, but usually relatively short and robust; coronoid process of mandible thick.

Comparisons.—This species lacks the black dorsal mane and inflated pterygoid sinuses characteristic of *B. torquatus. Bradypus tridactylus* has a pair of oblong foramina in the anterodorsal nasopharynx lacking in *B. variegatus* (although in young of Age class 1, the roof of the nasopharynx is poorly ossified, complicating the identification of newborn and juvenal individuals of *B. variegatus* and *B. tridactylus*). Also, *B. variegatus* has a brown throat (rarely frosted with golden), in contrast to *B. tridactylus,* which has a brilliant golden throat with hairs golden to the base of the hairs, or with only a slight smoky gray tint to the bases. See account of *B. pygmaeus* for comparisons with that closely related species.

Comments.—*Bradypus variegatus* is the only species of the genus that displays notable geographic variation. In Central America, it almost always has a tan face. Many specimens from South America—especially from southwestern Colombia, western Ecuador, and northcentral Brazil—possess strikingly golden faces, although the bases of the facial hairs are usually dark brown. A few populations in northern Brazil (e.g., on the lower Rio Tapajós) also show a strong golden frosting on the throat. This species also varies widely in the blotchiness of its dorsal coloration. Cranially, specimens from west of the Andes tend to have more elongated, strongly hourglass-shaped skulls, whereas many populations east of the Andes possess proportionately shorter, wider skulls. All populations agree with the diagnoses of Wetzel (1985) in lacking foramina in the anterodorsal nasopharynx.

Some populations show moderate dwarfing in size. The series from Mojui dos Campos represents one of the few such South American populations. In Central America, populations of *Bradypus variegatus* on several islands of the Laguna de Chiriquí in Bocas del Toro, Panamá average smaller than most but not all populations of the species that we examined from the mainland (Tables 2 and 6). If similar series were available from throughout the species' range, a detailed study of geographic variation might show that these populations deserve subspecific status. Given the present state of understanding of geographic variation within *B. variegatus,* however, it is premature to recognize subspecies of this wide-ranging and highly variable species.

Bradypus gorgon Thomas, 1926 (the only named insular form of the genus prior to this study) does not show dwarfing similar to that of *B. pygmaeus,* and it is conspecific with *B. variegatus. Bradypus gorgon* is from Isla Gorgona, an island with an area of 15.6 km^2 (Aguirre-C. & Rangel-Ch. 1990) approximately 30 km off the southwestern coast of Colombia. Isla Gorgona is located on the continental shelf of South America (von Prahl 1986) and has strong biological affinities with the lowlands of western Colombia and Ecuador (Alberico 1986, Rangel-Ch. 1990b). Although its geological history remains controversial (Aguirre-C. & Rangel-Ch. 1990), it may represent the tip of a sunken volcanic peak belonging to a fourth (coastal) Colombian cordillera (Haffer 1970, Alberico 1986). This coastal cordillera, or at least an arc of volcanic islands, was formed at the end of the middle Eocene, including the Serranía del Baudó, Serranía de los Saltos, and Alto de Nique, in western Colombia and extreme eastern Panamá (Haffer 1970, see also Hershkovitz 1969, Coates & Obando 1996). In the late Pliocene, the Atrato-San Juan sea corridor (= Bolívar Geosyncline) closed, uniting these volcanic blocks with the main body of South America (Alberico 1990, Coates & Obando 1996). Subsequently, glacial cycles alternately raised and lowered sea level; during one or more of these episodes, Isla Gorgona presumably became isolated from the adjacent Chocoan lowlands.

Thomas justified naming *Bradypus gorgon* partly on the basis of size: "Size small, about as in *tridactylus, infuscatus,* and *ephippiger,* the skull markedly smaller than in the Ecuadorean *macrodon*" (Thomas 1926:309–310). *Bradypus infuscatus, B. ephippiger,* and *B. macrodon* are currently considered junior synonyms of *B. variegatus* (see Gardner 1993). Three of the four taxa that Thomas compared with the sloth from Isla Gorgona occur only east of the Andes, making them poor comparisons. Thomas (1917) restricted the fourth one, *B. ephippiger,* to NW Colombia, and Cabrera

(1957) further restricted it to the Río Atrato region. Thus, a better comparison for the *Bradypus* from Isla Gorgona would have been with *B. epipphiger* rather than with *B. macrodon,* as the occurrence of *B. ephippiger* west of the Andes in Colombia places it in the biogeographic region from which the sloth on Isla Gorgona almost certainly was derived.

Contrary to Thomas' conclusions, in the two specimens from Isla Gorgona for which we have measurements (both adults), the greatest length of the skull averages near that of adults from the closest available mainland populations in southwestern Colombia (Isla Gorgona: GLS, $\bar{X}$ = 76.7, standard error of the mean (SEM) = 1.20, n = 2; Río Raposo & Bajo Calima: GLS, $\bar{X}$ = 73.7, SEM = 1.09, n = 6; Tumaco: GLS, $\bar{X}$ = 76.3, SEM = 2.85, n = 3). We agree with Wetzel & Avila-Pires (1980) and Gardner (1993) in considering *Bradypus gorgon* to be conspecific with *B. variegatus.*

Isla Gorgona is twice as far from the mainland as any of the islands of Bocas del Toro, falls within the size range of those islands, and surely has been isolated longer, since it is separated from the mainland by water about 70 m deep (Alberico 1986), whereas the greatest depth of water separating Isla Escudo from the adjacent mainland is ca. 29 m (Kalko & Handley 1994). This raises the question of why the three-toed sloth on Isla Gorgona has not undergone a decrease in size similar to that of *Bradypus pygmaeus* on Isla Escudo. We speculate that dwarfism in *B. pygmaeus* may be related to foraging in mangroves, which are absent from Isla Gorgona (Rangel-Ch. 1990a). Another scenario that should not be dismissed is the possibility that three-toed sloths could have been recently introduced to Isla Gorgona from the mainland by humans (Alberico 1986).

Specimens examined.—Bradypus variegatus, total 467. Argentina (1). Jujuy: no specific locality, 1 (FMNH 21672). Bolivia (13). Beni: Beni River [10°23′S, 65°24′W], 1 (USNM 238668); Río Mamoré [10°23′S, 65°23′W], 5 km S Guayaramerin, 1 (AMNH 209940); Río Mamoré [10°23′S, 65°23′W], 8 km N Exaltación, 1 (AMNH 211663). Cochabamba: Todos Santos [16°48′S, 65°08′W], 1 (AMNH 38784). Santa Cruz: Buena Vista [17°27′S, 63°40′W], 4 (AMNH 61792; FMNH 21393–21394, 21430); Buena Vista [17°27′S, 63°40′W], 450 m, 1 (FMNH 51871); Río Surutú [17°24′S, 63°51′W], 400 m, 1 (AMNH 61791); Río Yapacaní [16°00′S, 64°25′W], 1 (FMNH 51870); Santa Cruz de la Sierra [17°48′S, 63°10′W], 1 (AMNH 133435); 5 km E Río Palometillas, 300 m, 1 (AMNH 261304). Brazil (130). Amazonas: Rio Amazonas, Santo Antonio de Amatary, 1 (AMNH 93103); Rio Amazonas, south bank, Villa Bella Imperatriz [= Parintins, 2°36′S, 56°44′W], 12 (AMNH 93104–93115); Rio Madeira, Rosarinho [3°42′S, 59°08′W], 4 (AMNH 92335, 92828–92829, 92845); Rio Madeira, Rosarinho, Santo Antonio de Uayará, 3 (AMNH 92332–92334); Rio Negro, Cacao Pereira [3°08′S, 60°05′W], Igarapé, 2 (AMNH 80447–80448); Rio Negro, Iaunari [0°31′S, 64°50′W], 1 (AMNH 79396); Rio Negro, Manaus [3°08′S, 60°01′W], 1 (AMNH 91353); Rio Solimões, Codajás [3°50′S, 62°05′W], 1 (FMNH 50906); Solimões, 1 (AMNH 37155). Espíritu Santo: Lagoa Juparana [19°20′S, 40°04′W, Hershkovitz 1977], 4000 ft, 1 (AMNH 78844). Pará: Altamira, 85 km SW, east bank Rio Iriri (3°50′S, 52°40′W), 1 (USNM 549523); Belém [1°27′S, 48°29′W], 2 (MCZ 31001; USNM 393816); Belém [1°27′S, 48°29′W], Utinga, 2 (USNM 339631–339632); Curralinho, 2 (AMNH 133438, 133457); Curralinho, Ilha de Marajó [1°00′S, 49°30′W], 8 (AMNH 133406, 133415, 133419, 133421, 133426, 133432–133433, 133455); Ilha de Marajó [1°00′S, 49°30′W], 4 (FMNH 34401, 34712–34714); Patagonia, 12 mi, 2 (AMNH 75140–75141); Rio Amazonas, Igarapé Piaba [1°55′S, 55°33′W], 3 (MCZ 30993, 30995, 31002); Rio Majary, Recreio [1°42′S, 52°12′W], 1 (AMNH 95841); Rio Tapajós, Aramanay [2°45′S, 54°59′W, Hershkovitz 1977], 3

(AMNH 95101–95103); Rio Tapajós, Caxiricatuba [2°50′S, 55°08′W], 1 (AMNH 95104); Rio Tapajós, east bank, Fordlandia [3°40′S, 55°30′W], 1 (FMNH 94551); Rio Tapajós, lgarapé Amorin [2°26′S, 55°00′W, Hershkovitz 1977], 1 (AMNH 95329); Rio Tapajós, Igarapé Bravo [2°26′S, 55°00′W, Hershkovitz 1977], 2 (AMNH 95105–95106); Rio Tapajós, Inajatuba, 4, (AMNH 95325–95328); Rio Tapajós, Santarem [2°26′S, 54°42′W], nearby, 1 (FMNH 21551); Rio Tapajós, Tauarý [3°05′S, 55°06′W], 3 (MCZ 30996–30997, 31731); Rio Tapajós, west bank, São Raimundo [3°27′S, 55°17′W], 1 (FMNH 92079); Rio Tocantins, Baião [2°41′S, 49°41′W], 1 (AMNH 96255); Rio Tocantins, Cametá [2°15′S, 49°30′W], 1 (MCZ 30998); Rio Tocantins, Ilha do Taiuna [2°15′S, 49°30′W], 14 (AMNH 96241–96251, 96256, 97315); Rio Tocantins, Mocajuba [2°35′S, 49°30′W], 2 (AMNH 96253–96254); Santarém [2°26′S, 54°42′W], 5 (USNM 111636/49590, 111637/49591, 239454–239455, skin number 49592); Santarém, Cuiaba, km 35, 1 (USNM 461731); Santarém [2°26′S, 54°42′W], near, 2 (AMNH 40829–40830); Santarém, Mojui dos Campos (2°26′S, 54°42′W), 27 (USNM 545911–545937); no specific locality, 7 (FMNH 25315–25319, 34402; UMMZ 53929). São Paulo: Jaraguá [23°27′S, 46°44′W] 1 (FMNH 94296). Colombia (83). Amazonas: Leticia [4°09′S, 69°57′W], Río Amazonas, 1 (MLS 2213); no specific locality, 1 (IND-M 387). Antioquia: Dabeiba [7°01′N, 76°16′W], Río Sucio, 2000 ft, 2 (AMNH 37792–37793); Medellín [6°15′N, 75°35′W], 1 (MCZ 5015); Turbo [8°06′N, 76°43′W], 1 (ICN 800); Zaragoza, 23 km S, 22 km W, at Providencia [7°21′N, 75°03′W], 400 m, 1 (USNM 449524). Bolívar: San Juan Nepomuceno, 167 m [9°58′N, 75°04′W, Hershkovitz 1977], 2 (FMNH 68916–68917). Caquetá: no specific locality, 1 (FMNH 140254). Cauca: Isla Gorgona [2°59′N, 78°12′W], 2 (BM skin 24.12.6.17/skull 24.16.6.17 [holotype of *Bradypus gorgon* Thomas, examined by E. Kalko and N. Simmons]; IND-M 2613); Río Saija [2°52′N, 77°41′W], 100 m, 1 (FMNH 90060). Cesar: Colonia Agrícola de Caracolicito [10°18′N, 74°00′W, Hershkovitz 1947], 2 (USNM 281352–281353); Valledupar, Río Cesar, El Orinoco [10°09′N, 73°26′W, Hershkovitz 1947], 1 (USNM 281354). Chocó: Andagoya [5°06′N, 76°41′W], 1 (FMNH 86760); Juradó [7°07′N, 77°46′W], 100 m, 1 (UC 3909); Quibdó [5°42′N, 76°40′W], 1 (AMNH 42838); Río Baudó, Río Sandó [5°03′N, 76°57′W], 160 m, 2 (FMNH 90061, 90314); Riosucio, corregimiento de Cacaricas, Río Peranchó [7°40′N, 77°10′W], Parque Nacional Natural Los Katíos, 1 (IND-M 3907); Unguía [8°01′N, 77°07′W, Hershkovitz 1977], Golfo de Urabá, 4 (FMNH 69587–69590). Córdoba: Arboletes, 1 (ICN 12978); Catival [8°17′N, 75°41′W], upper Río San Jorge, 1 (FMNH 68921); Río San Jorge [9°07′N, 74°44′W], 2 (AMNH 32699–32700); Upper Río Sinú [7°51′N, 76°17′W, Hershkovitz 1977], 2 (FMNH 68919–68920). Cundinamarca: Salto del Tequendama [4°35′N, 74°18′W], 1 (IND-M 3906). Guainía: Caño Carbón, Puerto Inírida [3°52′N, 67°56′W], 1 (IND-M 3964). La Guajira: Puerto Estrella [12°21′N, 71°19′W], 1 (USNM 216665). Meta: Villavicencio [4°09′N, 73°37′W], 1 (ICN 801). Nariño: Barbacoas [1°41′N, 78°09′W], 1 (AMNH 34153); Tumaco [1°49′N, 78°46′W], 1 (IND-M 4112); Tumaco, Inguapí del Guadual, Río Mira, 2 (UV 8131, 10920); Tumaco, 15 km E, Inguapí del Guadual, 4 (UV 4657, 4658, 8132, 8133). Norte de Santander: Catatumbo, Petrólea [8°30′N, 72°35′W], 1 (MLS 576); Cúcuta [7°54′N, 72°31′W], “comprado en Cúcuta,” 1 (MLS 578). Putumayo: Puerto Leguízamo [0°12′S, 74°46′W], Caño Caucayá, Finca Velásquez, entrando por Limonconcho NW de Leguízamo, 1 (IND-M 590); Río Mecaya [0°28′N, 75°20′W], 185 m, 2 (FMNH 70812–70813). Santander: Barrancabermeja, Peroles, Caño Muerto [7°10′N, 73°55′W], 150–200 m, 1 (ICN 2952). Sucre: Chochó, Sincelejo [9°18′N, 75°24′W], 1 (IND-M 4133); Colosó [9°30′N, 75°21′W], Las Campanas, 1 (FMNH 68918). Valle del Cauca: Bajo Calima [4°00′N, 76°56′W, González-M.

& Alberico 1993], Quebrada La Brea, parte alta, ca. 250 m, 2 (UV 4078, 10919), Buenaventura, Bajo Calima [4°00′N, 76°56′W, González-M. & Alberico 1993], 35 m, 3 (UV 4079–4081); Buenaventura, Río Raposo [3°41′N, 77°05′W, Alberico 1983], ca. sea level, 17 (UV 4843–4859); Calima, 300 m, 1 (MSU 2077); Rockefeller Research Station, 5 mi up Río Raposo from the Pacific, 20 mi. SE Buenaventura, 1 (UMMZ 115803); Sabaletas, 500 m, 4 (MSU 2078–2081); Zabaletas, 500 m, 3 (FMNH 86761–86762, 86879). Costa Rica (8). Alajuela: Jabillo, San Carlos [= Vijagual and La Vieja de San Carlos, 10°20′N, 84°30′W, see also Goodwin 1946], 1 (AMNH 139833). Cartago: Angostura [9°53′N, 83°38′W], 1 (USNM 12871/14104). Heredia: Río Sarapiquí, Puerto Viejo [10°38′N, 84°01′W], 300 ft, 2 (UMMZ 112319–112320). Limón: Pacuare [9°55′N, 83°34′W], 1 (USNM 12870/15961); Talamanca, 2 (USNM 11381, 12103/14215). Puntarenas: Palmar [8°57′N, 83°28′W], 1 (AMNH 139313). Ecuador (20). El Oro: Portovelo [3°43′S, 79°39′W]; Cuatro Lomas, 1 (AMNH 46552). Esmeraldas: Achote, 1 (MSU 9339); Dogola, 1 (MSU 9338); Hacienda de Tinbre, near Quinindé [= Rosa Zárate, 0°20′N, 79°28′W], 1 (MSU 8675); Montaña de Cole, near Quinindé [= Rosa Zárate, 0°20′N, 79°28′W], 1 (MSU 8676); Montañas de Chancamita, 1 (MSU 8664). Los Ríos: Vinces [1°32′S, 79°45′W], 8 (AMNH 62877, 62879–62885); Vinces [1°32′S, 79°45′W], Hacienda Pijigual, 2 (AMNH 62876, 62878). Manabí: Río de Oro [0°28′S, 79°36′W], 1 (AMNH 34270). Napo: Río Suno [0°42′S, 77°08′W], below Loreto, 1 (FMNH 31119). Pastaza: Puyo, east of (1°29′S, 77°57′W), 2000 ft, 1 (MSU 3724). Pichincha: Santo Domingo de los Colorados [0°15′S, 79°09′W], bypass road, 1 (USNM 528706). Honduras (2). Gracias a Dios: Patuca River, 2 (USNM 21010/36058, 21011/36059). Nicaragua (44). Boaco: Chontales, 2 (AMNH 28477–28478). Jinotega/Nueva Segovia: Río Coco, 1 (AMNH 29441). Matagalpa: Finca Tepeyac [13°11′N, 85°56′W, Genoways 1973], 10.5 km N, 9 km E Matagalpa, 960 m, 5 (KU 97876–97880); Hacienda Tepeyac [13°11′N, 85°56′W, Genoways 1973], 3 (KU 104581; USNM 337556–337557). Río San Juan: Greytown [= San Juan del Norte, 10°56′N, 83°42′W], 2 (USNM 59010, 16352/23251); La Esperanza, 2 (KU 108389; USNM 361231). Zelaya: Bonanza [13°57′N, 84°32′W], 16 (KU 99451–99458; USNM 338773–338780); Bonanza [13°57′N, 84°32′W], 3.5 mi SW of, 780 ft, 1 (KU 96356); Bonanza [13°57′N, 84°32′W], 4 mi NE of, 800 ft, 1 (KU 96357); El Recreo [12°09′N, 84°26′W], 71 km ENE Bluefields, 5 (KU 104368–104369; USNM 337713–337715); El Recreo [12°09′N, 84°26′W], north side Río Mico, 25 m, 2 (KU 115212–115213); El Recreo [12°09′N, 84°26′W], south side Río Mico, 25 m, 3 (KU 106317, 111343–111344); Escondido River [12°09′N, 83°46′W], 1 (USNM 51273). Panamá (127; specimens collected in the former “Canal Zone” are now placed in Colón or Panamá provinces, as listed here] Bocas del Toro: Almirante (9°18′N, 82°24′W), 9 (USNM 315847–315852, 315855–315856, 399052); Cayo Agua (9°10′N, 82°02′W), 18 (USNM 324249–324260, 578414*, 578415–578419); Cayo Nancy (9°19′N, 82°11′W), 7.3 km ESE Bocas del Toro (town), 6 (USNM 464853–464855, 464856*, 464857–464858); Changuinola (9°27′N, 82°31′W), 2 (USNM 315853–315854); Elena Farm, 1 (USNM 291179); Isla Bastimentos (9°19′N, 82°08′W), 2 (USNM 324248, 324261); Isla Bastimentos, Cedar Creek (9°19′N, 82°08′W), 6 (USNM 335267–335172); Isla Colón (9°24′N, 82°16′W), La Gruta, 5 (USNM 464849*, 464850–464852, 464859); Isla Popa, south shore (9°10′N, 82°08′W), 1 km E Sumwood Channel, 7 (USNM 579164*, 579165–579170); Isla San Cristóbal, Bocatorito (9°15′N, 82°16′W), 7 (USNM 449525–449530, 449531*); Ñuri (8°56′N, 81°48′W), 10 (USNM 575379–575381, 575382*, 575383–575388); Península Valiente, Punta Alegre (9°10′N, 81°54′W), 8 (USNM 578412, 578420–578424, 578425*, 578426); Sibube (9°36′N, 82°47′W), 1 (USNM 335466); Tierra Oscura (9°11′N, 82°15′W), 3.5 km S Tiger Key, 8 (USNM 449542*, 449543–449549). Colón: Brujo Point, 3 (UMMZ 64942, 64950; USNM 256182); Frijoles [9°10′N, 79°49′W], 3 (UMMZ 56659, 58926, 59971); Fort Davis [9°15′N, 79°56′W], 3 (USNM 296408–296409, 298712); Gatún [9°15′N, 79°56′W], 2 (AMNH 36816; USNM 170889); Gatún, near, Río Indio [9°15′N, 79°59′W], 2 (USNM 170950–170951); Lion Hill [9°13′N, 79°54′W], 1 (USNM 172729); Loma de León [= Lion Hill, 9°13′N, 79°54′W], 1 (MCZ B8427), Monte Lirio, 1 (USNM 256178); Río Pequeni, Salamanca Hydrographic Station [9°17′N, 79°36′W], 1 (MCZ 34334). Darién: Cerro Tacarcuna (8°10′N, 77°18′W), 4600 ft, 2 (USNM 338124–338125); Cituro [8°00′N, 77°36′W], 1 (AMNH 38191); El Real [8°06′N, 77°45′W], 3 (AMNH 37619–37621); Marragantí [8°08′N, 77°44′W], about 2 mi above Real de Santa María, on the Río Tuyra, ca. sea level, 1 (USNM 179551 [holotype of *Bradypus ignavus* Goldman]); Mount Sapo [7°58′N, 78°22′W], 1 (MCZ 19844); Tapalisa [7°59′N, 77°26′W], 400 ft., 1 (AMNH 38102). Panamá: Balboa [8°57′N, 79°35′W], 1 (USNM 296410); Barro Colorado Island [9°09′N, 79°51′W], 2 (FMNH 30738; UMMZ 64943); Cerro Azul [= La Zumbadora], (9°14′N, 79°21′W), 1 (USNM 306856); La Chorrera [8°52′N, 79°48′W], 2 (AMNH 31427; USNM 324956); Fort Kobbe [8°54′N, 79°36′W], 2 (USNM 296293, 318366). San Blas: Mandinga (9°29′N, 79°05′W), 2 (USNM 305593–305594). Perú (31). Loreto: Alto Amazonas, Río Morona, boca Río Amaya [4°39′S, 77°07′W], 200 m, 1 (FMNH 88893); Boca Río Curarray [2°22′S, 74°05′W], 1 (AMNH 71822); Iquitos [3°46′S, 73°15′W], 6 (AMNH 98532–98533, 98536, 98542, 98545–98546); Nauta, Río Samiria, Santa Elena [4°50′S, 74°13′W], 130 m, 1 (FMNH 86896); Río Amazonas, Apayacu [3°19′S, 72°06′W], 1 (AMNH 74429); Río Amazonas, Orosa [3°26′S, 72°08′W], 2 (AMNH 73758–73759); Río Amazonas, Puerto Indiana [3°28′S, 73°03′W], 6 (AMNH 73571–73575, 73757); Río Samiria [4°42′S, 74°13′W], 4 (AMNH 188193–188196); Río Ucayali, Sarayacu [6°44′S, 75°06′W], 7 (AMNH 76402–76403, 76408, 76423, 76495–76497); Yurimaguas, Puerto Arturo [5°50′S, 76°03′W], 1 (FMNH 20132). Ucayali: Pucallpa [8°23′S, 74°32′W], 200 m, 1 (AMNH 147462). Venezuela (8). Amazonas: Mount Duida, Esmeralda [3°10′N, 65°33′W], left bank Río Orinoco, 1 (AMNH 76904); Río Casiquiare, orilla izquierda, El Merey [3°05′N, 65°55′W], 1 (AMNH 78515); San Juan (5°18′N, 66°13′W), Río Manapiare, 163 km ESE Puerto Ayacucho, 155 m, 1 (USNM 406693). Aragua: Rancho Grande [10°22′N, 67°41′W], 1 (AMNH 144824); Carabobo/Yaracuy: 10 km NW Urama (10°32′N, 68°23′W), 25 m, 1 (USNM 374817). Miranda: San Andrés (10°22′N, 66°50′W), 16 km SSE Caracas, 1144 m, 2 (USNM 372832–372833). Zulia: El Rosario (9°09′N, 72°36′W), 42 km WNW Encontrados, 24 m, 1 (USNM 443760).

Key to three-toed sloths (*Bradypus*)

1. Distinctive black mane originating at nape and extending halfway down the back; pterygoids inflated; two or three foramina present on each side of the anterodorsal nasopharynx; dorsal speculum never present; no differentiation between color or length of facial and dorsal pelage. Known only from the Atlantic forests of southeastern Brazil. . . . . subgenus *Scaeopus, Bradypus* (*S.*) *torquatus*

1′. No black mane on nape; pterygoids not inflated; no foramina present on lateral walls of the anterodorsal nasopharynx; orange speculum present on the dorsum of adult males; facial hair shorter than dorsal hair and of a different color. . . . . subgenus *Bradypus,* 2

2. Single pair of large oval foramina present on the dorsal roof of the anterodorsal nasopharynx; throat with stiff hairs golden-yellow to the base or with a slight smoky gray tint to the base, no dark stripe extending laterally from eye; face and forehead covered with golden-yellow hairs to the base; hair of fore-

head short. Known only from the Guianas and adjacent regions of Venezuela and Brazil. . . . . *Bradypus* (*B.*) *tridactylus*

2′. No foramina in any part of the anterodorsal nasopharynx; throat with soft hairs, typically brown or cream-colored, but occasionally dark brown frosted with golden; dark stripe usually present lateral to eye; face variable in color, with either tan or yellowish hair; long brownish hair of dorsum usually extending to forehead. . . . . *B. variegatus*-group, 3

3. Size small; skull small and gracile; external carotid foramen usually closed or minute; stylomastoid foramen minute; external auditory meatus both absolutely and relatively large; coronoid process of mandible strikingly falcate; long hair of forehead and shoulders forming an obvious hood around short facial hair. Known only from Isla Escudo de Veraguas, Panamá. . . *Bradypus* (*B.*) *pygmaeus*

3′. Size variable but usually large; skull robust; external carotid foramen large; stylomastoid foramen larger, usually visible to naked eye; external auditory meatus both absolutely and relatively smaller; posterior border of coronoid process of mandible straight or only moderately curved; hair of forehead not especially long, never giving the appearance of a hood. Wide-ranging in both Central and South America. . . . . *Bradypus* (*B.*) *variegatus*

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A remarkable new species of small falcon from the Quaternary of Cuba (Aves: Falconidae: *Falco*)

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Abstract.—An enigmatic small falcon, *Falco kurochkini,* new species, is described from postcranial bones from several Quaternary sites in western and central Cuba. It was approximately intermediate in size between *F. sparverius* and *F. columbarius* but had proportionately longer and more slender leg elements than any living species of *Falco.* It is hypothesized that *F. kurochkini* may have been terrestrial, pursuing prey on foot, and that its extinction could have been related to terrestrial nesting habits as well.

Falcons of the genus *Falco* are poorly represented in the West Indies today. Two species, the Merlin (*F. columbarius*) and the Peregrine (*F. peregrinus*) are migrant or wintering birds from North America, although there are single breeding records of the latter from Cuba (Regalado & Cables 2000) and Dominica (Raffaele et al. 1998). Thus, the only truly resident *Falco* is the American Kestrel (*F. sparverius*), the smallest New World falcon, which is found throughout the Antilles. There are three endemic subspecies, of which by far the most distinctive is the Cuban *F. s. sparverioides,* which has three plumage phases—dark, light, and intermediate (Berovides & Fernández 1984), whereas the other taxa have no phases and are all more similar to the light phase of the Cuban bird. The Cuban subspecies has expanded relatively recently into the southern Bahamas and possibly to Jamaica and Hispaniola (Wotzkow 1998), although its occurrence on the last two islands does not appear to have been documented by specimens.

Considering this dearth of Antillean falcons, the discovery of a highly distinctive new fossil species in Cuba, also of small size, assumes considerable interest. We first learned of the existence of such a falcon in 1981, when E. N. Kurochkin showed one of us (SLO) a tarsometatarsus that he had collected in Camagüey eight years before. This specimen was so long and slender that it clearly could not be referred to any known species (Fig. 2E). Recently, Suárez was able to collect a considerable series of bones of this species representing most of the major postcranial elements, so that there is now sufficient material to characterize the new species.

Materials and Methods

Material examined.—Skeletons of the following species of Falconidae in the collections of the National Museum of Natural History, Smithsonian Institution (USNM): *Herpetotheres cachinnans, Caracara plancus, C. cheriway, Milvago chimango, M. chimachima, Daptrius americanus, D. ater, Phalcoboenus australis, Spiziapteryx circumcinctus, Polihierax insignis, Microhierax caerulescens, Falco mexicanus, F. rusticolus, F. peregrinus, F. rufigularis, F. biarmicus, F. cherrug, F. tinnunculus, F. vespertinus, F. rupicoloides, F. femoralis, F. cuvieri, F. eleonorae, F. subbuteo, F.*

cenchroides, F. longipennis, F. berigora. Measurements included in Table 1 were from *F. columbarius* USNM 18083, 291176, 291862, 291880, 300351, 322363, 429864, 499430, 499431–32, 554205, 560083, 610377–80, 610756; *Falco sparverius sparverioides* USNM 555159–69, 555175, 555524–25, 562459. Catalog numbers of fossil specimens formerly in the collection of William Suárez are indicated by WS.

Systematics

Class Aves
Family Falconidae

The new fossil species is referable to the Falconidae by the three distal openings in the tibiotarsus (the third may be only a deep pit in *Micrastur* and *Herpetotheres*), and by the longer and more centrally placed inner calcaneal ridge of the hypotarsus as opposed to the very short and medially placed ridge in the Accipitridae.

Genus *Falco* Linnaeus, 1758

The fossil agrees with *Falco, Polihierax,* and *Microhierax* in the absence of a procoracoid foramen in the coracoid, and in having the inner calcaneal ridge of the hypotarsus much longer, tapering gradually and extending over half the length of the shaft. In all other genera of Falconidae the procoracoid foramen is present and the inner calcaneal ridge of the hypotarsus is short and ends abruptly distally. These characters are also present in the small falcon *Pediohierax* Becker (1987) from the Miocene of North America. The species of *Polihierax* and *Microhierax* are the smallest members of the family, are entirely Old World in distribution, and are not obviously distinct from *Falco* osteologically. There is no reason to consider the Cuban fossil to be related to any of these smaller Old World taxa and it is therefore referred to the genus *Falco,* within which it is highly distinctive.

Falco kurochkini, new species
Figs. 1–2

Holotype.—Complete left tarsometatarsus, Museo Nacional de Historia Natural de Cuba MNHNCu P3229, formerly WS 1054. Collected 4 May 1997 by William Suárez.

Type locality.—Cuba, La Habana province, municipality of Caimito, Llanura Meridional Habanera, about 4 km south of the town of Vereda Nueva, "Cueva de Sandoval," in a small sink within the cave known as "El Sumidero" (see Suárez 2000).

Chronology.—Quaternary, probably Pleistocene but not directly dated.

Measurements (mm) of holotype.—See Table 1.

Paratypes.—The following are topotypes. Right coracoid MNHNCu P3209 (WS 1071); left coracoid USNM 510237 (WS 1070). Humerus: complete left MNHNCu P3210 (WS 1068), USNM 510238 (WS 1046), left lacking pectoral crest USNM 510239 (WS 1055), incomplete left MNHNCu P3211 (WS 0195), proximal lefts MNHNCu P3212, P3213, P3214 (WS 1056, 1057, 1069), right lacking proximal end MNHNCu P3215 (WS 1049), proximal right USNM 510238 (WS 1058), distal right USNM 510241 (WS 1078). Ulna: proximal right MNHNCu P3217 (WS 1065), USNM 510242 (WS 1063); distal right MNHNCu P3219 (WS 1072); proximal left MNHNCu P3216 (WS 1064); distal left MNHNCu P3218 (WS 1073), USNM 510249 (WS 1074). Carpometacarpus: proximal right MNHNCu P3220 (WS 1045). Notarium: MNHNCu P3221 (WS 1080). Femur: complete left MNHNCu P3222 (WS 1048), USNM 510243 (WS 1067); distal half of right MNHNCu P3226 (WS 0198); left lacking distal end MNHNCu P3223 (WS 0196); proximal left MNHNCu P3224 (WS 1077), MNHNCu P3225 (WS 1047), USNM 510244 (WS 1061). Tibiotarsus: complete right MNHNCu P3227 (WS 1066); complete left USNM 510245 (WS 1053); proximal half of left USNM 510246 (WS 1043);

Table 1.—Measurements (mm) of skeletal elements of small species of Cuban *Falco*. Sequence is: range (mean) n.

Measurement	*F. kurochkini*, n. sp.	*F. sparverius sparverioides*	*F. columbarius*
NOTARIUM			
Length	20.9	14.5–19.1 (18.2) 14	24.1–27.7 (26.2) 16
CORACOID			
Head to internal distal angle	27.3	21.6–23.2 (22.3) 15	27.0–31.5 (29.2) 17
Procoracoid to internal distal angle	19.0–20.6 (19.8) 2	15.9–17.2 (16.5) 15	19.6–23.5 (21.6) 17
HUMERUS			
Length	45.8–49.4 (47.7) 3	39.5–43.1 (41.1) 14	43.7–51.0 (48.1) 16
Proximal width from internal to external tuberosities	8.7–9.8 (9.2) 7	7.8–8.8 (8.4) 15	9.3–12.5 (11.0) 16
Shaft width at midpoint	3.6–4.2 (4.0) 7	2.3–2.6 (2.5) 15	4.1–4.8 (4.4) 16
Distal width	7.4–8.4 (7.9) 5	7.0–7.4 (7.2) 15	8.5–10.2 (8.8) 16
ULNA			
Proximal width	4.0–4.5 (4.2) 3	3.8–4.1 (3.6) 15	4.7–6.1 (5.1) 16
Width of shaft at midpoint	2.8–3.2 (3.0) 5	2.3–2.6 (2.5) 15	4.1–4.8 (4.4) 16
Distal width	5.1–5.2 (5.1) 3	4.5–5.1 (4.8) 15	5.1–6.7 (6.0) 15
CARPOMETACARPUS			
Proximal width	3.1	2.9–3.4 (3.1) 15	3.3–4.1 (3.7) 17
Proximal depth	7.0	6.4–7.2 (6.8) 15	8.0–9.5 (8.6) 17
FEMUR			
Length	45.7–48.2 (46.9) 2	34.5–37.2 (35.9) 15	41.1–47.2 (44.3) 17
Proximal width	6.6–7.3 (7.1) 5	5.5–6.2 (5.9) 15	6.8–8.2 (7.3) 18
Shaft width at midpoint	3.5–3.9 (3.7) 5	2.7–3.2 (2.9) 15	3.4–4.3 (3.7) 18
Distal width	6.7–7.4 (7.2) 3	4.5–5.1 (4.8) 15	6.8–8.0 (7.3) 18
TIBIOTARSUS			
Length	60.8–68.9 (64.4) 2	47.6–51.8 (49.9) 11	52.3–60.7 (56.8) 17
Proximal width	6.5	4.7–5.6 (5.1) 14	5.6–7.1 (6.3) 17
Length of fibular crest	9.5–10.7 (10.0) 4	6.4–8.3 (7.6) 14	6.9–9.3 (8.2) 17
Shaft width at midpoint	3.0–3.4 (3.3) 4	2.3–2.9 (2.6) 13	2.6–3.3 (2.9) 17
Distal width	5.5–6.3 (6.0) 3	5.0–5.6 (5.3) 14	5.9–7.0 (6.5) 17
TARSOMETATARSUS			
Length	49.6*	34.5–37.3 (36.0) 15	34.6–39.9 (37.2) 17
Proximal width	6.6*	5.2–5.7 (5.5) 15	6.1–7.4 (6.7) 17
Shaft width at midpoint	3.0–3.1* (3.1) 3	2.1–2.6 (2.3) 15	2.2–2.9 (2.6) 17
Distal width	5.9–6.7* (6.3) 2	5.2–6.1 (5.7) 15	5.9–7.3 (6.7) 17

* Holotype.

distal right MNHNCu P3228 (WS 1062). Tarsometatarsus: right, lacking proximal end USNM 510247 (WS 1059); shaft of left USNM 510248 (WS 1060).

Cuba, La Habana province, municipality of Caimito, ca. 3 km SE of Ceiba del Agua, "Cueva de Paredones" (see Arredondo 1971, 1976), in a sink known as "Salón del Pozo," collected 5 March 1994 by William Suárez: right tibiotarsus lacking proximal end MNHNCu 3230 (WS 1081).

Cuba, Camagüey province, 28.5 km NE of Camagüey, "Cueva de los Fósiles" (see Olson 1985, Olson & Kurochkin 1987), collected in 1973 by E. N. Kurochkin: left tarsometatarsus lacking distal end (Fig 2E) Instituto de Geología y Paleontología, Habana, Cuba, 406-3.

Measurements (mm) of paratypes.—See Table 1.

Etymology.—Dedicated to our colleague and friend Evgeny N. Kurochkin, of the Paleontological Institute of the Russian Academy of Sciences, for his many contributions to avian paleontology and in recognition of his paleontological explorations in Cuba during which he found the first known specimen of the new species described here.

Diagnosis.—A small species of *Falco,* larger than *F. sparverius sparverioides* and with some measurements within the size range of *F. columbarius* but hindlimb elements proportionately much longer and more slender than in any known species of *Falco.*

Description.—Coracoid with shaft more slender, sternal facet in dorsal view narrower, deeper, and more rounded than in *F. columbarius* or *F. sparverius.* Humerus with shaft more slender, elongate, and sigmoid, resulting in a proportionately greater distance between the distal extent of pectoral crest and the distal extremity. Pectoral crest and entepicondylar process not as expanded as in *F. columbarius.* Lack of complete specimens of the ulna and carpometacarpus prevent adequate comparisons, except to note that the shaft is more robust in the new species than in *F. sparverius.*

Notarium more slender and slightly larger than in *F. sparverius.* Femur with very long slender shaft, head more constricted at base and more distinctly set off from the neck, depression for ligamentum teres less distinct, distal end of femur relatively narrower. Tibiotarsus with shaft extremely slender, proximal and distal ends relatively narrower, fibular crest longer, distal point of fusion of fibula much higher on the shaft, most proximal tendinal opening of distal end higher on the shaft. Tarsometatarsus also extremely long and slender, proximal end of inner calcaneal ridge of hypotarsus situated lower on shaft relative to proximal articular surface, distal portion of shaft relatively wider so that trochleae appear less flared, wing of inner trochlea less distinct and pointed.

Substantial size variation between some of the elements (e.g., tibiotarsi USNM 510245 and MNHNCu 3230) are strongly suggestive of sexual dimorphism in size, with presumed males being smaller as in many species of raptors.

Remarks.—There are no obvious clues to the derivation of *F. kurochkini* within the genus *Falco,* as no other species has such an elongate, slender hindlimb. The Australian Brown Falcon *F. berigora* has the most elongated tarsometatarsus of any living species of the genus, but this is a much larger bird in which the other elements of the hindlimb are not as slender proportionately as in *F. kurochkini.* The general similarity of the fossil species is closer to that of *F. sparverius* than to the stronger and more robust *F. columbarius,* but this similarity could be the result of both being smaller, weaker birds.

The singular nature of *F. kurochkini* naturally raises obvious questions concerning its habits, ecology, and extinction. It is unlikely that climatic fluctuations in the Quaternary or overhunting by paleoindians would cause the disappearance of a small, volant predatory bird, particularly considering that *Falco sparverius* still thrives and is abundant in Cuba (Garrido & García Montaña 1975).

Falco sparverius had previously been reported in Cuba in a Quaternary cave deposit in Habana Province (Jiménez Vázquez 1997). It occurs in association with *F. kurochkini* at the type locality (Suárez 2000) and at Paredones Cave as well (Suárez, pers. obs.), where its remains probably accumulated as prey items of the extinct barn owl *Tyto noeli.* Thus, these two small falcons co-existed in both time and space and presumably either exploited different food sources, or obtained similar prey species in a different manner.

How did *F. kurochkini* hunt and what was its prey? In some raptors (Accipitridae, Strigidae), elongation of the hindlimb, particularly the tarsometatarsus, is thought to

Fig. 1. Pectoral elements of *Falco kurochkini,* new species (middle bone in each group), compared with *F. sparverius sparverioides* USNM 555167 (left in each group) and *F. columbarius* USNM 291880 (right in each group): A, right coracoids in ventral view (paratype MNHNCu P3209); B, left humeri in anconal view (paratype MNHNCu 3210); C, left ulnae in internal view (paratypes MNHNCu 3216 and USNM 510249); D, right carpometacarpi in external view (paratype MNHNCu P3220). Scale = 2 cm.

be associated with preying on birds (Olson & James 1991), but *F. columbarius* feeds almost exclusively on birds and has no such adaptation. *Falco sparverius* is primarily insectivorous; *F. kurochkini* was not much larger and quite likely also fed on insects, and perhaps on lizards. Why then, does it have such remarkable leg proportions?

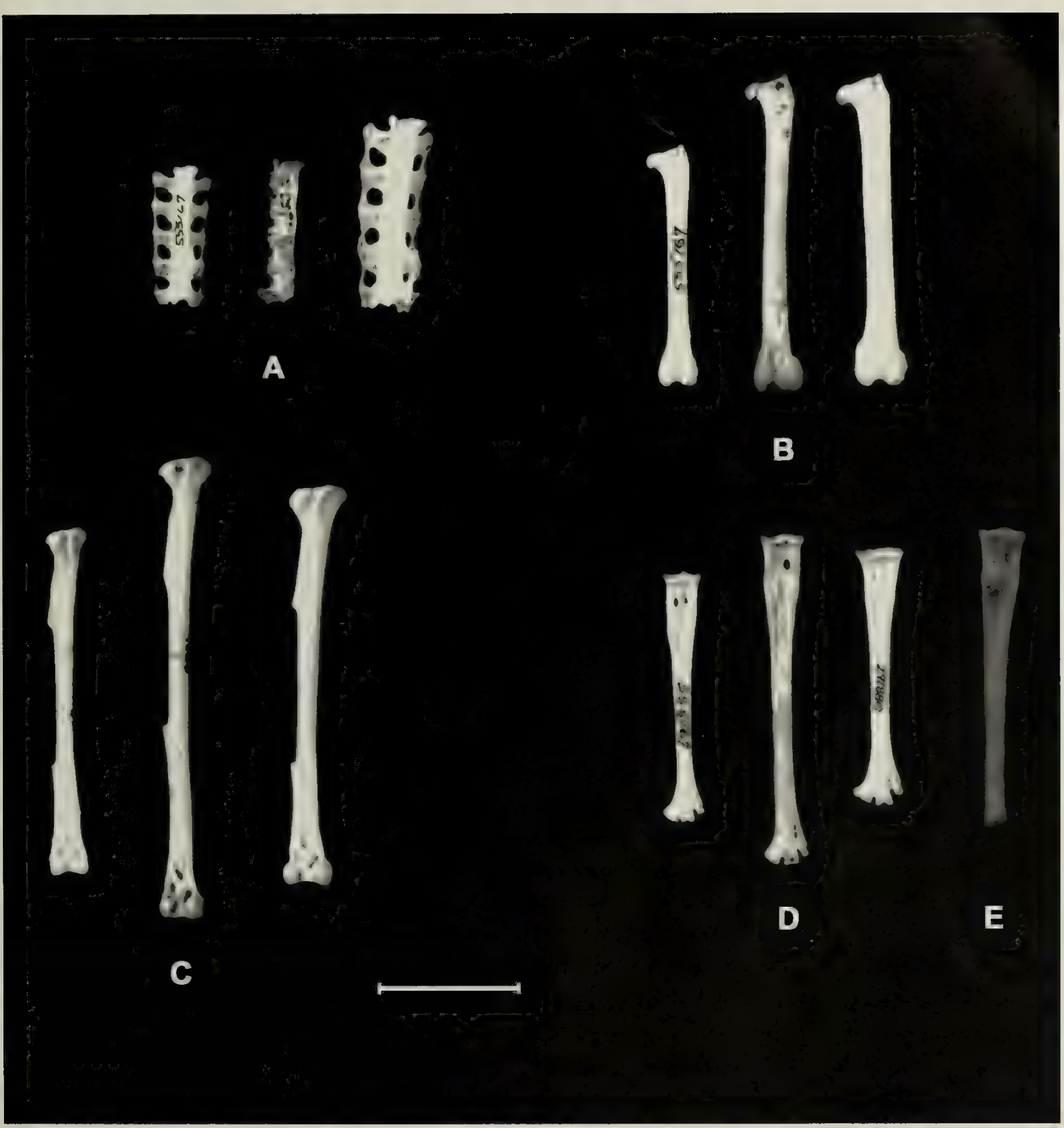

Fig. 2. Notarium and hindlimb elements of *Falco kurochkini,* new species (middle bone in each group), compared with *F. sparverius sparverioides* USNM 555167 (left in each group) and *F. columbarius* USNM 291880 (right in each group): A, notaria in ventral view (paratype MNHNCu P3221); B, left femora in anterior view (paratype MNHNCu P3222); C, right tibiotarsi in anterior view (paratype MNHNCu 3227); D, tarsometatarsi in external view (holotype MNHNCu P3229); E, left tarsometatarsus lacking distal end from Camagüey (paratype Instituto de Geología y Paleontología 406-3). Scale = 2 cm.

The habits of the long-legged Australian *Falco berigora* may provide a clue to the adaptations of *F. kurochkini.* The former is an opportunistic carnivore and scavenger that may feed upon prey from the size of rabbits to insects (Marchant & Higgins 1993). It uses various methods of hunting including soaring, low quartering, or sallying from a perch. More interestingly, however, it also hunts on the ground, where it may run after prey (Fig. 3), which is quite unlike other species of *Falco.* We suggest, therefore, that *F. kurochkini* may have been a terrestrial bird of open country, stalking

Fig. 3. Stances of the Australian Brown Falcon *Falco berigora* when feeding on the ground. It is hypothesized that perhaps the adaptations of the extinct Cuban fossil *Falco kurochkini* new species, may have been for a more terrestrial existence than in other species of the genus. (Figure from Marchant & Higgins, 1993, p. 240).

prey such as insects and lizards on the ground. It could then be viewed as occupying the niche of a diminutive caracara (e.g., *Caracara, Milvago*), the caracaras being more terrestrially adapted members of the Falconidae.

Species of *Falco* do not usually build their own nests. *Falco sparverius* nests in cavities, usually in trees, but most other species appropriate the disused nests of other raptors, or nest on ledges, hollows in rocks, or even on the ground. In Australia, *F. berigora* usually uses old nests of other raptors but may lay its eggs in a depression in the "ground, ledges, or in holes" (Marchant & Higgins 1993: 247). The New Zealand Falcon *F. novaeseelandiae,* which evolved on islands with no native terrestrial predators, places its nest "on ledges of cliffs . . . on ground on steep broken hillsides, easily accessible, at foot of rocky overhang and usually screened by vegetation . . . on ground under log without much screening vegetation . . . in epiphytes on trees" (Marchant & Higgins 1993: 287).

In Cuba, where the only native mammalian predators were two genera of Insectivora, *Falco kurochkini* likewise may have nested on the ground or in holes or crevices in embankments or hillsides. Such nesting habits may have made it more vulnerable to increased burning after the arrival of Amerindians and to destruction by introduced mammals such as rats (*Rattus*) following European colonization in the 16th century.

Acknowledgments

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 9. Confirmation of the hybrid origin of *Coeligena purpurea* Gould, 1854

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Abstract.—*Coeligena purpurea* Gould, 1854 is shown to be a hybrid between *Coeligena coeligena* and *Coeligena prunellei.* The geographic distribution of the parental species suggests that the two hybrid specimens were collected in the Eastern Cordillera of the Colombian Andes. The hybrids exhibit a blended mosaic of plumage characters of the postulated parental species. External measurements of the hybrids fall within the cumulative ranges of characters of the parental species.

The taxonomic validity of *Coeligena purpurea* Gould 1854, supposedly from the vicinity of Poyayán, Colombia, was first questioned by Elliot (1876:60):

> "Two specimens of this form are in Mr. Gould's collection, no others being known to exist. The characters these examples present are not sufficiently satisfactory to entitle them to an independent specific rank without giving rise to great doubts regarding the propriety of such an acknowledgment. . . . until we have further evidence that will substantiate its claim to a distinctive rank, *L. purpurea* cannot but hold a very doubtful position among the species of this group."

Elliot (1878) later opined that *C. purpurea* represented a melanistic variant of *C. wilsoni,* a species restricted to the Pacific slope of the Andes in Colombia and northwestern Ecuador. Subsequent catalogs have listed it several ways—as a valid species (Salvin 1892, Cory 1918, Simon 1921), an immature male of *C. prunellei* (Boucard 1893), or as a hybrid, *C. coeligena* × *C. prunellei* (Berlioz 1936; Peters 1945; Meyer de Schauensee 1949, 1966). Schuchmann (1999) ambiguously concluded that *C. purpurea* was either a dark variety of *C. wilsoni* or a hybrid between *C. coeligena* and *C. prunellei.* Not surprisingly, none of the aforementioned treatments provided documentation or evidence in support of taxonomic conclusions. Here I confirm the hybrid origin of *Coeligena purpurea,* employing the methods and assumptions of Graves (1990) and Graves & Zusi (1990) as modified by insights on plumage color aberrations associated with hybridization (Graves 1996, 1998, 1999).

Methods

The type (BMNH 1888.7.25.165, listed as "syntype" by Warren 1966) and a second specimen (uncataloged until recently, BMNH 2000.1.9) of *Coeligena purpurea* were obtained by The Natural History Museum, Tring (formerly British Museum of Natural History) as part of the Gould Collection. I compared these specimens (Figs. 1, 2) with all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997), in that museum. Both specimens appear to be adult males in definitive plumage as judged by the absence of striations on the maxillary ramphotheca, the presence of iridescence on the crown and back, and a moderately forked tail (fork depth in type = 12.1 mm). Unless otherwise noted, subsequent descriptions in this paper refer to definitive male plumage. I discovered no evidence that *C. purpurea*

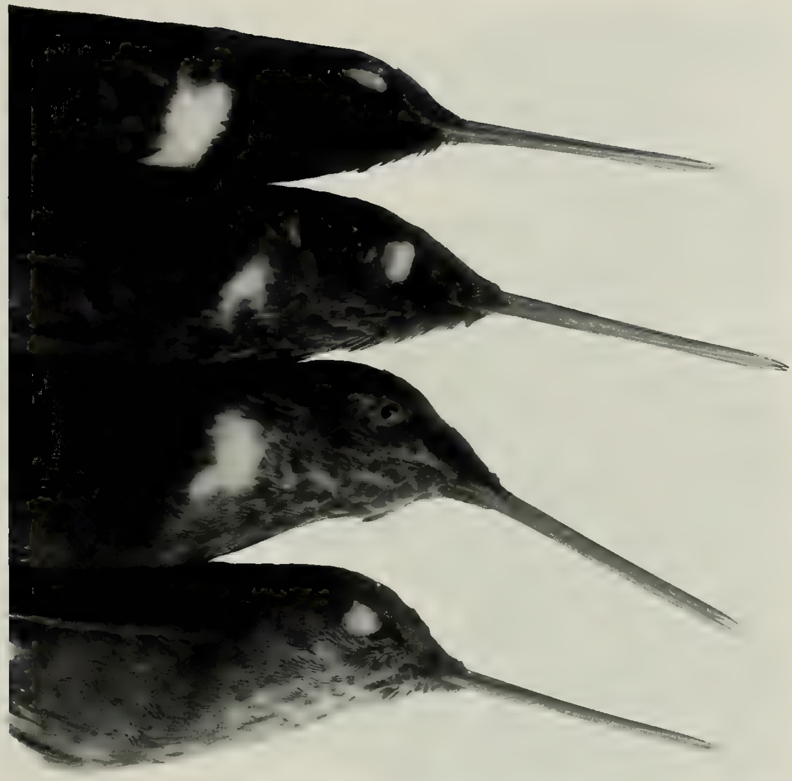

Fig. 1. Lateral views of males in definitive plumage (top to bottom): *Coeligena prunellei*; *C. coeligena colombiana* × *C. prunellei,* BMNH 2000.1.9; *C. coeligena colombiana* × *C. prunellei,* BMNH 88.7.25.165 (type of *Coeligena purpurea* Gould, 1854); and *C. coeligena colombiana.*

represented a subdefinitive plumage, aberrant color morph, or geographic variant of any known taxon (see Results and Discussion). In assessing the possibility of hybridization, I considered all species in the genus *Coeligena* (*coeligena, wilsoni, prunellei, torquata, phalerata, eos, bonapartei, helianthea, lutetiae*; taxonomy of Schuchmann 1999) that occur in Colombia and Ecuador (Hilty & Brown 1986, Fjeldså & Krabbe 1990, Krabbe et al. 1992) as potential parental species.

Measurements were taken with digital calipers and rounded to the nearest 0.1 mm: wing chord; bill length (from anterior extension of feathers); and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5).

General color descriptions presented in Appendix 1 were made under natural light. I evaluated the color of the crown, center of back, and dorsal surface of rectrix 4 with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent feathers are acutely dependent on the angle of measurement, the curvature of plumage surfaces in museum skins, and the degree of pressure applied to the plumage surface by the

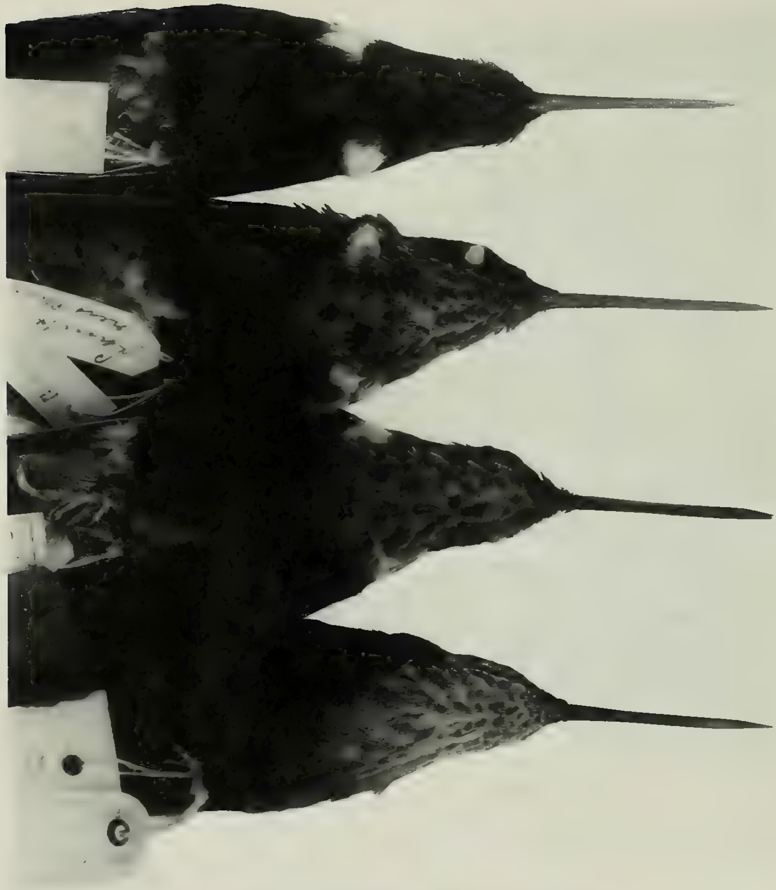

Fig. 2. Ventral views of males in definitive plumage (top to bottom): *Coeligena prunellei*; *C. coeligena colombiana* × *C. prunellei*, BMNH 2000.1.9; *C. coeligena colombiana* × *C. prunellei*, BMNH 88.7.25.165 (type of *Coeligena purpurea* Gould, 1854); and *C. coeligena colombiana*.

Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the plumage surface without depressing it. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure three times for each area of plumage, removing the aperture between trials. Each datum summarized in Table 2 thus represents the mean of three independent measurements.

Colorimetric characters were described in terms of opponent-color coordinates (*L*, *a*, *b*) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (*L*), red-green (*a*), and yellow-blue (*b*). The rationale is that a color cannot be perceived as red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value *a*, which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by *b* for yellows and $-b$ for blues. The third coordinate, *L*, ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage, the higher the *L* value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans. The relevance

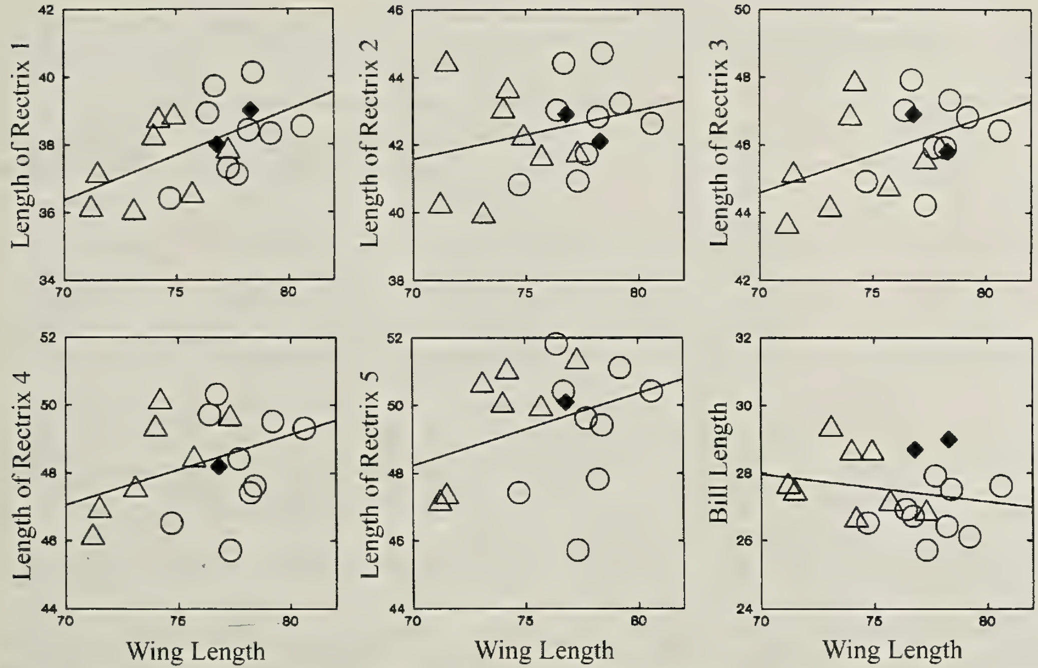

Fig. 3. Bivariate plots of measurements (see Table 1) of males in definitive plumage: *Coeligena prunellei* (○); *C. coeligena colombiana* (△); and putative hybrids (♦), *C. coeligena colombiana* × *C. prunellei* (BMNH 2000.1.9; BMNH 88.7.25.165).

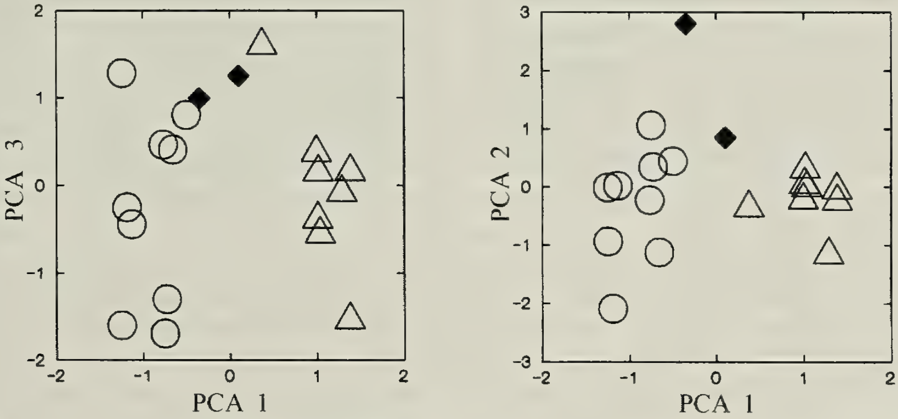

Fig. 4. Bivariate relationships of factor scores (see Table 3) from a principal components analysis of crown and breast color (*L, a, b*) of males in definitive plumage: *Coeligena prunellei* (○); *C. coeligena colombiana* (△); and putative hybrids (♦), *C. coeligena colombiana* × *C. prunellei* (BMNH 2000.1.9; BMNH 88.7.25.165).

of opponent color coordinates to colors perceived by hummingbirds is unknown.

I used principal components analysis (PCA) on untransformed colorimetric variables to reduce the dimensionality of data. Unrotated principal components were extracted from correlation matrices (Wilkinson 1989). Factor scores were projected on bivariate plots to illustrate the relationship of plumage color variables in postulated hybrids and parental species. Scatter plots of mensural characters and least squares re-

Table 1.—Ranges (mean ± standard deviation) of measurements (mm) of adult males of *Coeligena prunellei, C. coeligena colombiana,* and two specimens of a probable hybrid, *C. c. colombiana* × *C. prunellei* (= *Coeligena purpurea* Gould; type, BMNH 1888.7.25.165 and BMNH 2000.1.9).

	Coeligena prunellei (*n* = 9)	*Coeligena coeligena colombiana* (*n* = 8)	BMNH 1888.7.25.165	BMNH 2000.1.9
Wing chord	74.7–80.6 (77.7 ± 1.7)	71.2–77.3 (74.0 ± 2.1)	76.8	78.3
Bill length	25.8–28.0 (26.9 ± 0.7)	26.6–29.3 (27.8 ± 1.0)	28.7	29.0
Rectrix 1	36.5–40.2 (38.4 ± 1.2)	36.0–38.8 (37.4 ± 1.1)	38.0	39.0
Rectrix 2	40.9–44.8 (42.8 ± 1.4)	39.9–44.4 (42.1 ± 1.6)	42.9	42.1
Rectrix 3	44.3–48.0 (46.4 ± 1.8)	43.6–47.8 (45.4 ± 1.5)	46.9	45.8
Rectrix 4	45.8–50.4 (48.4 ± 1.6)	46.1–50.1 (48.3 ± 1.5)	48.2	—
Rectrix 5	45.8–51.9 (49.4 ± 2.0)	47.1–51.3 (49.6 ± 1.7)	50.1	—

gression lines were used to illustrate size differences among specimens.

Results and Discussion

I considered four hypotheses proposed by previous authors: *Coeligena purpurea* represents (a) a melanistic plumage of *C. wilsoni*; (b) a subdefinitive plumage of *C. prunellei*; (c) an intrageneric hybrid; or (d) a valid species. For brevity I use the epithet, *purpurea,* in the remainder of the paper.

Melanistic plumage of Coeligena wilsoni?—The hypothesis of melanism (Elliot 1878) is contradicted by the fact that *C. wilsoni* and *purpurea* differ in external measurements (unpublished data). Both sexes of *C. wilsoni* have significantly shorter wings but marginally longer bills than *purpurea.* Additionally, the length of rectrix 5 of the type of *purpurea* exceeds the maximal values observed in *C. wilsoni.*

Subdefinitive plumage of Coeligena prunellei?—As previously noted, both specimens of *purpurea* appear to be in definitive

Table 2.—Maxima, minima, and means (± standard deviation) of opponent color coordinates (*L, a, b*) of crown, breast and rectrix of adult males of *Coeligena prunellei, C. coeligena colombiana,* and two specimens of a probable hybrid, *C. c. colombiana* × *C. prunellei* (= *Coeligena purpurea* Gould; type, BMNH 1888.7.25.165 and BMNH 2000.1.9).

		Coeligena prunellei (*n* = 9)			*Coeligena coeligena colombiana* (*n* = 8)			BMNH 88.7.25.165	BMNH 2000.1.9
Variables		Min.	Max.	Mean (± *SD*)	Min.	Max.	Mean (± *SD*)		
	L	13.1	18.9	16.4 (± 1.7)	20.1	25.6	23.4 (± 1.6)	19.0	15.4
Crown	*a*	−1.1	2.6	0.7 (± 1.5)	3.5	5.9	4.7 (± 0.8)	3.3	4.6
	b	2.1	5.2	4.0 (± 1.0)	5.0	16.7	12.1 (± 3.8)	3.3	3.5
	L	11.7	20.3	15.4 (± 3.4)	37.0	46.9	41.7 (± 3.6)	31.9	23.8
Breast	*a*	1.6	4.2	3.0 (± 0.8)	2.4	3.4	3.0 (± 0.3)	3.6	4.3
	b	2.0	6.4	3.7 (± 1.7)	9.2	12.7	10.8 (± 1.0)	3.3	7.8
	L	7.2	11.6	9.6 (± 1.5)	18.4	24.0	21.2 (± 1.8)	13.1	12.9
Rectrix	*a*	3.3	3.8	3.6 (± 0.2)	5.4	5.9	5.7 (± 0.2)	5.0	5.1
	b	2.1	3.8	3.1 (± 0.5)	12.6	18.3	16.0 (± 1.8)	3.6	9.3

Table 3.—Factor loadings from a principal components analysis (PCA) of crown and breast color (L, a, b) of *Coeligena prunellei, C. coeligena colombiana,* and hybrids, *C. coeligena colombiana* × *C. prunellei* (BMNH 2000.1.9; BMNH 88.7.25.165).

Variables		PCA 1	PCA 2	PCA 3
Crown	L (dark/light)	0.96	−0.14	−0.15
	a (red/green)	0.88	0.13	0.35
	b (yellow/blue)	0.89	−0.23	−0.32
Breast	L (dark/light)	0.95	−0.08	0.03
	a (red/green)	0.01	0.98	−0.17
	b (yellow/blue)	0.91	0.31	0.09
Percent variance explained		70.4%	19.2%	4.7%

plumage. Specimens of *C. prunellei* in definitive and subdefinitive plumages differ in numerous ways from *purpurea* (see Appendix 1).

Hybrid?—Because hybrids lack formal standing in zoological nomenclature, hybridity must be ruled out before species status is conferred. In this instance, the evidence is consistent with the hypothesis that *purpurea* represents an intrageneric hybrid, *Coeligena coeligena* × *C. prunellei* (Berlioz 1936). Several characters of *purpurea* facilitate the identification of its parental species: (a) throat feathers conspicuously margined with pale buffy-white; (b) elliptical white spots on both sides of the upper breast; (c) unmarked rectrices; (d) absence of rufous or buff pigmentation on the secondaries; (e) absence of a brilliant frontlet or coronal patch; and (f) the absence of strong iridescence on the lower breast and belly (see Appendix I).

Here I present a synopsis of the critical steps of the hybrid diagnosis. The pool of potential parental species may be quickly narrowed by focusing on the scalloped pattern of chin and throat feathers of *purpurea.* Among the potential parental species, this character is shared only by *C. coeligena.* The white breast spots of *purpurea* were inherited from the other parental species. Three species in the source pool either have white breast spots (*C. wilsoni, C. prunellei*) or a white pectoral band (*C. torquata*). *Coeligena torquata* can be eliminated from further consideration because its rectrices (1–4) are predominately white (rectrices are dark and unmarked in *purpurea*). Only one of the two remaining pairs of species (*C. coeligena* × *C. prunellei*) could have contributed the unique combination of characters exhibited by *purpurea* (Appendix).

The hybrid diagnosis focuses on the identification of apomorphic character states in putative hybrids (Graves 1990). Complete dominance and polygenic inheritance of plumage characters, however, may preclude or obscure the expression of parental apomorphies in hybrids. When parental apomorphies are not identifiable, the parentage of a hybrid may be indicated, although less conclusively, by the presence or absence of a suite of plesiomorphic characters. In this case, rejection of taxa whose prominent plesiomorphic characters were not identified (even as traces) in *purpurea* reduces the species pool to the same couplet of species that share apomorphic characters with *purpurea.* For example, hybridization of *C. wilsoni* and *C. coeligena* would likely produce offspring with plumage that is significantly less melanized than that of *purpurea.* In a similar fashion, *Coeligena eos* (brilliant frontlet, cinnamon secondaries and rectrices, brilliant iridescence on lower breast), *C. bonapartei* (brilliant frontlet, brilliant iridescence on lower breast), *C. helianthea* (brilliant frontlet, brilliant iridescence on lower breast), *C. phalerata* (brilliant frontlet, completely white rectrices), and *C. lutetiae* (brilliant frontlet, buff secondaries) are exceedingly unlikely to be parental species because they possess a combination of characters not observed in *purpurea.*

External measurements.—As a second step, the restrictive hypothesis was tested with an analysis of size and external proportions (Table 1, Fig. 3). Measurements of avian hybrids fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic mode of inheritance (see Buckley 1982). External measurements of adult male *Coeligena coeligena* and *C. prunellei* overlap and the percent difference in character means is small (larger species divided by smaller): wing chord (5.0%), bill length (3.3%), rectrix 1 (2.7%); rectrix 2 (1.7%), rectrix 3 (2.2%), rectrix 4 (0.2%), and rectrix 5 (0.4%). Nevertheless, measurements of *purpurea* fall within the cumulative ranges of measurements of the postulated parental species, and, in many cases, approximate the values predicted by least squares regression (Fig. 3).

Colorimetric measurement.—Colorimetric values of *purpurea* fall within the range of values exhibited by the postulated parental species. The intermediate appearance of *purpurea* is neatly summarized by bivariate plots of factor scores from a principal components analysis (Fig. 4, Table 3) of crown and breast color. In particular, factor scores for *purpurea* are bracketed by those of *Coeligena coeligena* and *C. prunellei* along PCA 1, which explains 70.4% of the variance in color among specimens.

In summary, evidence obtained from plumage color and pattern, as well as from external size and shape, is consistent with the hypothesis that *Coeligena purpurea* is an intrageneric hybrid between *Coeligena coeligena* and *Coeligena prunellei. Coeligena purpurea* Gould, 1854 is thus available in taxonomy only for the purposes of homonymy.

Geographic origin.—As noted by Gould (1854; opposite plate 256), the geographic origin of *Coeligena purpurea* is indeterminate: "I have lately received from M. Parzudaki, of Paris, a fine specimen of this bird, which I believe to be from the neighbourhood of Popayan; a second example forms part of the collection of Edward Wilson, Esq., and is said to have been killed in Peru." I suspect both specimens were collected in the Eastern Cordillera of the Colombian Andes for the simple reason that one of its parental species, *Coeligena prunellei,* is restricted to this region (Hilty & Brown 1986, Collar et al. 1992). Collar et al.'s (1990) report of a single specimen of *C. prunellei* from the Central Cordillera at Salento, Department of Quindío, is unconfirmed. *Coeligena prunellei* (~1400–2600 m elevation) and *Coeligena coeligena colombiana* (1500–2600 m) overlap geographically in humid montane forest in the Department of Cundinamarca (Snow & Snow 1980, Hilty & Brown 1986, Fjeldså & Krabbe 1990, Collar et al. 1992).

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Appendix 1

Comparative description of selected characters of adult male *Coeligena prunellei, C. coeligena colombiana,* and two specimens of a probable hybrid, *C. coeligena colombiana* × *C. prunellei* (= *Coeligena purpurea* Gould; type, BMNH 1888.7.25.165; BMNH 2000.1.9). Unless noted otherwise, descriptions of *purpurea* refer to the type (BMNH 1888.7.25.165).

Viewed "head-on," the dorsum of *prunellei* is matte black. When viewed from a "tail-on" position, the dorsum exhibits weak iridescence, which varies in color from silvery-green on the forecrown and crown, to dark purple on the hindneck and mantle, to coppery-purple on the upper back, and bronze-green on the lower back and rump. The lesser wing coverts are iridescent steel blue. The median wing coverts and primary coverts are tipped with dark purple. Upper tail coverts are black faintly tinted with purple iridescence.

The dorsum of *coeligena*, which generally can be characterized as dark olive-bronze, exhibits weak bronze to coppery-bronze iridescence when viewed head-on. Exposed portions of dorsal feathers, all of which are narrowly or broadly tipped with rufous barbs, vary in color from bronze on the forecrown to coppery-bronze on the wing coverts, scapulars, and mantle, to olive-bronze or green on the back and rump. The imbrication of rufous-tipped feathers produces a subtly banded appearance on the back and rump. When viewed tail-on, the anterior dorsal plumage emits a dull golden-bronze iridescence which shifts to brighter bluish-green on the back and rump. The upper tail coverts are dark olive-bronze, narrowly edged with rufous.

The dorsum of *purpurea* is nearly intermediate in appearance between that of *prunellei* and *coeligena*. Crown, nape, and mantle are black, faintly tinted with brownish-purple; feathers are narrowly fringed with rufescent barbs. Purplish and coppery iridescence appears on the upper back. Viewed head-on, the forecrown of the type of *purpurea* exhibits a very faint purple iridescence, much less pronounced than in *prunellei*. The second specimen of *purpurea* (BMNH 2000.1.9) differs from the type in exhibiting a more intense iridescence (purple) on the crown and hindneck. Feathers on the rump are subtly banded, but significantly darker, than in *coeligena:* dark neutral grayish-brown basally, bordered distally by an iridescent band which changes spectrally toward the tip from dull coppery red through gold to green. The terminal barbs are tipped with rufescent barbs. The extent of green iridescence increases posteriorly from the lower back to the rump. Viewed tail-on, the mantle and back emits weak coppery-purple iridescence, shifting to golden-bronze on the lower back and rump. The upper tail coverts are dark purplish-brown (same color as crown), narrowly tipped with rufous.

Wing coverts and flight feathers of *purpurea* are intermediate in color and degree of melanism to those of *coeligena* and *prunellei*. The lesser wing coverts of *purpurea* are dark iridescent purple, whereas the margins of the adjacent upper scapulars are dark coppery-purple. Posterior scapulars are banded as in the middle back. Margins of the median wing coverts, primary coverts, and coverts at the bend of the wing are dark purple (darker than lesser wing coverts). Tiny coverts at the edge of the wing (best seen by raising the wing slightly) are tipped with chestnut. Greater wing coverts are dark bronzy purplish-brown. Flight feathers are dull black, tinted with purplish-brown. Outer vane of outermost primary is buff proximally, gradually darkening toward the tip to dark brown (similar to *prunellei* and *coeligena*). Underwing coverts dark brownish-black, intermediate between *prunellei* and *coeligena*.

Auriculars of *coeligena* are brown with some buffy-white barbs. Feathers of the chin, throat, malar region, and upper breast are scalloped; feathers are brownish-black with wide pale margins, either white or white faintly tinted with grayish-buff. Feathers of the lower breast, flanks, and abdomen are bronze to dark brown, paler and grayer toward the midline. Undertail coverts are dark brown, broadly edged with buff.

Auriculars, throat and upper breast of *prunellei* are black. Feathers of the central throat are tipped with brilliant steel blue to light purple disks, forming a gorget. An elliptical white patch occurs at the side of breast anterior to the bend of the wing in museum skins. The lower breast, flanks, and belly are black, less lustrous near the midline. The undertail coverts are black, broadly margined with white.

The ventral plumage of *purpurea* is nearly intermediate to that of *coeligena* and *prunellei*. Feathers of the chin, auricular margins, and throat are dark brownish-black (margined on the lower chin, throat, and malar area with pale buffy-white. When viewed head-on, the dark subterminal disks of the central throat emit a dull purple iridescence—iridescence was not observed at other angles of inspection. In *prunellei*, the exposed portions of the longest feathers that compose the white shoulder patch are silky white throughout their length. The shoulder patch of *purpurea* is similar to that of *prunellei*, but the margins are less well defined, the feathers less lustrous, narrowly to broadly fringed with dark brownish-black (same color as rest of ventral plumage). The breast, flanks, and abdomen of *purpurea* are dark brownish-black, with scattered buff or brown barb tips, especially along the midline. The undertail coverts are almost perfectly intermediate in color between those of *prunellei* and *coeligena*. The density of melanin in the central lanceolate spot increases with covert size. A couple of very short coverts are mostly buff (with dark brownish-black bases). Feather margins become progressively paler with increasing feather size, buffy to rufous in short feathers, very pale buffy-white in the longest feather. The second specimen of *purpurea* differs from the type in having the smaller undertail coverts more extensively fringed with buff and rufescent. The tibial plumes are dark brownish-black, tipped with brown barbs.

The unmarked rectrices of *purpurea* are intermediate in color and intensity of iridescence between those of *prunellei* (black, faintly tinted with purple) and *coeligena* (bronze or olive-bronze).

Feet and tarsi of *prunellei* are pale brownish-yellow (rose red in life, Hilty & Brown 1986), the claws are dark brown, but, on occasion, may be yellow. The feet and tarsi of *coeligena* are light brown with dark brown scutes, whereas the claws are dark brown. The feet and tarsi of *purpurea* are yellowish brown with medium brown scutes (claws brown). The maxillary ramphotheca is black in *prunellei, coeligena,* and *purpurea*. The mandibular ramphotheca is black in *prunellei*, medium brown in *coeligena*, and brownish-black in *purpurea*.

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Prognatholiparis ptychomandibularis, a new genus and species of the fish family Liparidae (Teleostei: Scorpaeniformes) from the Aleutian Islands, Alaska

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Abstract.—A new species representing a monotypic genus of liparid fishes is described from the central Aleutian Islands. The new genus differs from all known liparid genera by its strongly protruding lower jaw and prominent folds and flaps of skin on the jaws and snout. It is similar to *Allocareproctus jordani* and *Careproctus pycnosoma,* which are also moderately slender liparids with large pelvic disks, but it is further distinguished from these species by its lower meristics, more slender body, and absence of pyloric caeca. *Ptychomandibularis* also differs from *Allocareproctus* in its possession of an eighth preoperculomandibular pore, absence of coronal and post-coronal pores, two epurals, and autogenous hypural plates.

A single specimen of a new liparid (Fig. 1) was collected during the 1997 triennial groundfish survey of the Aleutian Islands, conducted by the Alaska Fisheries Science Center of the U.S. National Marine Fisheries Service. The specimen was captured in Seguam Pass in the central Aleutians at 455 m depth (Fig. 2). The new species possesses unique morphological features that indicate its distinctiveness as the only known member of a new genus.

Methods

The holotype was fixed at sea in 10% formalin-seawater solution and later transferred to 70% ethanol. Counts and measurements follow Burke (1930) and Pitruk (1991), with the exception of pore and pectoral-fin ray counts. Pore counts follow Stein and Andriashev (1990). In pectoral-fin ray counts, the upper lobe includes the dorsalmost ray to the ray dorsal to the shortest ray; the lower lobe includes the shortest ray in the notch to the ventralmost ray. Caudal-fin morphology and counts of dorsal- and anal-fin rays, branchiostegals, epipleural and pleural ribs, and vertebrae were obtained by examining radiographs. Osteology of the pectoral fin was not visible in radiographs. The holotype was deposited in the University of Washington Fish Collection (UW).

Prognatholiparis, new genus

Type species.—*Prognatholiparis ptychomandibularis,* new species, by monotypy.

Diagnosis.—Lower jaw projecting anterior to upper jaw (Fig. 3); prominent flaps and folds of skin on snout, upper jaw, and ventral portion of mandible; pelvic disk large, 37.4% head length (Fig. 4); body slender, depth at pectoral-fin base 20.5% SL, depth at anal-fin origin 19.0% SL; cephalic lateralis pores in 2-6-8-1 pattern, coronal and post-coronal pores absent (Fig. 5); epurals two, fused at base; hypural plates autogenous (Fig. 6); pleural ribs present; pseudobranchiae absent; subcutaneous ge-

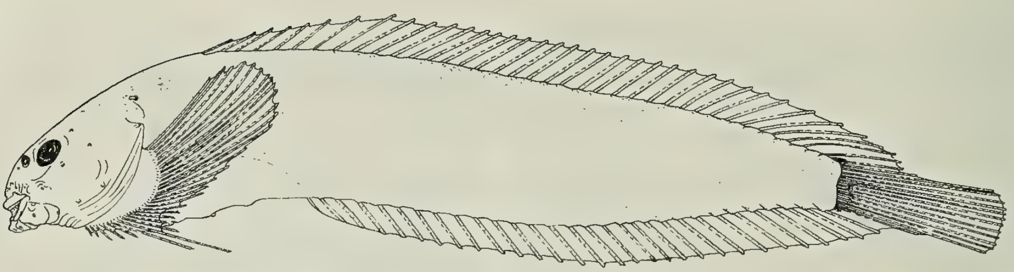

Fig. 1. *Prognatholiparis ptychomandibularis,* holotype, UW 042341, 88.0 mm SL, male. Illustration by B. Vinter.

latinous layer absent; pyloric caeca absent (Table 1).

Description.—See species account.

Etymology.—*Prognatholiparis* from the Greek *pro* (προ) = in front of + *gnathos* (γναθοζ) = jaw + *Liparis,* a genus of snailfishes, applied in reference to the protruding lower jaw, which distinguishes this genus from all other known liparid genera.

Prognatholiparis ptychomandibularis, new species

Wrinkle-jaw snailfish
Figs. 1–6, Table 1

Holotype.—UW 042431, 88 mm SL, male, Seguam Pass, east of Seguam Island, 52.31836°N, 172.7453°W, 455 m depth, W. Flerx, collector, R/V *Vesteraalen,* Cruise

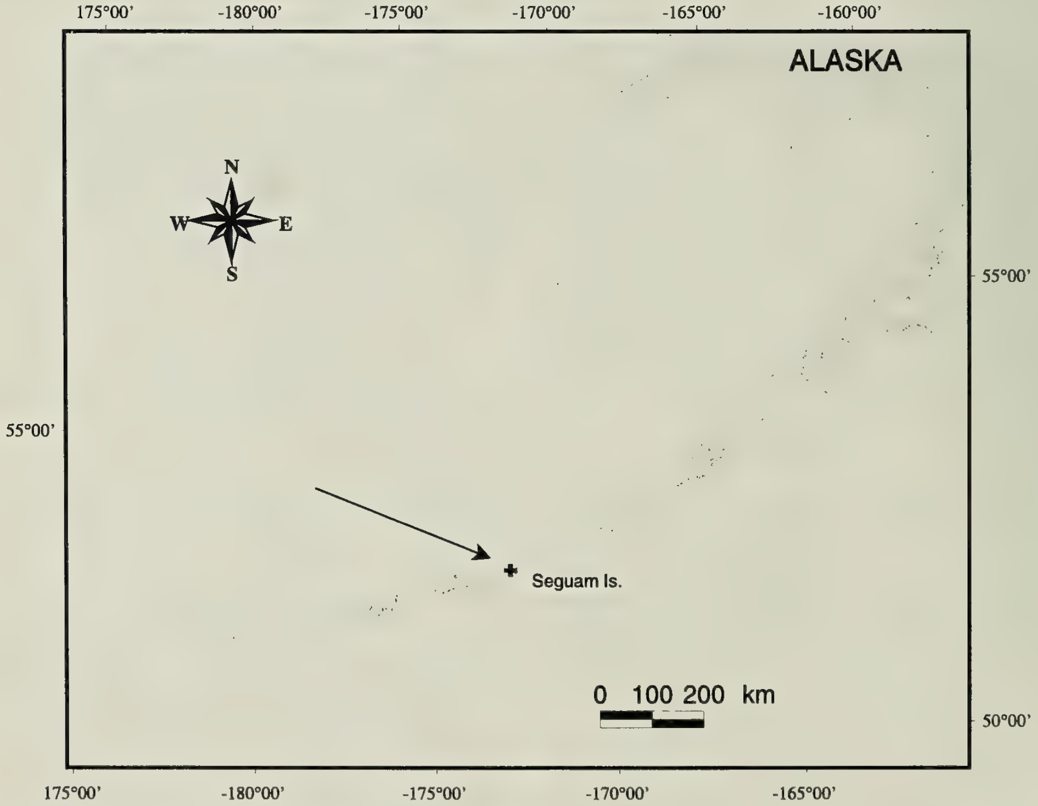

Fig. 2. Collection locality of *Prognatholiparis ptychomandibularis,* holotype, UW 042341, 88.0 mm SL, male, Seguam Pass, central Aleutian Islands, Alaska.

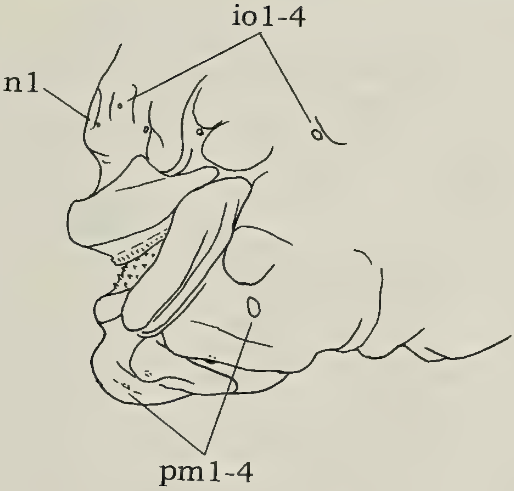

Fig. 3. *Prognatholiparis ptychomandibularis*, holotype, UW 042341, 88.0 mm SL, male. Left lateral view of snout and lower jaw. n1 = nasal pore 1; io1-4 = infraorbital pores 1–4; pm1–4 = preoperculomandibular pores 1–4. Illustration by B. Vinter.

199701, T. Cosgrove, Captain, haul 58, 22 Jun 1997.

Diagnosis.—Same as for genus.

Counts.—See Table 1.

Description of holotype.—Body slender, depth at pectoral-fin base 20.5% SL, depth at anal-fin origin 19.0% SL; predorsal length 28.2% SL; preanal length 35.7% SL; head slightly depressed; maxilla 18.5% HL, ending well anterior to orbit; mandible 25.6% HL, articulation with quadrate anterior to orbit; fleshy lip originating well posterior to the tip of the mandible leaving a narrow anterior edge on lower jaw; snout and mandible with longitudinal folds of skin bracketing pores of the cephalic lateralis, folds on snout broadened distally with slightly constricted base, folds on mandible formed as strong ridges (Fig. 3); mandible projecting anterior to snout, with 4 rows of weakly trilobate teeth tapering to a single row posteriorly; teeth in 4 rows at tip of

Fig. 4. *Prognatholiparis ptychomandibularis*, holotype, UW 042341, 88.0 mm SL, male. Ventral view of anterior portion of body, including lower jaw and pelvic disk. pm1–7 = preoperculomandibular pores 1–7 (Pore 4 of right side is not visible; see text for discussion). Illustration by B. Vinter.

Table 1.—Meristics and morphometrics of the holotype of *Prognatholiparis ptychomandibularis* n. sp., UW 042431. Pectoral-fin ray counts are presented with upper + lower lobe in parentheses; caudal-fin ray counts are presented as dorsal procurrent, dorsal principle + ventral principle, ventral procurrent rays. Vertebral counts are presented with precaudal + caudal in parentheses.

Character	Counts	Percent	Measurement (mm)
Dorsal-fin rays	37		
Anal-fin rays	30		
Pectoral-fin rays	30 (21+9)		
Branchiostegal rays	6		
Caudal-fin rays	3, 5+7, 2		
Vertebrae	41 (10+31)		
Pyloric caeca	0		
Cephalic pores	2-6-7-1		
Standard length			88.0
Head length			19.5
Caudal-fin length			17.9
% SL			
Head length		22.2	19.5
Predorsal length		28.2	24.8
Preanal length		35.7	31.4
Snout-to-anus length		23.9	21.0
Snout-to-disk length		11.6	10.2
Disk-to-anus length		4.1	3.6
Body depth at pectoral-fin base		20.5	18.0
Body depth at anal-fin origin		19.0	16.7
Pectoral-fin upper lobe length		15.1	13.3
Pectoral-fin lower lobe length		13.1	11.5
Disk diameter		8.3	7.3
Caudal-fin length		20.3	17.9
% HL			
Maxilla length		18.5	3.6
Mandible length		25.6	5.0
Snout length		33.8	6.6
Orbit diameter		22.1	4.3
Gill slit length		20.0	3.9
Disk diameter		37.4	7.3
% CL			
Dorsal fin overlap on caudal fin		33.0	5.9
Anal fin overlap on caudal fin		25.1	4.5

upper jaw tapering to a single row posteriorly. Eye small, orbit diameter 22.1% HL. Pyloric caeca absent.

Cephalic lateralis in 2-6-8-1 pattern on left side, preoperculomandibular pore 4 not opened on right side (Figs. 3–5). Nasal pores small, without tubes. Infraorbital pores small, only pore 6 on short tube. Mandibular canal from opposing sides united on dental symphysis at a single pore. Preoperculomandibular pores 1–5 large, without projecting tube; pores 6–8 small, on short tubes. Supratemporal pore one, on short tube.

Gill opening small, 20% HL, slit extending to above first pectoral-fin ray. Branchiostegal rays six.

Dorsal fin with 37 soft rays gradually increasing in length from anterior to posterior, membrane of posteriormost ray connected to dorsalmost ray of caudal fin for about 33.0% of caudal-fin length. Anal fin with

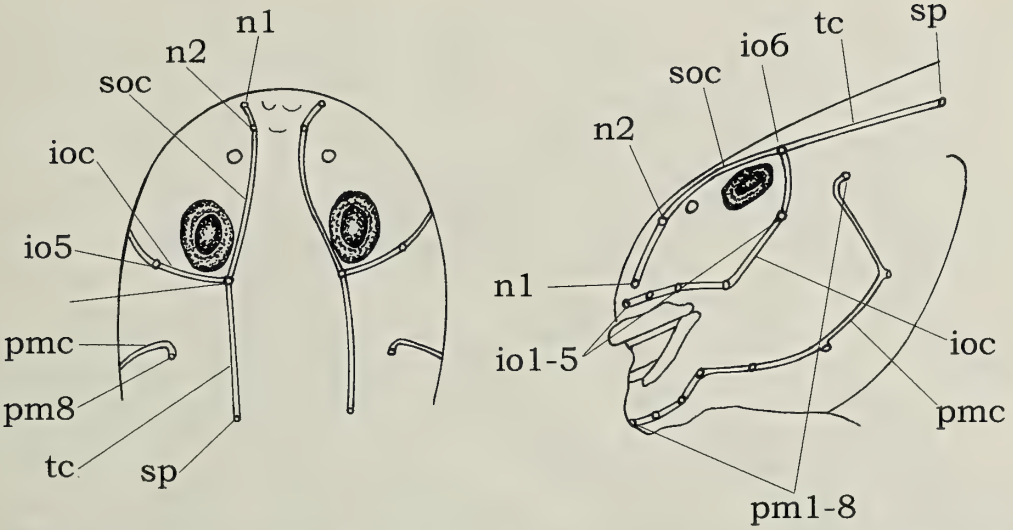

Fig. 5. *Prognatholiparis ptychomandibularis,* holotype, UW 042341, 88.0 mm SL, male. Diagrammatic view of cephalic pores. Abbreviations from anterior to posterior: n1 and n2 = nasal pores 1 and 2; soc = supraorbital canal; ioc = infraorbital canal; io1–6 = infraorbital pores 1–6; pm1–8 = preopercularmandibular pores 1–8; pmc = preoperculomandibular canal; tc = temporal canal; sp = suprabranchial pore. Illustration by B. Vinter.

30 rays gradually increasing in length from anterior to posterior, membrane of posteriormost ray connected to ventralmost ray of caudal fin for 25.1% of caudal-fin length.

Pectoral fin with 30 rays in two lobes, lobes separated by shallow notch with 21 rays in upper lobe and 9 rays in lower lobe. Pectoral-fin rays in notch spaced as in rays of lobes. Upper lobe rounded, extending to anal-fin origin, length 15.1% SL, with rays 3–10 longest; length of rays gradually shortening from ray 10 to ray 22; lower lobe pointed, extending beyond anus, length 75% of upper lobe length, 13.1% SL, with ray 24 longest; rays 25–30 shortening ventrally; tips of lower rays of dorsal lobe and all rays of lower lobe exserted.

Pelvic disk large, 37.4% HL and 8.3% SL, length about equal to width, fleshy covering obscuring internal structure (Fig. 4). Anus located midway between pelvic disk and origin of anal fin; distance from disk to anus 49.4% disk length (4.1% SL).

Caudal fin 20.3% SL, with 12 principal and 5 procurrent rays (3 + 5/7 + 2). Neural and haemal spines of preural centrum 2 complete and fused to centrum. Epurals 2, partially fused together at base. Hypural plates autogenous; parhypural fused to ventral hypural (Fig. 6). Vertebrae 41, precaudal vertebrae 10, caudal vertebrae 31. Pleural ribs present on vertebrae 8–10, epipleurals on vertebrae 1–20, epineurals on vertebrae 1–19.

Color in alcohol pale brown, with scattered melanophores over body beneath translucent cutaneous layer, darker on nape and at anterior base of dorsal fin. Orobranchial cavity, stomach, peritoneum, and intestines pale.

Ecology.—The single known specimen of *Prognatholiparis ptychomandibularis* was captured at 455 m depth with species typical of moderately deep waters of the Aleutian Islands. The haul was dominated by *Reinhardtius hippoglossoides* and *Bathyraja maculata.* The holotype had a full stomach that contained ostracods and rocks.

Etymology.—*ptychomandibularis* from the Greek *ptyx, ptychos* (πτυξ, πτυχοζ) = a fold + Latin *mandibula* = jaw, in reference to the skin folds on the snout and along the ventral margin of the mandible.

Comparisons.—Some 25 genera of lipar-

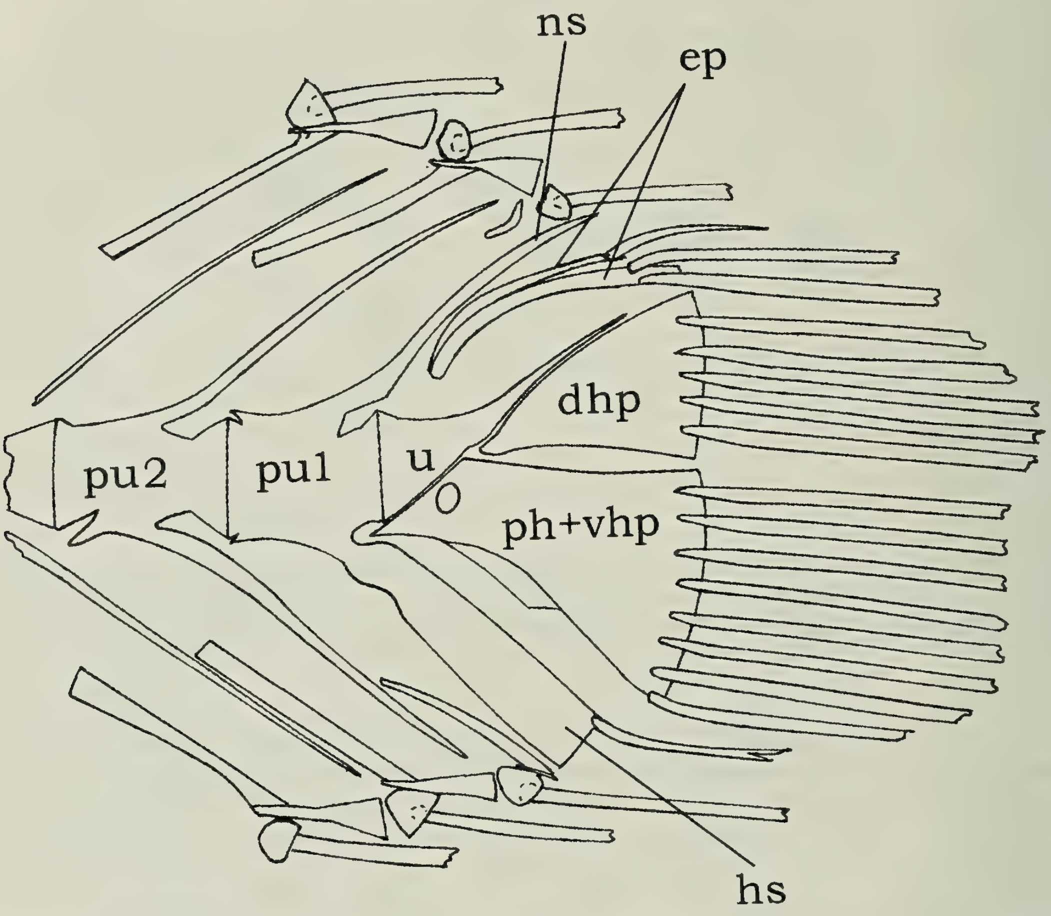

Fig. 6. *Prognatholiparis ptychomandibularis,* holotype, UW 042341, 88.0 mm SL, male. Caudal skeleton as illustrated from radiograph. pu1 and pu2 = preural centrum 1 and 2; u = urostyle; dhp = dorsal hypural plate; vhp = ventral hypural plate; ph = parhypural; ns = neural spine; hs = haemal spine; ep = epural. Illustration by B. Vinter.

ids are recognized worldwide, and the phylogenetics of the Liparidae are poorly understood (Kido 1988, Balushkin 1996, Andriashev & Stein 1998). However, *Prognatholiparis* is easily distinguished from all other liparid genera on the basis of its strongly projecting lower jaw and the folds of skin on the upper and lower jaws. Generally, among species of the North Pacific, it is phenetically most similar to the species *Allocareproctus jordani* and *C. pycnosoma,* which are also characterized by a moderately slender body, pale coloration, large disk, and small gill slit. Both species possess either trilobed teeth as in *Prognatholiparis* or both simple and trilobed teeth (Burke 1930, Kido 1985, 1988; Pitruk & Fedorov 1993).

Prognatholiparis differs from both these species in its lower meristics, including dorsal-, anal-, and pectoral-fin rays, and vertebrae. Both *A. jordani* and *C. pycnosoma* have at least 41 dorsal-fin rays, 33 anal-fin rays, 36 pectoral-fin rays, and 46 vertebrae. *Prognatholiparis* also differs in several other characters, including the absence of fleshy flaps on the rim of the cephalic pores (present in *Allocareproctus* and *C. pycnosoma*), and a longer lower pectoral-fin lobe that extends beyond the anus (does not reach the anus in *Allocareproctus* and *C. pycnosoma*).

In addition to characters of the lower jaw and snout, these species may differ from *Prognatholiparis* in the configuration of the anterior dorsal-fin rays, which project above the fin membrane. In the holotype of *Prognatholiparis,* the anterior rays appear to have been connected by membrane to their tips but were damaged during the specimen's collection.

Prognatholiparis differs from most liparids (Kido 1988, Balushkin 1996), including *Allocareproctus jordani* (Pitruk & Federov 1993), in the structure of its caudal skeleton, which includes hypural plates autogenous from the preural centrum and two epurals. Most liparids, especially those considered more derived, possess a relatively consolidated caudal skeleton, with fused hypural plates and a single epural (Kido 1988; Balushkin 1996).

Kido (1985, 1988) and Burke (1930) also considered *C. curilanus* and *C. ectenes* similar to *C. pycnosoma,* and therefore possibly similar to *Prognatholiparis. Careproctus ectenes* is a very slender and elongate species with exerted anterior dorsal rays and is similar to *C. curilianus* in its possession of an elongate protruding snout, a character that distinguishes both species from *Prognatholiparis.*

With the exception of *Allocareproctus jordani,* which was recently redescribed by Pitruk & Fedorov (1993) on the basis of 15 additional specimens, each of these species is known from less than five individuals. For each of these, the cephalic pore morphology, caudal skeleton, and features of the axial skeleton are not known. Recent surveys and collections of additional liparids from the Aleutian Islands may serve to shed light on these similar species and their relationships.

Acknowledgments

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Dendrochirote and dactylochirote sea cucumbers (Echinodermata: Holothuroidea) of China, with descriptions of eight new species

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Abstract.—The dendrochirote and dactylochirote holothurian fauna of China is now known to comprise 56 species in 16 genera. An annotated checklist of species is included here. Eight species are described as new: *Actinocucumis chinensis, Phyllophorus* (*Phyllothuria*) *donghaiensis, P.* (*Isophyllophorus*) *orientalis, Neothyonidium spiniferum, Stolus crassus, S. micronodosus, Thyone purpureopunctata* and *T. sinensis. Phyllophorus* (*Isophyllophorus*), a new subgenus, is also diagnosed. Preliminary analysis reveals that affinities of the dendrochirote/dactylochirote fauna lie with the tropical Indo-West-Pacific, for approximately 70% of the species are more or less widely distributed in the Indo-West-Pacific. Ten species are now known from the Yellow Sea, 26 from the East China Sea, and 39 from the South China Sea.

Until recently, the dendrochirote and dactylochirote holothurians of China have not been studied as a group. There are a number of scattered records in publications by Chang (1934, 1935, 1943, 1948), Yang (1937), Chang et al. (1964). Other records can be found in Liao & Clark (1995) and Liao (1997). In the present paper an attempt is made to list all of the dendrochirotes and dactylochirotes currently known from China. Eight new species are described, and new material sheds light on the systematic status of 14 already-described species. A new phyllophorid subgenus is also defined. Broad distribution patterns are briefly discussed. The classification of the Dendrochirotida and Dactylochirotida employed here is that of Pawson & Fell (1965). Type and other specimens are deposited at the Institute of Oceanology, Academia Sinica (IOAS), Qingdao, People's Republic of China. A few type specimens and some non-type material are deposited at the USNM, as noted in the text.

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Order Dendrochirotida

Family Cucumariidae Ludwig, 1894
Subfamily Thyonidiinae Heding & Panning, 1954
Actinocucumis chinensis, new species

Fig. 1

Material examined.—Holotype IOAS E1064, off Sanya, Hainan Island, 18°N, 109°E, 14 May 1960, 45 m, shelly sand.

Diagnosis.—Small form, length 25 mm, with stout, barrel-shaped body. Tubefeet large, restricted to five double rows in radii. Tentacles 20, varying in size, in a single ring. Calcareous ring simple, no posterior projections. Color in alcohol uniformly

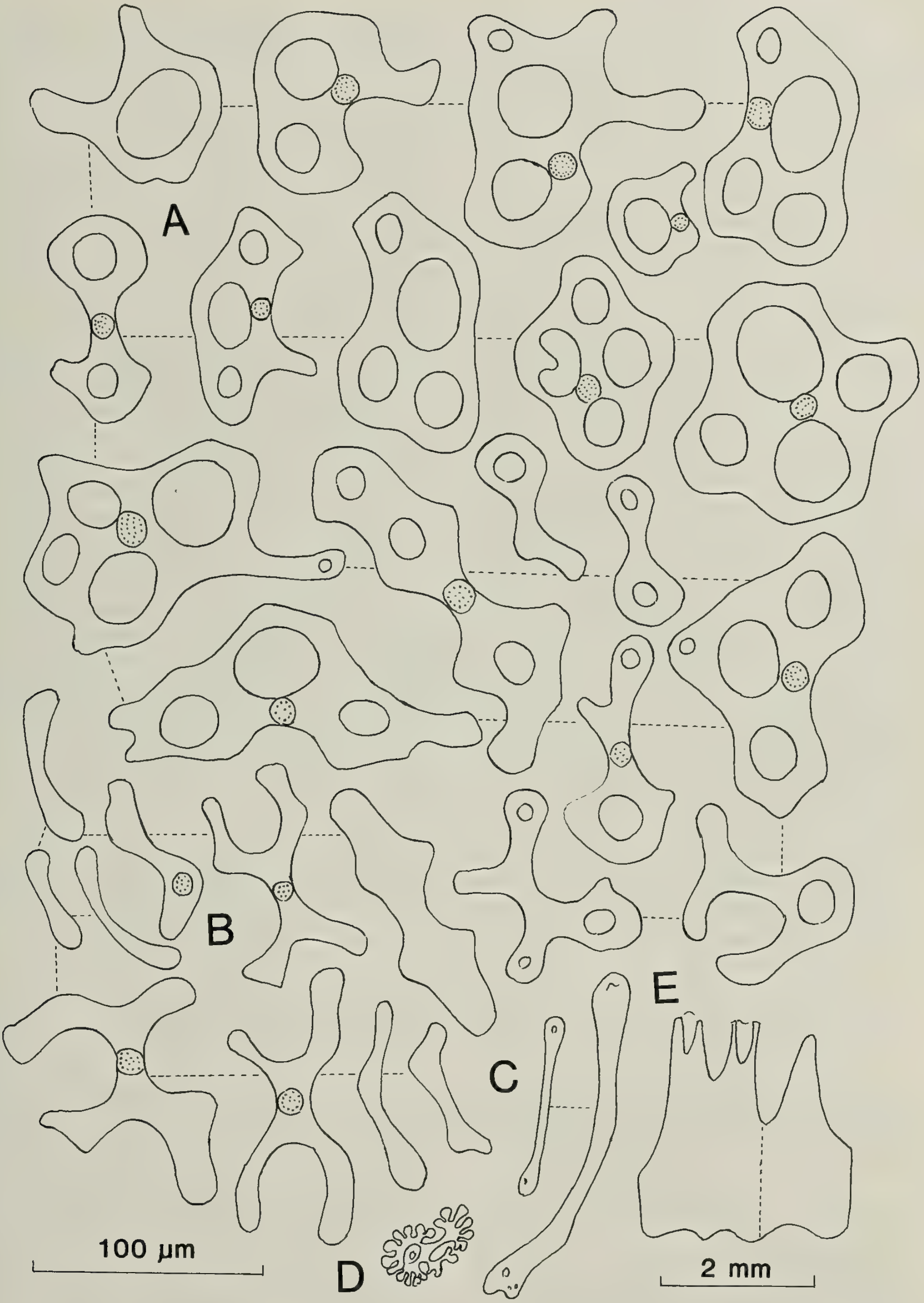

Fig. 1. *Actinocucumis chinensis* new species. A, perforated plates from body wall; B, rods from body wall; C, rods from tentacles; D, rosette from introvert; E, radial and interradial pieces of calcareous ring.

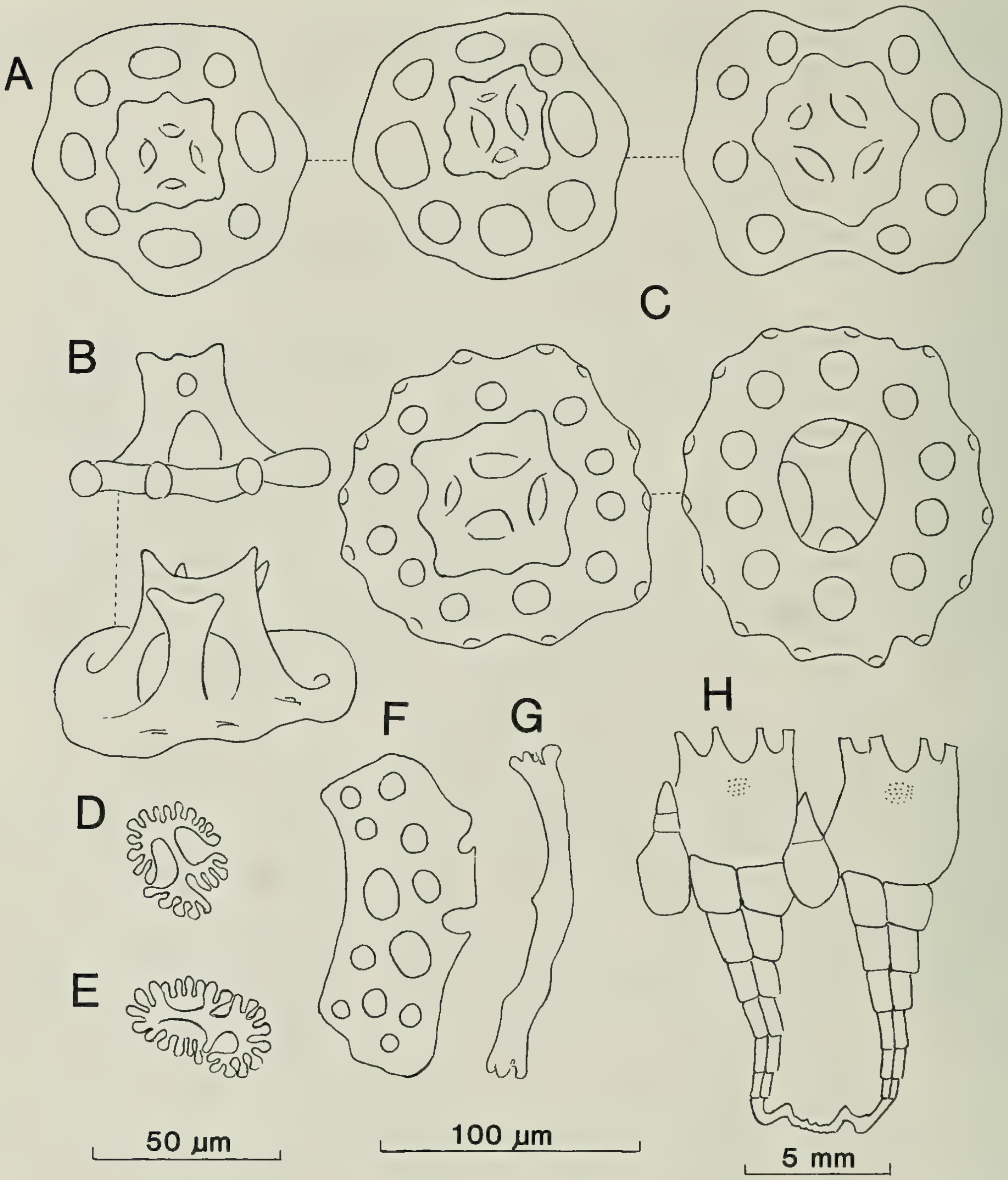

Fig. 2. *Anthochirus loui* Chang. A, tables from body wall; B, lateral view of tables from body wall; C, tables from posterior end; D, rosette from tentacles; E, rosette from introvert; F, perforated plate from tube feet; G, rod from tentacles; H, radial and interradial pieces of calcareous ring.

brown. Body wall ossicles irregular perforated plates and rods.

Description.—Total length 25 mm, diameter 15 mm. Body barrel-shaped, rounded anteriorly and posteriorly. Tentacles 20, of unequal size, in a single ring. Large tubefeet arranged in five double rows in radii; feet absent from interradii. Anus surrounded by five minute papillae. Calcareous ring simple, without posterior projections (Fig. 1E). Single Polian vesicle and stone canal. Body wall thin, soft, with numerous ossicles of diverse forms, usually as perforated plates and rods. Plates very numerous, 50–

170 μm long and 35–100 μm wide, very variable in shape and number of perforations (Fig. 1A). Rods (precursors of plates, probably) 40–110 μm long, variable in shape, often X-shaped (Fig. 1B). Plates and rods often bear a knob on their surface. Tubefeet with well-developed end plates and no other ossicles. Tentacles with rosettes and supporting rods of variable size (Fig. 1C). Introvert with rosettes (Fig. 1D).

Remarks.—The combination of characters—number of tentacles, simple calcareous ring and arrangement of tube feet place this specimen in the genus *Actinocucumis* Ludwig. In their monograph of the Phyllophoridae as it was then characterized, Heding and Panning (1954) noted that *Actinocucumis* was monotypic, containing the single species *A. typicus* Ludwig. The new species differs from *A. typicus* in the structure of its ossicles; those of *A. typicus* are figure-eight shaped fenestrated ellipsoids and irregular tables with a strong four-pillared spire (Clark & Rowe 1971). Further investigation of a wider range of material may require that these two species be referred to separate genera, but for the present it is preferred that they remain within the genus *Actinocucumis.*

Family Phyllophoridae Östergren, 1907

Subfamily Phyllophorinae Östergren, 1907

Anthochirus loui Chang

Figs. 2, 20F, G

Anthochirus loui Chang, 1948:79–80, text fig. 21, pl. 10 figs. 6–8; Chang et al., 1964:29.

Material examined.—Yellow Sea, 33°30′N, 122°30′E, 36 m, 4 specimen; Yellow Sea, 33°N, 123°E, 57 m, 2 specimens; Yellow Sea, 33°N, 123°15′E, 1 specimen.

Diagnosis.—Medium-sized form, about 50 mm in total length. Body slender, tubefeet numerous, scattered on body wall. Tentacles 30, of variable size, in two rings, outer ring with 20 tentacles, inner ring with 10. Calcareous ring compact; radials with well-developed posterior projections composed of 5–8 pieces; interradials much smaller than radials, more or less pentagonal, anterior end often composed of one or two small pieces. Ossicles in body wall sparsely scattered four-pillared and low-spired tables (Fig. 2A, B).

Remarks.—This remarkable holothurian was described by Chang in 1948 on the basis of four fragmentary specimens taken in the vicinity of Qingdao in about 20–30 m. It was a great pleasure to study seven entire specimens from the Yellow Sea, collected at depths between 33 and 57 meters. In his original description, Chang (1948:79) noted that "no deposits can be detected in body wall". Our material has sparsely scattered ossicles (Fig. 2A, B) in the form of tables with low four-pillared spires, and re-examination of Chang's type-material showed that he had overlooked the scattered ossicles. Tables in mid-body have smooth discs; those from the posterior end (Fig. 2C) have some small marginal knobs. Introvert with rosettes (Fig. 2E). Tube feet have perforated plates (Fig. 2F). Tentacles with rods (Fig. 2G) and rosettes (Fig. 2D). Details of the calcareous ring are illustrated here (Fig. 2H); posterior projections of present material are more delicate than those illustrated by Chang (1948).

In the structure of the ossicles, *Anthochirus* resembles *Selenkiella* Heding & Panning (1954), but *Anthochirus* differs in having more numerous tentacles and a more compact calcareous ring with single rather than bifurcated "tails" on the radial pieces.

Phyllophorus (Phyllophorella) dubius Cherbonnier

Figs. 3, 20A

Phyllophorus (*Phyllophorella*) *dubius* Cherbonnier, 1960:434, fig. 5c–k, fig. 6a–b; Clark & Rowe, 1971:184.

Phyllophorus (*Phyllophorella*) *kohkutiensis* (in part).—Liao & Clark, 1995:508, fig. 309. Non: *Phyllophorus* (*Phyllophorella*) *kohkutiensis* Heding & Panning, 1954.

Material examined.—Gulf of Tonkin, 20°15′N, 108°E, 50 m, 1 specimen; Gulf of Tonkin, 20°15′N, 108°30′E, 57 m, 1 speci-

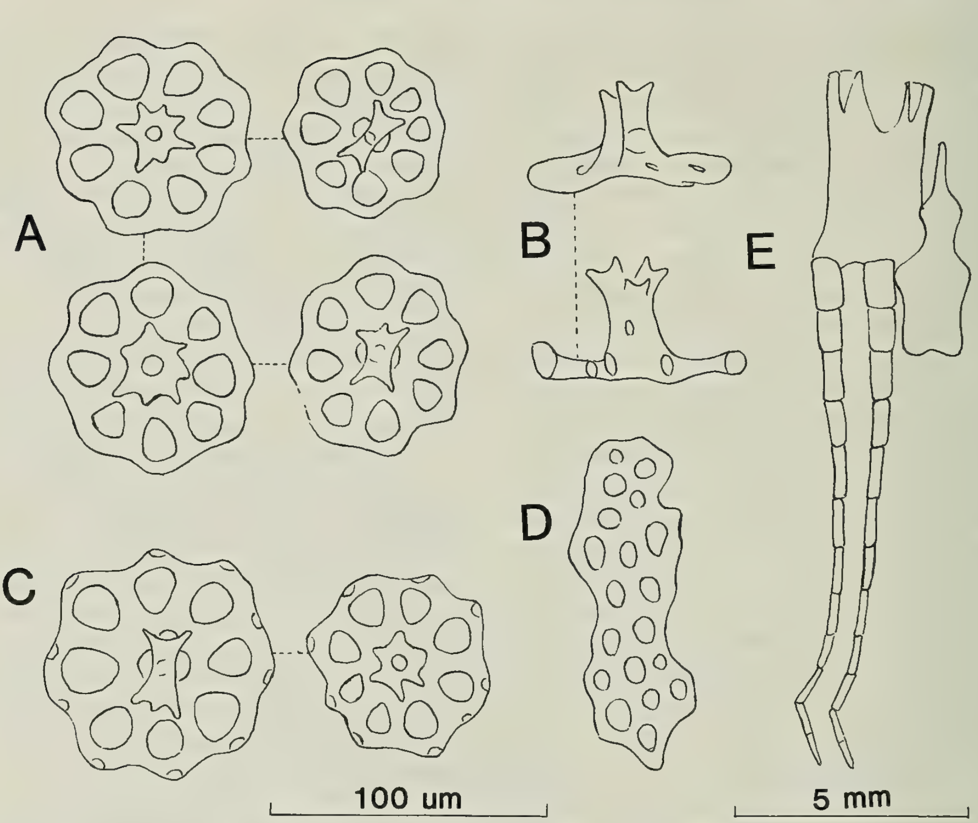

Fig. 3. *Phyllophorus* (*Phyllophorella*) *dubius* Cherbonnier. A, tables from body wall; B, tables from body wall, lateral view; C, body wall tables with marginal knobs; D, perforated plate from tube feet; E, radial and interradial pieces of calcareous ring.

men; Gulf of Tonkin, 18°N, 107°E, 63 m, 1 specimen; Gulf of Tonkin, 19°45′N, 108°30′E, 62 m, 1 specimen; Gulf of Tonkin, 19°45′N, 108°E, 63 m, 2 specimens; off Hainan Island, 19°45′N, 111°15′E, 106 m, 1 specimen; off southern end of Hainan Island, 17°30′N, 110°E, 125 m, 1 specimen; off Shanchuan Island, 21°15′N, 113°E, 43 m, 1 specimen; off Macao, 21°15′N, 113°30′E, 51 m, 1 specimen; off Macao, 21°30′N, 113°45′E, 43 m, 1 specimen; Taiwan Strait, 24°30′N, 119°45′E, 50 m, 6 specimens.

Diagnosis.—Small form, total length up to 50 mm, with spindle-shaped body. Tentacles 20, of varying size. Fine tube feet scattered on body wall. Calcareous ring with very long posterior projections on radials, each column composed of about 10 small pieces. Ossicles in body wall tables with circular disc perforated by eight holes (Fig. 3A–C); margin often knobbed; low four-pillared spire crowned by eight sharp teeth. Tube feet with flat plates (Fig. 3D).

Remarks.—These are undoubtedly representatives of the species originally described by Cherbonnier (1960) on the basis of a small and incomplete specimen from Vietnam. Our material ranged in length from 6–45 mm, and in diameter from 9–12 mm. Chinese specimens were previously confused with *Phyllophorus* (*Phyllophorella*) *kohkutiensis* Heding & Panning, 1954 (see Liao & Clark 1995, p. 508), but the calcareous rings (Fig. 3E, 4E) of the two species are quite different. The body wall ossicles of *P.* (*P.*) *kohkutiensis* are similar to those of the present species, but the posterior projections on the radials of the calcareous ring are decidely shorter and broader. The localities given here extend the known distribution area, and it is likely that this species will prove to be more widespread in the Indo-west-Pacific region.

Phyllophorus (*Phyllophorella*) *kohkutiensis* Heding & Panning
Figs. 4, 20B

(?) *Thyonidium cebuense.* Theel, 1886:95, pl. 9 fig. 4 (Non *T. cebuense* Semper, 1868)

Phyllophorus (Phyllophorella) kohkutiensis Heding & Panning, 1954:156, fig. 69; Liao & Clark, 1995:508, fig. 309 (in part).

Phyllophorus (Phyllophorella) cebuense.—Cherbonnier, 1960:431, fig. 4b–i, fig. 5a–b (Non *T. cebuense* Semper, 1868).

Material examined.—Gulf of Tonkin, 20°30′N, 108°30′E, 46 m, 1 specimen; Gulf of Tonkin, 19°N, 108°30′E, 36 m, 1 specimen; Gulf of Tonkin, 20°15′N, 108°E, 45 m, 2 specimens; Gulf of Tonkin, 20°N, 108°E, 53 m, 1 specimen; Gulf of Tonkin, 20°15′N, 108°E, 42 m, 1 specimen; Gulf of Tonkin, 20°30′N, 107°30′E, 32 m, 1 specimen.

Diagnosis.—Small form, 20 mm in length, body crescent-shaped, often stout. Tentacles 20, in three circles 10 + 5 + 5. Calcareous ring compact, radials with short posterior projections, composed of about five pieces (Fig. 4E). Ossicles in body wall exclusively tables, sparsely scattered, with smooth disc with one central and eight peripheral holes; spire low, slender, with several blunt apical teeth (Fig. 4A–C). Tube feet with flat plates (Fig. 4D).

Remarks.—Some confusion has surrounded this species. On account of tables with high spires and several crossbars, Heding & Panning (1954) referred *cebuense* to their new subgenus *Phyllothuria* Heding & Panning, 1954. Cherbonnier (1960) referred a specimen from Vietnam with a single crossbar on spires of the tables to the subgenus *Phyllophorella.* Heding & Panning were correct in referring specimens with high spires and several crossbars to *cebuense,* while specimens with low spires and a single crossbar on the tables are actually *kohkutiensis.* Cherbonnier's (1960) specimen is conspecific with *kohkutiensis* from Thailand. The seven specimens from the Gulf of Tonkin agree completely with the description and figures of *kohkutiensis* (Heding & Panning, 1954). Thus the species is now known from Vietnam, Thailand, and the Gulf of Tonkin.

Phyllophorus (*Phyllothuria*) *cebuensis* (Semper)
Fig. 5

Thyonidium cebuense Semper, 1868:67, Pl. 12 fig. 5, pl. 13 fig. 25, pl. 15 fig. 8; Lampert, 1885:173.

Phyllophorus cebuensis.—Ludwig, 1892: 347; Sluiter, 1901:112; Pearson, 1903: 144, pl. 2 fig. 22–24; Clark, 1946:409.

Phyllophorus (Phyllothuria) cebuensis.—Heding & Panning, 1954:147, fig. 62; Liao, 1997:210, fig. 125.

(Non *Thyonidium cebuensis* Théel, 1886: 95, 146, pl. 9 fig. 4; Sluiter, 1914:15, fig. 10; Clark, 1938:487; Cherbonnier, 1960: 431, fig. 4b–i, fig. 5a–b).

Material examined.—off Hong Kong, 21°30′N, 113°30′E, 42 m, 1 specimen; off Hainan Island, 18°15′N, 110°30′E, 125 m, 1 specimen.

Diagnosis.—Small form, approximately 30 mm in length, with scattered tube feet. Tentacles 20, varying in size, in two rings, outer ring with 15, inner ring with five tentacles. Calcarous ring with posterior projections on radials, each column consisting of four pieces (Fig. 5E). Ossicles in body wall exclusively four-pillared tables with circular disc perforated by large central and eight peripheral holes (Fig. 5A); spire high, with 2–5 crossbars (Fig. 5B), crowned by numerous closely crowded teeth. Tube feet with plates (Fig. 5D), and tables (Fig. 5C).

Remarks.—Material consists of two small specimens 25 and 16 mm in length.

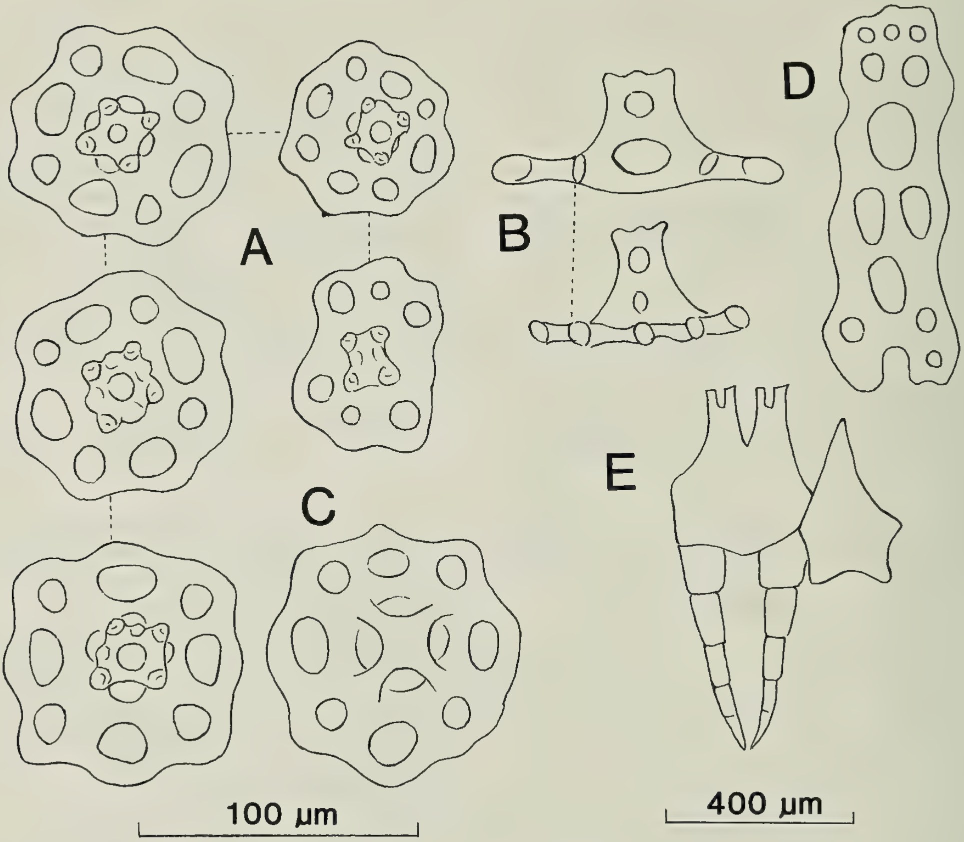

Fig. 4. *Phyllophorus* (*Phyllophorella*) *kohkutiensis* Heding & Panning A, tables from body wall; B, tables from body wall, lateral view; C, inner surface of body wall table; D, perforated plate from tube feet; E, radial and interradial pieces of calcareous ring.

They agree perfectly with the specimens recorded by Heding & Panning (1954) from Thailand and the Kei Islands. The species is now known from the Philippines, Sri Lanka, Thailand, Indonesia and China.

Phyllophorus (*Phyllothuria*) *donghaiensis*, new species

Figs. 6, 20C

Material examined.—Holotype IOAS E1075, East China Sea, 30°30′N, 127°E, 1 Jul 1978, 100 m, sand and broken shell bottom.

Diagnosis.—Medium-sized form, 45 mm in total length, with spindle-shaped body. Body wall rigid, filled with ossicles. Tube feet numerous, conical, papilliform and scattered on body wall. Calcareous ring small, radials with short posterior projections, each made up of four pieces. Ossicles in body wall four-pillared tables with 18–30 perforations. Tube feet ossicles tables with disc forming two to five lobes.

Description.—Body spindle-shaped, slightly curved, gently tapering towards ends. Length along dorsal surface 45 mm, along ventral surface 56 mm; diameter at middle 20 mm. Tentacles 20 in two rings, outer ring with 15, inner with 5. Tube feet numerous, conical, papilliform, and scattered all over body. Anus surrounded by five groups of small papillae. Body wall

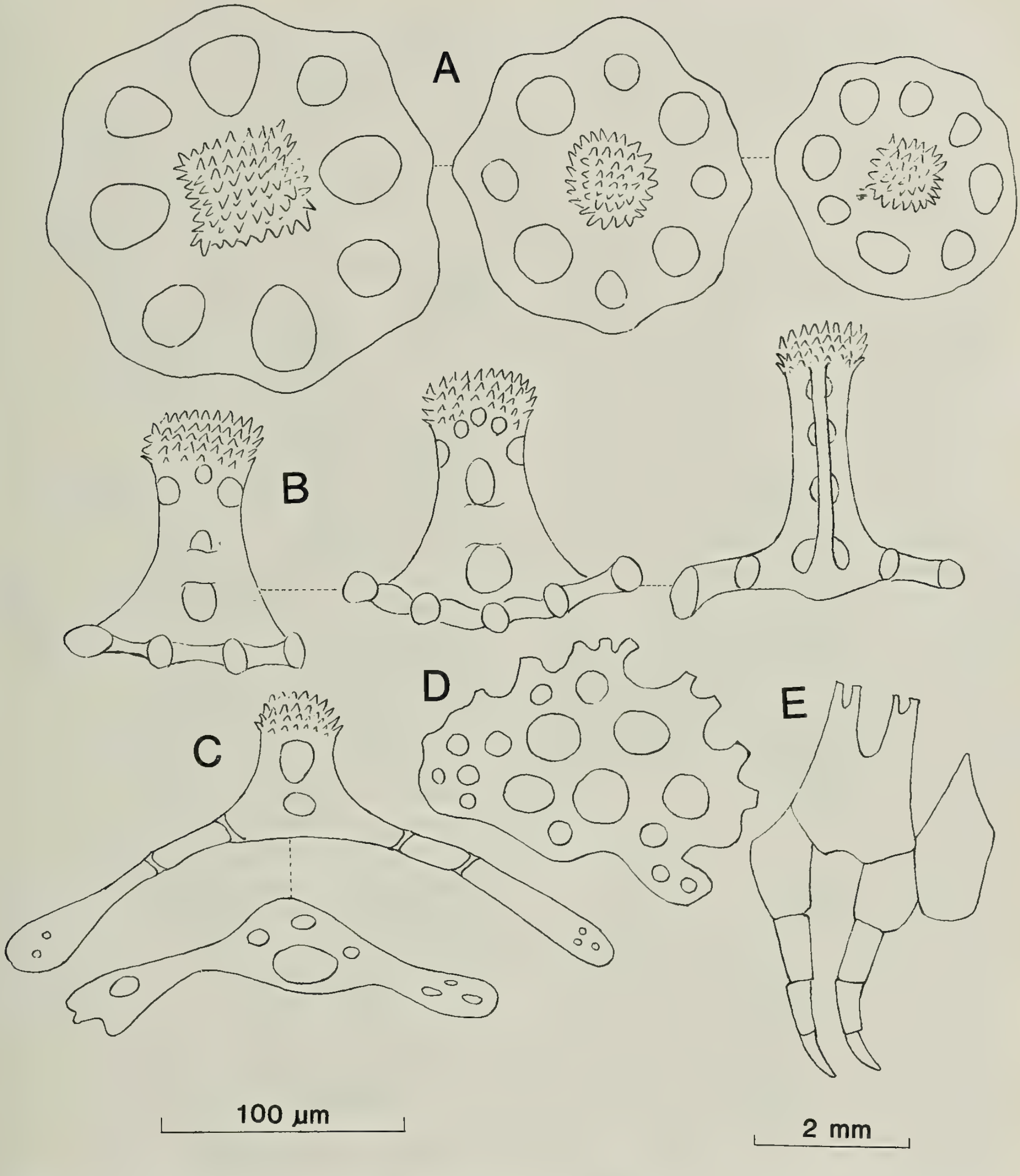

Fig. 5. *Phyllophorus* (*Phyllothuria*) *cebuensis* (Semper). A, tables from body wall; B, tables from body wall, lateral view; C, tables from tube feet; D, perforated plate from tube feet; E, radial and interradial pieces of calcareous ring.

rigid, rough. Calcareous ring small, total height 5 mm, radials with short posterior projections, each composed of four pieces; interradials pentagonal, anteriorly tapering to a point (Fig. 6H). One Polian vesicle; no stone canal detected. Ossicles abundant in body wall, four-pillared tables (Fig. 6A) with circular discs perforated by 18–30 holes; spire high with two crossbars, crowned by about eight teeth (Fig. 6B). Ossicles in tube feet irregular tables with disc forming two to five lobes; spire high with two to five crossbars, crowned by about eight teeth (Fig. 6C, D). Disc diameter

100–200 μm, height of spire 60–80 μm. Introvert with numerous rosettes (Fig. 6G). Tentacles with large supporting rods (Fig. 6E) and less common minute rods (Fig. 6F). Color in alcohol grayish, more or less whitish ventrally.

Remarks.—This is one of the most distinctive species in the family. Its ossicles are unique. The lobed extensions of the discs in the tube feet ossicles are reminiscent of species in the genus *Thorsonia* (Thyoninae).

Subfamily Phyllophorinae Heding & Panning, 1954

Genus *Phyllophorus* Grube, 1840

Remarks.—In their revision of the Phyllophoridae, Heding & Panning (1954) referred three genera to the Subfamily Phyllophorinae, and the genus *Phyllophorus* Grube, 1840 was diagnosed as having 20 tentacles (15 + 5), and towers or rosettes in the body wall. We wish to expand the concept of the genus to include a new subgenus, which has 20 tentacles in a single ring.

Isophyllophorus, new subgenus

Diagnosis.—Tentacles 20, subequal, arranged in single circle. Ossicles in body wall four-pillared tables with high spire; disc irregular, with marginal knobs.

Type species.—Phyllophorus (*Isophyllophorus*) *orientalis* new species.

Remarks.—See under description of *Phyllophorus* (*Isophyllophorus*) *orientalis* new species.

Phyllophorus (Isophyllophorus) orientalis, new species

Figs. 7, 20D, E

Material examined.—Holotype IOAS E1058, Yellow Sea, 33°N, 123°30′E, 4 Jul 1959, 41 m, sandy mud, grab sample.

Diagnosis.—Medium-sized form, total length about 40 mm. Tentacles 20, subequal, in single circle. Color in alcohol grayish-white, tube feet brownish. Calcareous ring small, low, posterior projections on radials composed of five small pieces. Ossicles in body wall four-pillared tables; disc irregular with numerous perforations and with few marginal knobs; spire high with three crossbeams, crowned by numerous teeth.

Description.—Body nearly cylindrical, 38 mm long, 12 mm in diameter, tapering towards posterior end. Tentacles 20, fully expanded, subequal, arranged in single circle. Tube feet numerous, contracted, scattered over body. Calcareous ring small, low, total height 4.5 mm; radials with posterior projections composed of five small pieces (Fig. 7F); interradials relatively large, pentagonal. Anus surrounded by five groups of papillae. Body wall thick, transversely wrinkled, rough to touch, with numerous ossicles.

Ossicles in body wall numerous tables with large disc 120–300 μm across, highly variable in shape and in number of perforations; all have few marginal knobs (Fig. 7A, B). Spire high, 70–120 μm, with four pillars, three crossbars and numerous apical teeth (Fig. 7C). In tube feet ossicles similar to those in body wall; no obvious endplate. Few rosettes in introvert (Fig. 7D). Tentacles with robust supporting rods (Fig. 7E).

Remarks.—The unique specimen differs from all other phyllophorus-like holothurians, and must be placed in a distinct subgenus as defined above. In most phyllophorids with 20 tentacles the tentacles are arranged in two circles. Only Pawson (1970) reported *Neothyonidium* species from New Zealand as having 20 tentacles in a single ring, but in that case the ossicles had two-pillared spires.

Subfamily Semperiellinae Heding & Panning, 1954

Neothyonidium inflatum (Sluiter)

Fig. 8

Phyllophorus inflatus Sluiter, 1901:114, pl. 2 fig. 10, pl 6 fig. 16.

Neothyonidium inflatum.—Heding & Panning, 1954:1293, fig. 95.

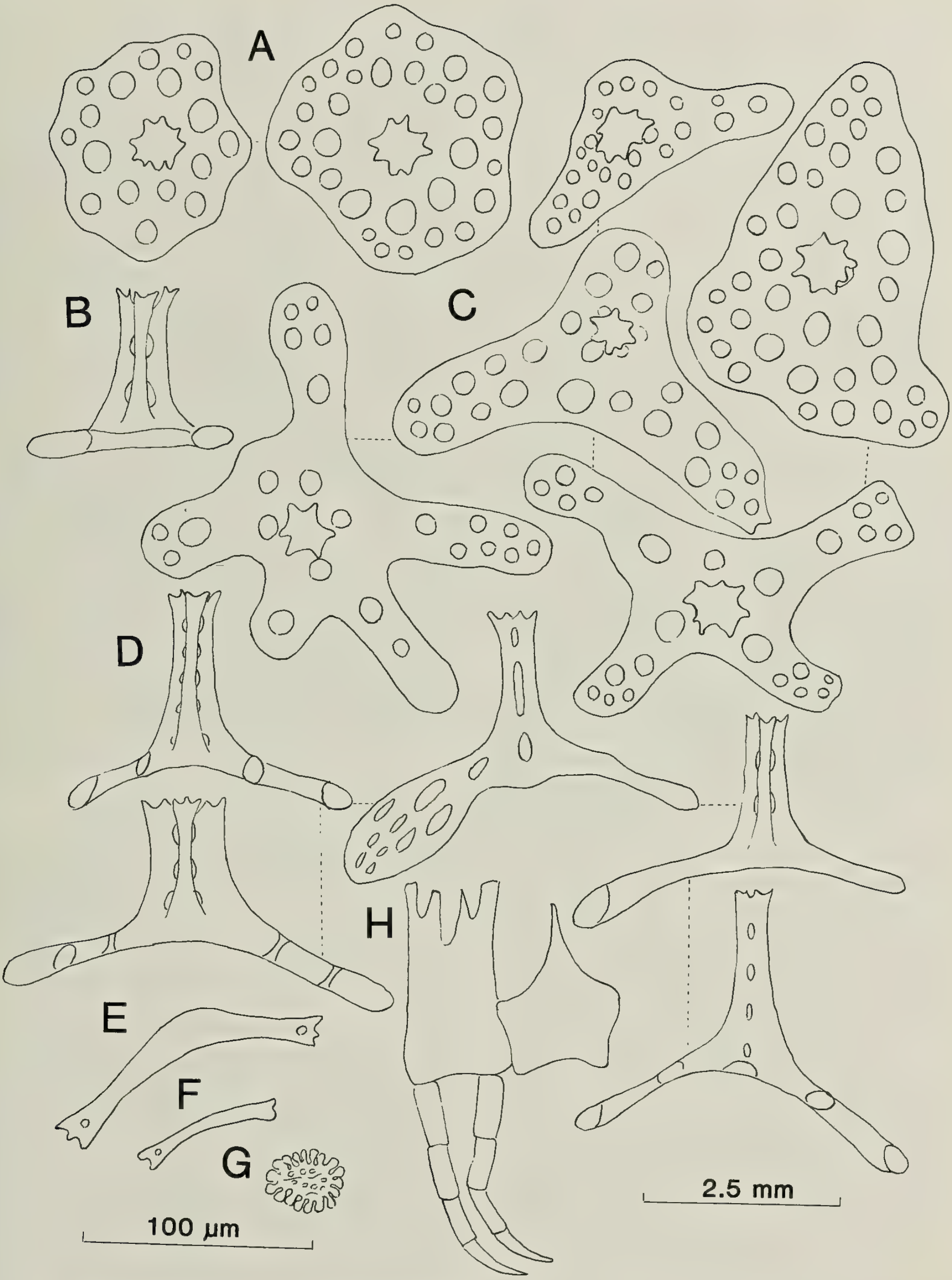

Fig. 6. *Phyllophorus* (*Phyllothuria*) *donghaiensis* new species. A, Tables from body wall; B, tables from body wall, lateral view; C, tables from tube feet; D, tables from tube feet, lateral view; E, rod from tentacles; F, minute rod from tentacles; G, rosette from introvert; H, radial and interradial pieces of calcareous ring.

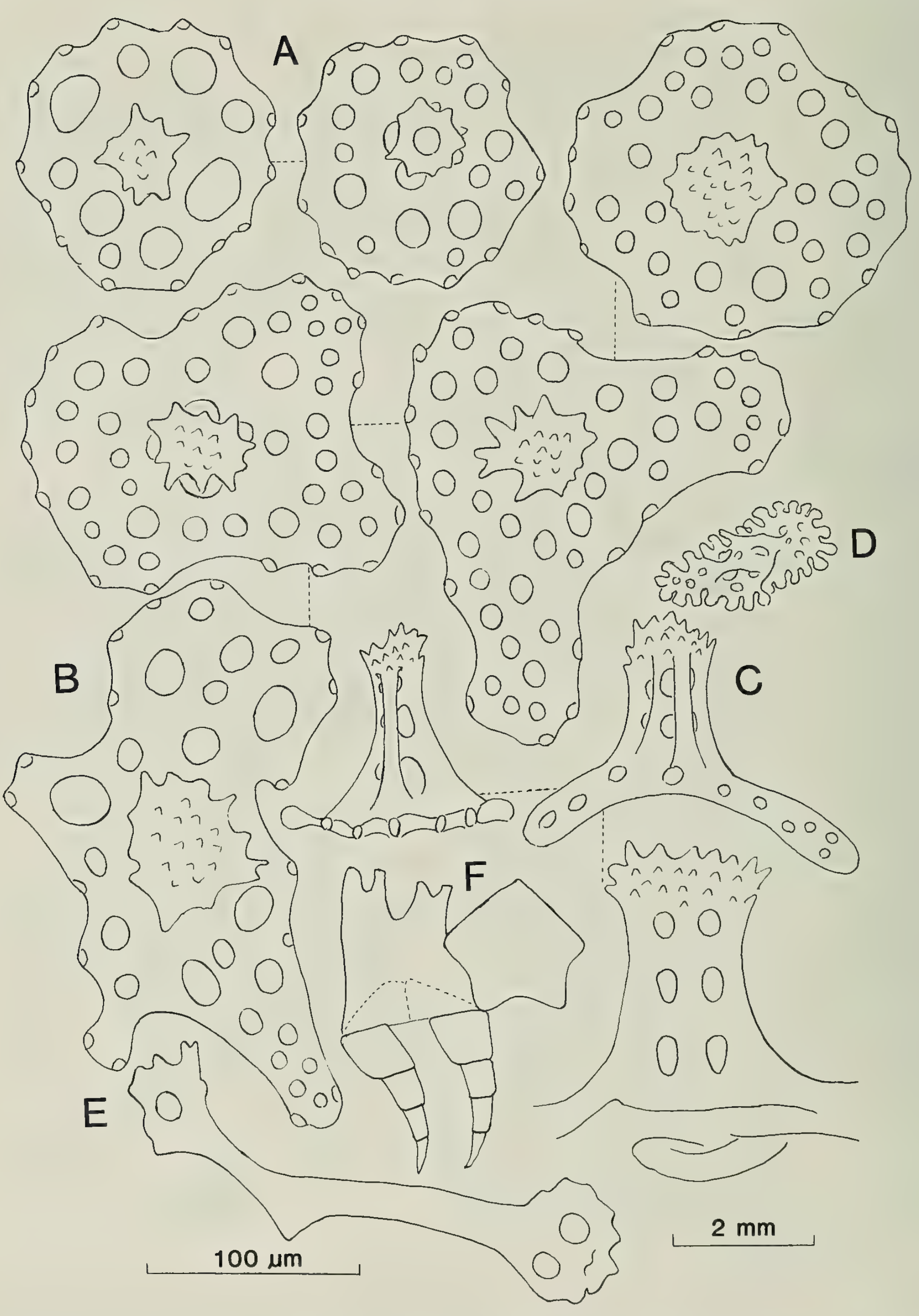

Fig. 7. *Phyllophorus* (*Isophyllophorus*) *orientalis* new subgenus, new species. A, tables from body wall; B, larger tables from body wall; C, tables from body wall, lateral view; D, rosette from introvert; E, rod from tentacles; F, radial and interradial pieces of calcareous ring.

Material examined.—Off Shantou, 23°30′N, 117°30′E, 37 m, 1 specimen; off Macao, 21°N, 117°30′E, 37 m, 1 specimen; off Guangdong Province, 20°30′N, 112°30′E, 74 m, 1 specimen. Diagnosis: Small to medium-sized form, up to 60 mm in length, body ovoid. Tentacles 20, arranged in two circles. Body wall thin, transparent. Tube feet thinly scattered over the body wall, more numerous ventrally than elsewhere. Calcareous ring very high, tubular, composed of a mosaic of small pieces; posterior projections on radials short, indistinct (Fig. 8D). Ossicles in body wall two-pillared tables (Fig. 8A, B) with low spire crowned with four diverging teeth; disc regular in outline, generally with eight perforations. Tube feet with well-developed end plates (Fig. 8C).

Remarks.—This species was previously known only from the unique holotype collected from Indonesia (Sluiter 1901). The current material is smaller (largest 20 mm in length). Coloration is striking—light yellow and transparent. The present record considerably extends the known range of the species.

Neothyonidium minutum (Ohshima)

Phyllophorus minutus Ohshima 1915:279, pl. 11 fig. 31a–b.

Neothyonidium minutum.—Heding & Panning, 1954: 194, fig. 96; Rho & Won, 1993:129, pl. 5 fig. 1–4.

Material examined.—East China Sea, 28°30′N, 126°E, 116 m, 1 specimen.

Diagnosis.—Small form, about 15 mm in length, with slender body. Tentacles 20, in two circles of 10 + 10. Calcareous ring composed of a mosaic of small pieces; radials fused with interradials. Ossicles in body wall two-pillared tables with low spires crowned with four to eight teeth; disc regular with four or eight holes.

Remarks.—The type locality for this species is the east China Sea, off Goto Islands, Japan (Ohshima 1915); other records are from the Sagami Sea and South Korea. Our specimen is 15 mm long and slender, and it is decalcified; we hesitantly refer it to this species, but we note that it was collected near the type locality of the species.

Neothyonidium spiniferum, new species

Figs. 9, 20H

Material examined.—Holotype IOAS E1061, Spratly Islands, South China Sea, 4°02′N, 109°59′E, 16 May 1987, 99 m, muddy sand bottom. Paratypes: IOAS E1083 Gulf of Tonkin, 18°15′N, 107°E, 8 Jan 1962, 69 m, 1 specimen; IOAS E1084, Gulf of Tonkin, 19°45′N, 108°45′E, 5 Jul 1960, 56 m, 1 specimen; IOAS E1085, Gulf of Tonkin, 19°N, 107°30′E, 9 Jul 1960, 66 m, 1 specimen; IOAS E1086, Gulf of Tonkin, 18°30′N, 107°E, 10 Dec 1969, 62 m, 1 specimen; IOAS E1087, Gulf of Tonkin, 18°N, 107°E, 14 Feb 1960, 63 m, 1 specimen; IOAS E1088, Gulf of Tonkin, 20°45′N, 107°30′E, 15 Feb 1960, 31 m, 1 specimen; IOAS E1089, Gulf of Tonkin, 19°N, 107°30′E, 9 Jul 1960, 66 m, 1 specimen; IOAS1090, Gulf of Tonkin, 20°30′N, 108°30′E, 27 Aug 1962, 45 m, 1 specimen. Additional 8 specimens from Gulf of Tonkin, 31–91 m.

Diagnosis.—Small to medium-sized form, 40 mm in length, body ovoid, more or less upcurved with mouth and anus dorsal. Tentacles 20 in two circles (10 + 10). Tube feet papilliform, sparsely scattered over body. Calcareous ring high, tubular, composed of mosaic of small pieces; radials fused with interradials, radials carrying short posterior projections. Three types of ossicles in body wall: tables characteristic, with high excentric solid spire ending in a point; button-like plates spiny, with distinct spines on margin and surface; smooth perforated plates with varying number of small holes.

Description.—Body ovoid, length 40 mm, diameter 25 mm at middle of body. Extremities upturned, mouth and anus therefore dorsally oriented. Tentacles 20 in two rings of 10. Body wall thin, soft, more or less transparent. Tube feet papilliform, sparsely scattered over body, more numer-

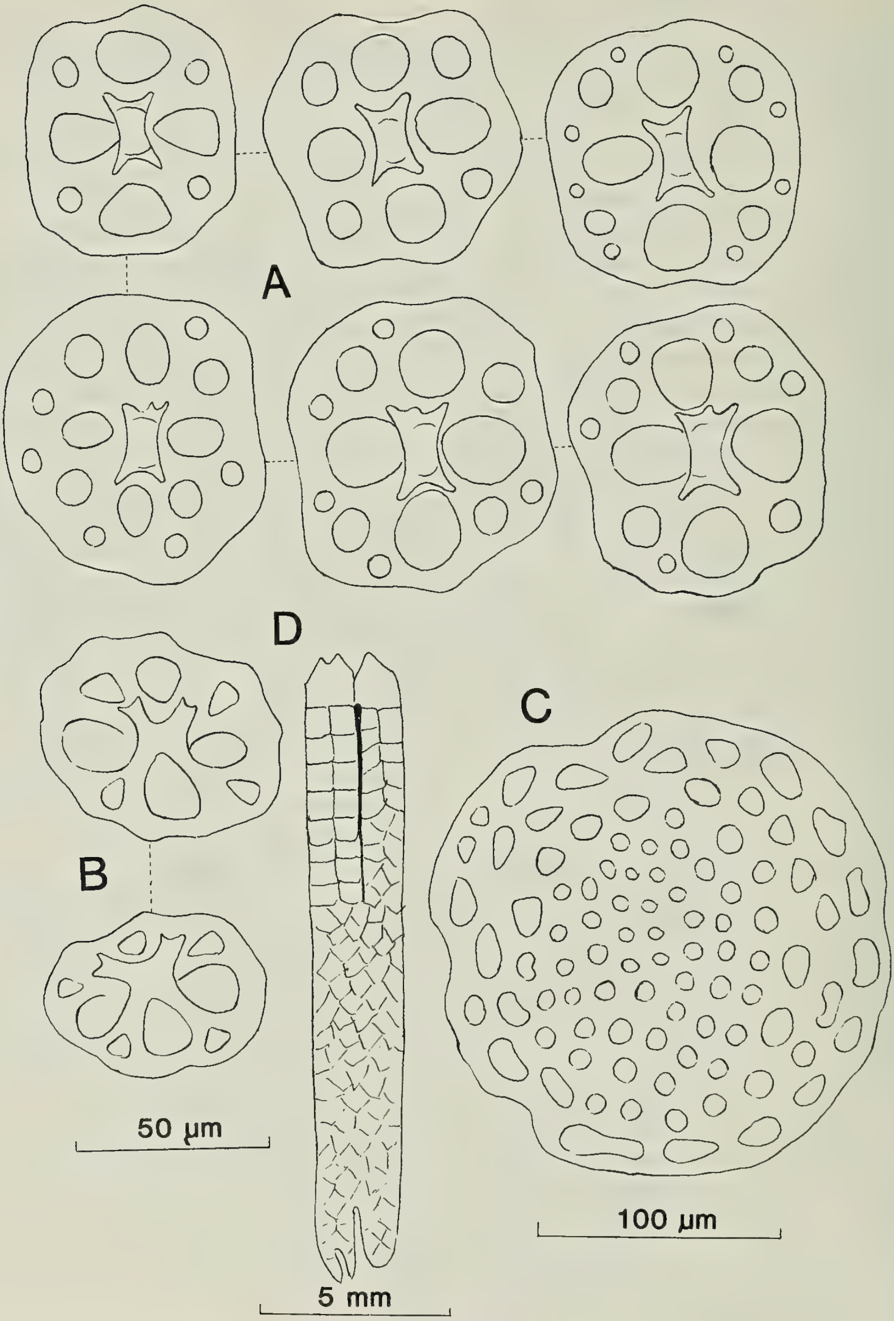

Fig. 8. *Neothyonidium inflatum* (Sluiter). A, tables from body wall; B, tables from body wall, oblique view; C, endplate from tube foot; D, radial and interradial pieces of calcareous ring.

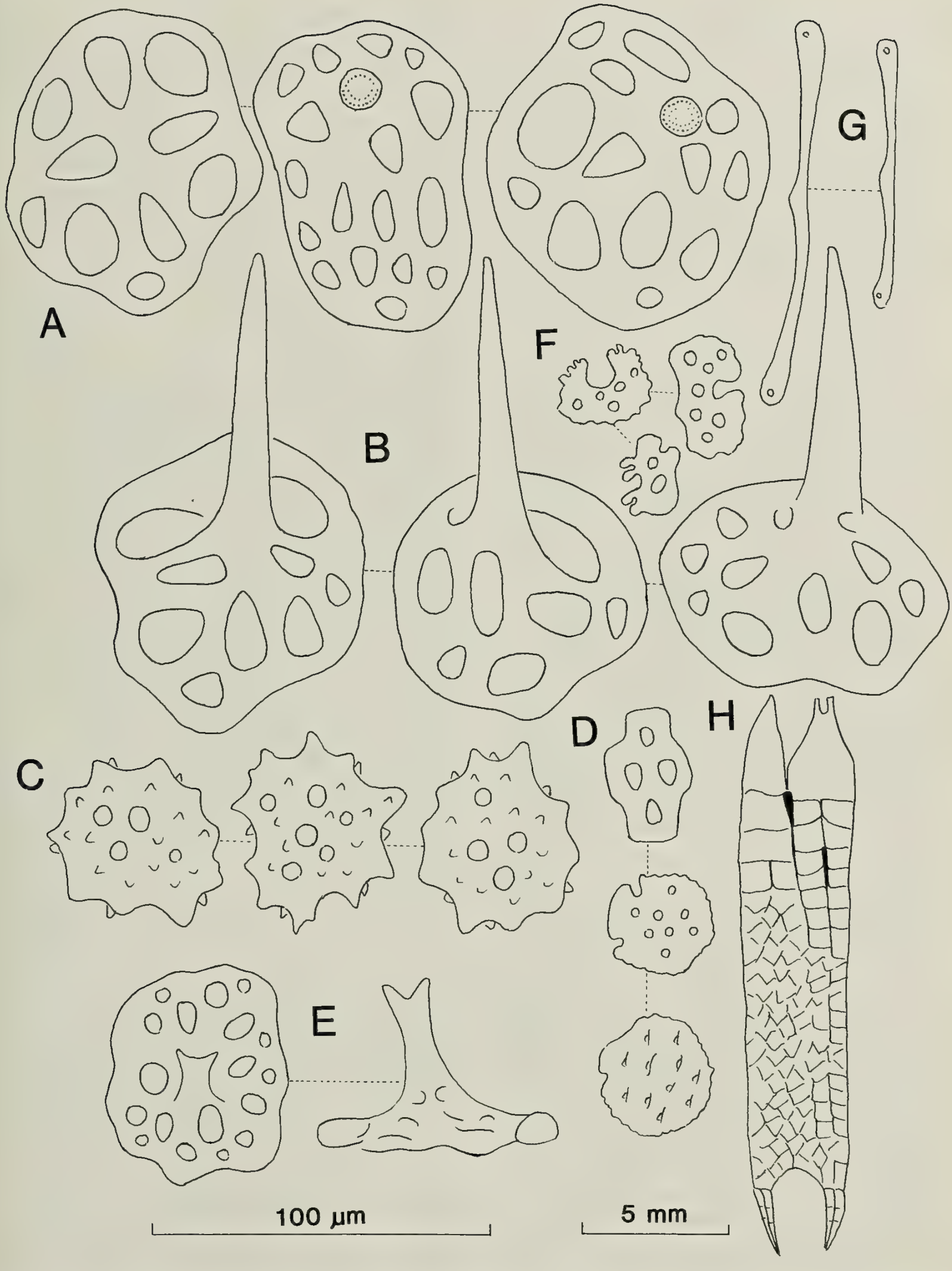

Fig. 9. *Neothyonidium spiniferum* new species. A, tables from body wall; B, tables from body wall, lateral view; C, spiny buttons from body wall; D, smooth plates from body wall; E, tables from introvert; F, rosettes from introvert; G, rods from tentacles; H, radial and interradial pieces of calcareous ring.

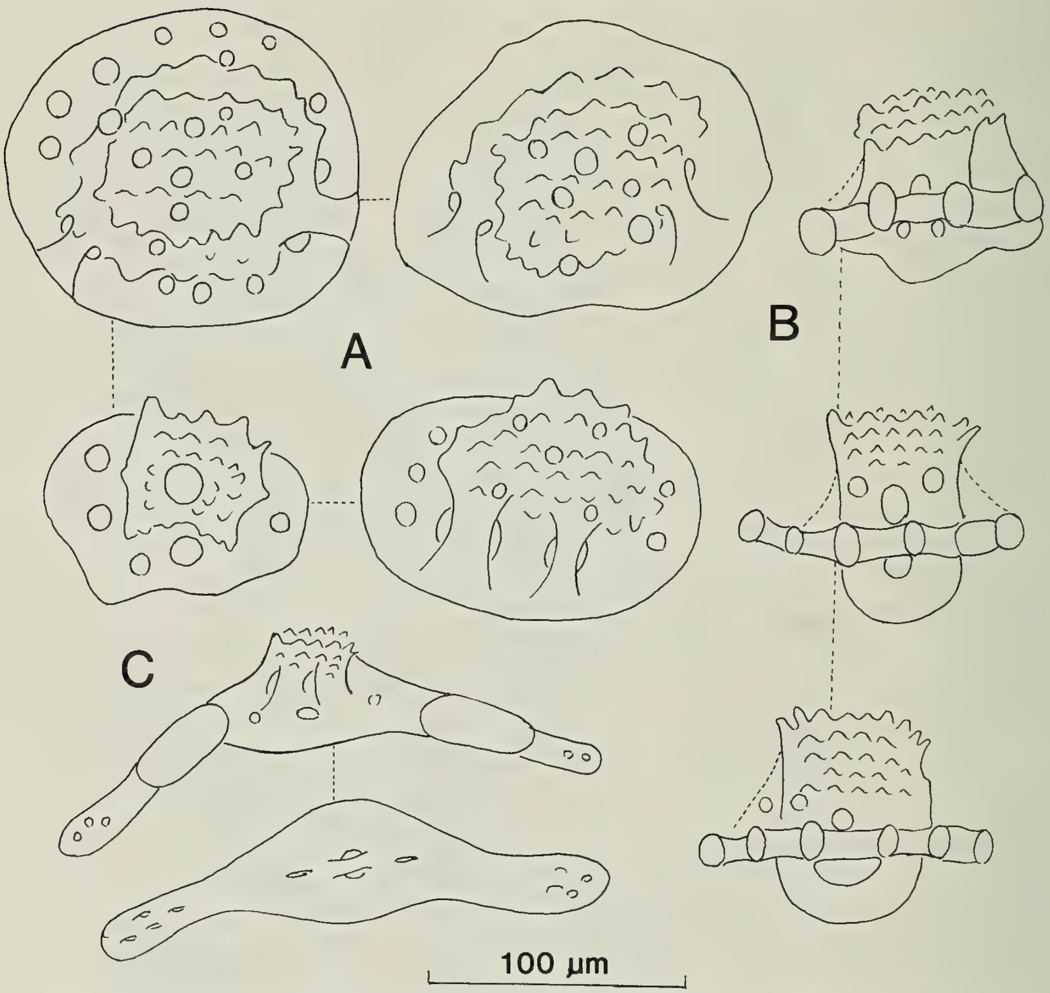

Fig. 10. *Allothyone longicauda* (Östergren). A, tables from body wall; B, tables from body wall, lateral view; C, tables from tube feet.

ous ventrally than dorsally. Anus surrounded by small papillae. Color in alcohol whitish. Calcareous ring tubular, high (20 mm long), entirely composed of mosaic of small pieces; radials fused with interradials; posterior projections on radials short (Fig. 9H). Polian vesicle and stone canal single.

Body wall ossicles of three kinds: tables, button-like plates and smooth perforated plates. Tables scarce in the body wall, but occur in numbers at bases of tube feet; discs smooth, circular 80–100 µm in diameter, with varying number of perforations. Spires excentric, solid, high (70–90 µm), terminating in a single point (Fig. 9A, B). Button-like plates very numerous, spiny, 40–70 µm long, 30–60 µm wide, very variable in shape and in number of perforations, usually with distinct projections on margins and on surface (Fig. 9C). Smooth perforated plates of average diameter 30 µm, roundish or oblong with varying number of holes (Fig. 9D). In introvert tables (Fig. 9E) and rosettes (Fig. 9F). In tentacles delicate supporting rods of variable size (Fig. 9G).

Remarks.—The number of tentacles and shape of the calcareous ring require that this species be placed in *Neothyonidium* Deichmann, 1938. The species is distinctive in that no other known species in this genus possess the three kinds of body wall ossicles described here.

Subfamily Thyoninae Panning, 1949

Allothyone longicauda (Östergren)

Figs. 10, 20I

Cucumaria longicauda Östergren, 1898: 108–109, fig. 1.
Allothyone longicauda.—Panning, 1949: 466.
Cucumaria chronhjelmi.—Chang & Woo, 1954: 137–138, text fig. 6, pl. 2 fig. 3–4; Chang et al., 1964:23.
(Non *Cucumaria chronhjelmi* Théel, 1886).

Material examined.—Off Dalian, 26 Jul, 1957, 47.5 m, 1 specimen; Xiaopingdao, Dalian, intertidal zone, 1953, 1 specimen.

Diagnosis.—Medium-sized form, up to 60 mm in length, body barrel-shaped, posteriorly tapering into a caudal portion. Tube feet restricted to radii, in double rows. Ossicles in body wall tables with circular discs; spire low, four-pillared, with numerous crowded apical teeth; spire pillars sometimes connected to margin of disc thus forming complex fenestrated bodies; on inner surface of disc a distinct half-ring or handle is present.

Remarks.—The occurrence of this remarkable holothurian on the northern coast of China is of great interest, as it was hitherto known only from the holotype, collected from "Japan or China" (Östergren 1898). There are two specimens in the collection of the IOAS. A specimen 18 mm in length had been identified by Chang & Woo (1954) and by Chang and Liao (1964) as *Cucumaria chronhjelmi* Théel, 1886. Another specimen is larger, 59 mm in length and 10 mm in diameter with a distinctly narrowed posterior end. In both specimens tentacles and introvert are missing. The body wall is moderately thick but not hard. Color in alcohol is yellowish. Ossicles are numerous in the body wall; they are exclusively tables with circular disc and many obscured perforations; the low four-pillared spires tend to fuse with the outer edge of the table disc producing a complex fenestrated body (Fig. 10A). On the inner surface of the table disc is a half-ring or "handle" (Fig. 10B). Tube feet with supporting tables. This material belongs to Östergren's distinctive species *Cucumaria longicauda.*

Allothyone mucronata (Sluiter)

Fig. 11

Cucumaria mucronata Sluiter, 1901:88, pl. 7 fig. 7.
Allothyone mucronata.—Panning, 1949: 466; Liao, 1997:189, fig. 111.

Material examined.—Many specimens from the Gulf of Tonkin, 30–60 m. Depth.

Diagnosis.—Small form up to 30 mm in length, body slender, curved, tapering anteriorly and posteriorly, more or less pentagonal in cross section. Tube feet delicate, confined to radii, most numerous and larger on the ventral surface. Calcareous ring (Fig. 11D) with long posterior projections on radials, each column composed of many small pieces. Ossicles in body wall exclusively tables with rounded disc with numerous perforations; spires heavy, four-pillared, with numerous apical teeth. Supporting tables in tube feet distinctive, with very slender high spire.

Remarks.—This species, originally described by Sluiter on the basis of two specimens taken by the *Siboga* Expedition in Indonesia, has proved to be common in the Gulf of Tonkin. Numerous specimens are in the collections of IOAS. Body size is small, total length 10–30 mm, diameter 3–6 mm. Ossicles of body wall (Fig. 11A, B) and tube feet (Fig. 11C) are distinctive and comply well with Sluiter's (1901) description. The range extension for this species implies that it may occur in many areas of the Indo-west-Pacific.

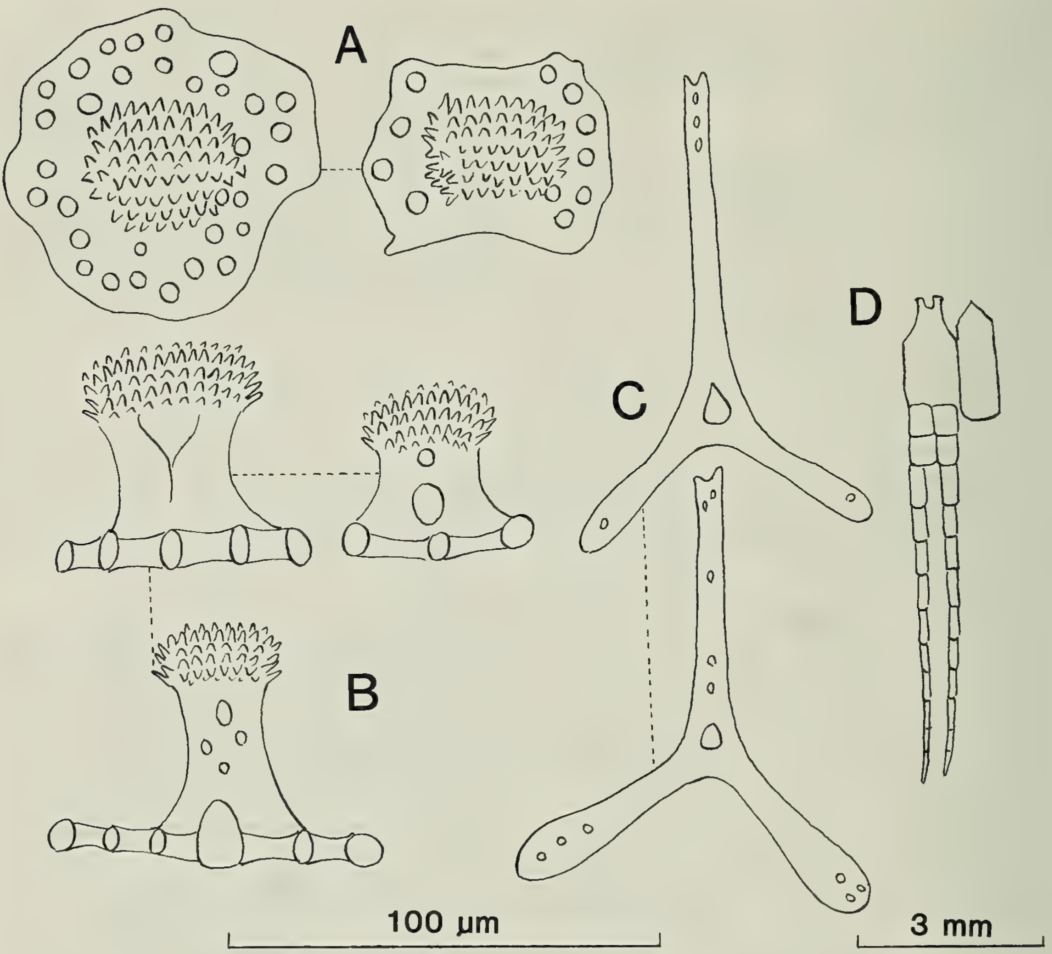

Fig. 11. *Allothyone mucronata* (Sluiter). A, tables from body wall; B, tables from body wall, lateral view; C, tables from tube feet; D, radial and interradial pieces of calcareous ring.

Pentamera constricta (Ohshima)
Fig. 12

Cucumaria constricta Ohshima, 1915:263, pl. 10 fig. 22a–b; 1916–19:277, pl. 6 fig. 40, text-fig. 63.

Pentamera constricta.—Panning, 1949: 465.

Material examined.—East China Sea, 26°30′N, 124°30′E, 150 m, 1 specimen; East China Sea, 29°30′N, 126°30′E, 100 m, 1 specimen; East China Sea, 31°30′N, 123°40′E, 55 m, 2 specimens.

Diagnosis.—Small form, approximately 25 mm in length, body slender, curved. Tube feet confined to radii in double rows. Tentacles 10, ventral pair smaller. Calcareous ring with two long posterior projections on radials (Fig. 12E). Ossicles in body wall two-pillared tables (Fig. 12A) and perforated plates (Fig. 12C), discs of tables with smooth edge and varying number of perforations, spires moderately high, with 6–8 apical teeth (Fig. 12B). Tube feet with supporting tables.

Remarks.—This species was hitherto known only from off southern Japan; its range now extends to the East China Sea. The four specimens are all small, largest 15 × 6 mm, the smallest 9 × 7 mm. They

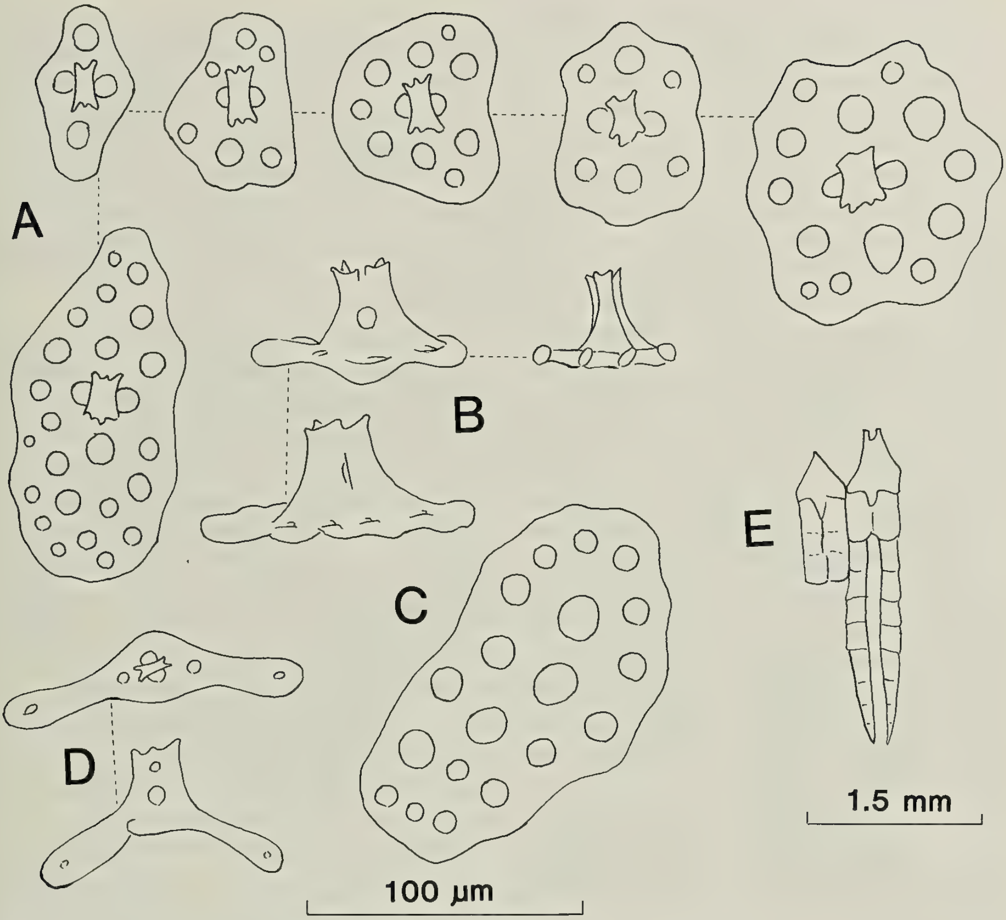

Fig. 12. *Pentamera constricta* (Ohshima). A, tables from body wall; B, tables from body wall, lateral view; C, perforated plate from body wall; D, supporting table from tube feet; E, radial and interradial pieces of calcareous ring.

agree in all essential features with the description and measurements given by Ohshima (1915), except that the diameter of the table ossicles in the Chinese specimens (about 100 μm) is smaller than in Ohshima's (1915) material (160 μm).

Stolus crassus, new species
Figs. 13, 20J

Material examined.—Holotype IOAS E1060, off Hong Kong, 21°N, 113°30′E, 14 Jul 1959, 74 m, muddy sand bottom. Paratype IOAS E1076, same locality as Holotype, 7 Feb 1960, 1 specimen.

Diagnosis.—Large form, total length exceeding 100 mm, body spindle-shaped. Tentacles 10, 2 ventral smaller. Tube feet not numerous, papilliform, sparsely scattered on body wall. Calcareous ring long, tubular, composed of a mosaic of small pieces, with short posterior projections on radials. Body wall thick and hard, with crowded large knobbed button-like tables.

Description.—Total length of single specimen approximately 130 mm, diameter at middle 30 mm. Body spindle-shaped, moderately curved, tapering anteriorly and posteriorly. Papilliform tube feet scattered on body, slightly more numerous ventrally than dorsally. Body wall thick, rough to touch due to abundant ossicles. Tentacles 10, ventral pair markedly smaller. Anus surrounded by minute papillae. Color in alcohol whitish. Calcareous ring 20 mm long, tubular, all pieces composed of a mosaic of small elements; radials with short posterior projections; interradials well-developed, wider than radials; radials with membranous space in middle of anterior part (Fig. 13J). Stone canal and Polian vesicle single.

Ossicles in body wall large, knobbed button-like tables; discs rounded or triangular in outline, averaging about 100 μm in diameter, strongly knobbed, with 6 small perforations (Fig. 13A), two-pillared spires low, about 90 μm high, with 2–3 apical teeth (Fig. 13B). Inner surface of disc with a handle or half ring with large central perforation (Fig. 13B). Tube feet with numerous supporting tables (Fig. 13C, D) and perforated plates (Fig. 13E). In introvert, delicate tables with oblong disc, knobbed margin, and low spires (Fig. 13F, G). In tentacles rosettes (Fig. 13H) and rods of various sizes (Fig. 13I).

Remarks.—This new species is distinctive in the genus *Stolus* in having peculiar button-like tables with knobbed margins, and a calcareous ring with some unusual features.

Stolus micronodosus, new species
Fig. 14

Material examined.—Holotype IOAS E1063, South-China Sea, 20°30′N, 113°E, 20 Oct 1959, 92 m, sandy mud bottom.

Diagnosis.—Medium-sized form, total length 50 mm, body spindle-shaped, more or less pentagonal in cross-section. Extremities attenuate. Tentacles 10, ventral pair smaller. Tube feet delicate, numerous, often in indistinct bands on radii but also scattered in interradii. Calcareous ring very high, composed of a mosaic of small pieces; interradials almost as long as radials; radials with short posterior projections. Ossicles in body wall small knobbed buttons, usually with 4 holes and minute knobs.

Description.—Length 50 mm, diameter at mid-body 35 mm. Body spindle-shaped, tapering markedly anteriorly and posteriorly; ends pentagonal in cross-section. Tube feet numerous, delicate, often in indistinct rows, but also scattered in interradii. Tentacles 10, ventral pair markedly smaller. Anus closed by 5 valves. Color in alcohol whitish, with numerous grayish spots. Body wall thin, soft.

Calcareous ring exceedingly long, 25 mm, tubular, pentagonal in cross-section. Radials only slightly shorter than radials, all composed of mosaic of small pieces, radials with short posterior projections (Fig. 14G). Polian vesicle and stone canal single.

Ossicles in body wall delicate buttons, 30–65 μm long, 30–50 μm wide, with 4 or more holes, with about 8 knobs on margin and 2 at center (Fig. 14A, B). Few buttons smooth, without knobs (Fig. 14C). Ossicles in tube feet elongate buttons (Fig. 14D). Introvert with tables (Fig. 14E) with knobbed disc, 8–20 perforations in disc, low two-pillared spire with about 8 apical teeth. Tentacles with small, simple rods (Fig. 14F).

Remarks.—*Stolus micronodosus* is unique in the genus in having a pentagonal body in cross-section, an exceedingly long calcareous ring, and ossicles in the form of delicate buttons with small knobs.

Thyone crebrapodia Cherbonnier
Figs. 15, 20K

Thyone crebrapodia Cherbonnier, 1988: 197, fig. 84A–I.
Thyone cf. *villosa* Liao, 1997:206.
Non: *Thyone villosa* Semper, 1868.

Material examined.—Off eastern Guangdong Province, 22°30′N, 116°30′E, 43 m, 2 specimens; off Hong Kong, 21°15′N, 113°30′E, 52 m, 1 specimen; off Shantou, 23°30′N, 117°E, 47 m, 1 specimen; East China Sea, 29°N, 124°E, 73 m, 1 specimen.

Diagnosis.—Small form, approximately 30 mm in length. Tube feet numerous, closely crowded. Calcareous ring long, tubular, radials and interradials composed of

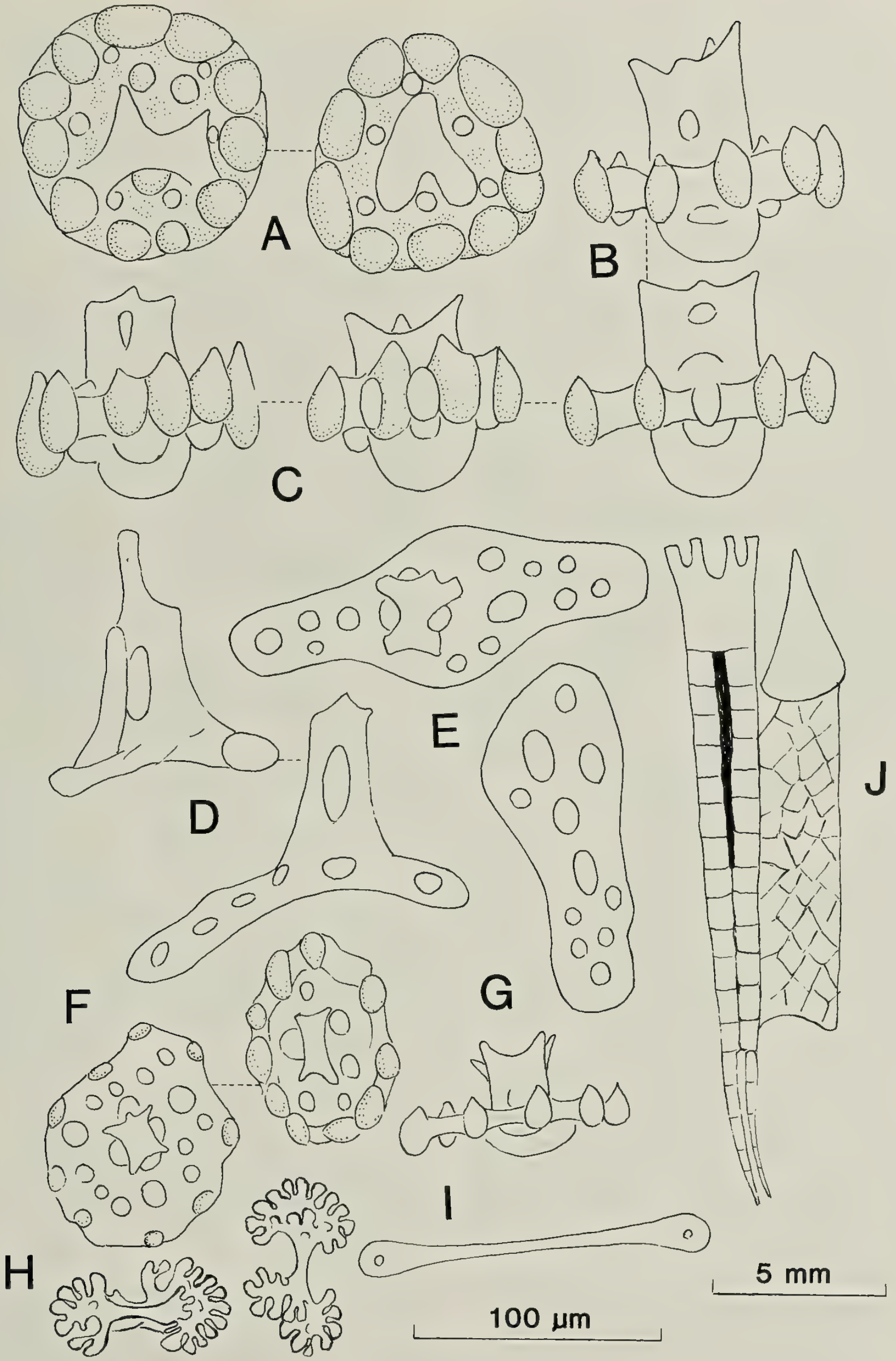

Fig. 13. *Stolus crassus* new species. A, table-like buttons from body wall; B, table-like buttons from body wall, lateral view; C, table from tube feet; D, tables from tube feet, lateral view; E, perforated plate from tube feet; F, tables from introvert; G, tables from introvert, lateral view; H, rosettes from tentacles; I, rod from tentacles; J, radial and interradial pieces of calcareous ring.

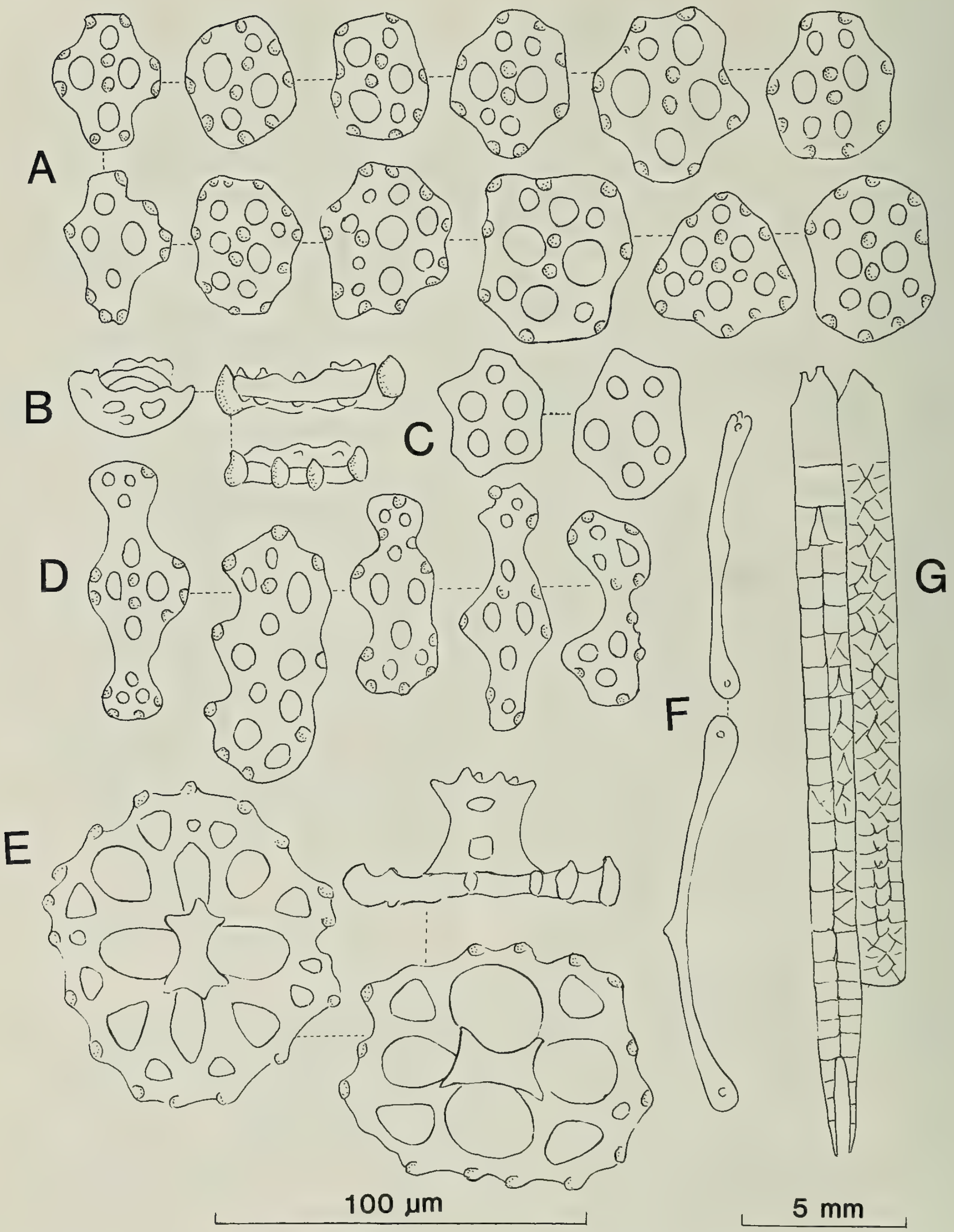

Fig. 14. *Stolus micronodosus* new species. A, knobbed buttons from body wall; B, knobbed buttons from body wall, lateral view; C, smooth buttons from body wall; D, buttons from tube feet; E, tables from introvert; F, rods from tentacles; G, radial and interradial pieces of calcareous ring.

a small number of pieces (Fig. 15E). Ossicles in body wall numerous two-pillared tables (Fig. 15A, B), disc oblong with 4–8 holes, spire low or moderately high with four apical teeth. Tube feet with supporting tables (Fig. 15C, D).

Remarks.—Of the five specimens the largest is 24 × 13 mm, the smallest 7 × 3.5 mm. They strongly resemble the Philippines species *Thyone villosa* Semper, 1868, and were referred to that species by Liao (1997). During a visit to the Hamburg Museum in Germany in 1993, YL examined the type of *T. villosa,* and decided that the Chinese material was not conspecific with that species. The characters of the calcareous ring and ossicles argue for referral of the specimens to *T. crebrapodia,* recently described by Cherbonnier (1988) from Madagascar.

Thyone papuensis Théel
Fig. 16

Holothuria dietrichii Ludwig, 1875:105, fig. 31.

Thyone fusus var. *papuensis* Théel, 1886: 92, pl. 17 fig. 1.

Thyone papuensis.—H. L. Clark, 1921:167; H. L. Clark, 1932:221; Clark & Rowe, 1971:182; A. M. Clark, 1982:489, 495, fig. 2; Cannon & Silver, 1987:32, fig. 9g; Rowe & Gates, 1995:316; Liao, 1997: 203, fig. 119.

Material examined.—Gulf of Tonkin, 20°15′N, 108°30′E, 58 m, 1 specimen; off Qingdao (Jiaozhou Bay), 25 m, 1 specimen; Yellow Sea, 33°30′N, 123°E, 14 m, 1 specimen; Yellow Sea, 33°15′N, 123°30′E, 46 m, 3 specimens.

Diagnosis.—Small to medium-sized form, up to 50 mm in length. Body spindle-shaped with numerous tube feet scattered all over body wall. Calcareous ring complex, both radials and interradials composed of mosaic of small pieces; radials with long posterior projections (Fig. 16G). Ossicles in body wall sparsely scattered small two-pillared tables with oblong disc, 4 large and 4 small perforations, low spire with 2 apical teeth (Fig. 16A, C). Feet with large end-plates and curved supporting tables (Fig. 16D). Introvert with rosettes (Fig. 16E) and tables with numerous holes (Fig. 16B). Tentacles with rods (Fig. 16F).

Remarks.—There are six specimens of this species in the collections of IOAS. Total length 30–50 mm, diameter near mid-body 6–10 mm. Color in alcohol uniformly light yellowish. There is no doubt that the specimens from the Gulf of Tonkin are identical with those from the Yellow Sea, even though these two areas do not have many species in common. Clark's (1982) specimen from Hong Kong had tube feet that tended to be aligned in longitudinal series, especially in the radii, and tables in the dorsal body wall had a low spire of two separate columns. It is with some trepidation that we refer this Hong Kong specimen to this species.

Thyone purpureopunctata, new species
Figs. 17, 20L

Material examined.—Holotype IOAS E1059, off Sanya, Hainan Island, 21 Mar 1992, 32–37 m, muddy bottom. Paratypes IOAS E1080 Gulf of Tonkin, 20°30′N, 107°30′E, 20 Apr 1960, 34 m, 1 specimen; IOAS F1081, Gulf of Tonkin, 20°N, 109°E, 11 Jul 1960, 30.5 m, 1 specimen; IOAS E1082, Gulf of Tonkin, 19°30′N, 108°E, 60 m, 1 specimen.

Diagnosis.—Medium-sized form, up to 60 mm in length, body spindle-shaped, more tapered posteriorly than anteriorly. Tentacles 10, ventral pair smaller. Tube feet delicate, numerous, scattered all over body wall. Calcareous ring tubular, composed of mosaic of small pieces, radials with short posterior projections (Fig. 17I). Ossicles in body wall two-pillared tables with irregularly elongated discs, low arched spires terminating in conical solid point (Fig. 17C). Supporting tables in tube feet with elongate discs and high solid spires (Fig. 17E).

Description.—Length 60 mm, diameter

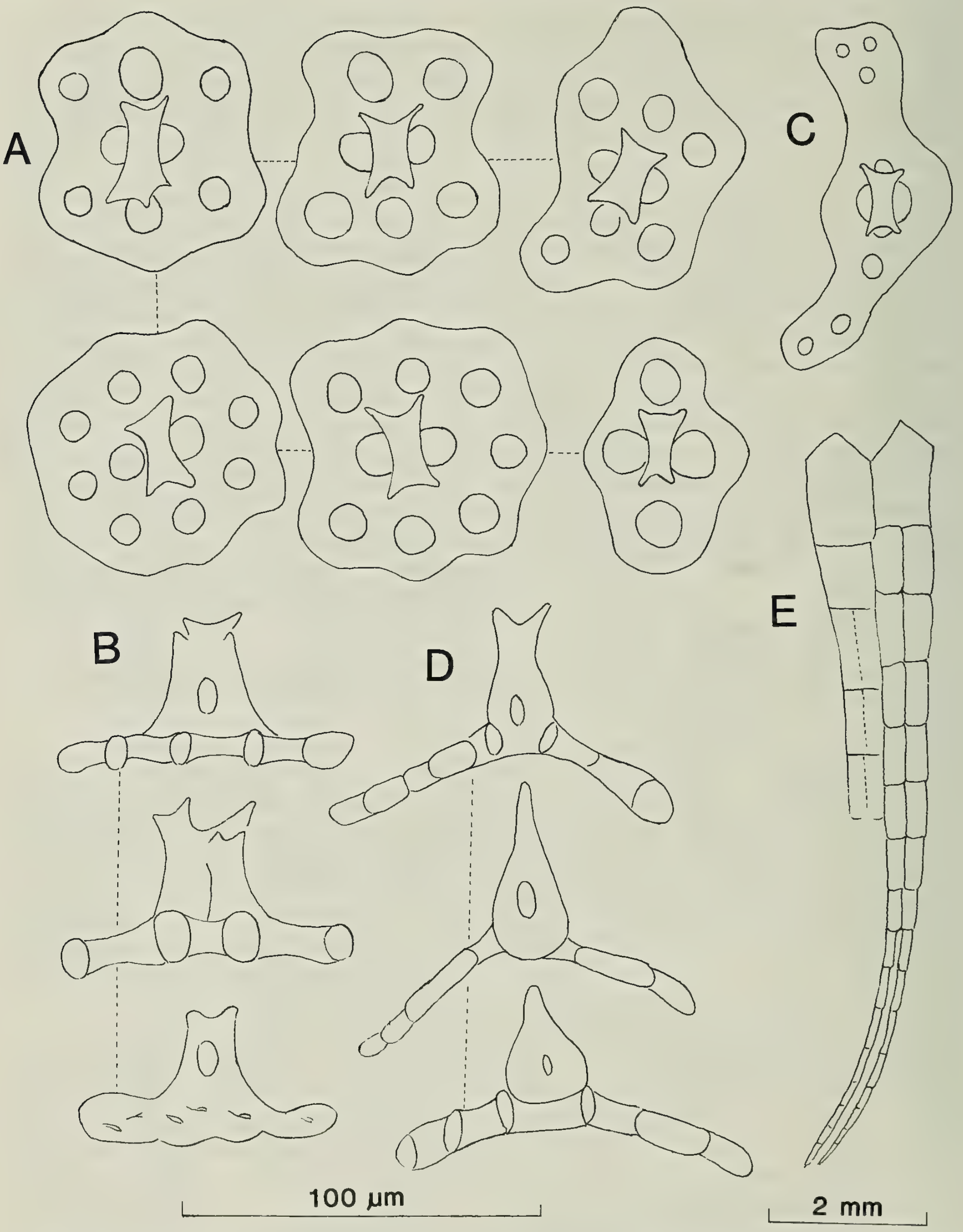

Fig. 15. *Thyone crebrapodia* Cherbonnier. A, tables from body wall; B, tables from body wall, lateral view; C, tables from tube feet; D, tables from tube feet, lateral view; E, radial and interradial pieces of calcareous ring.

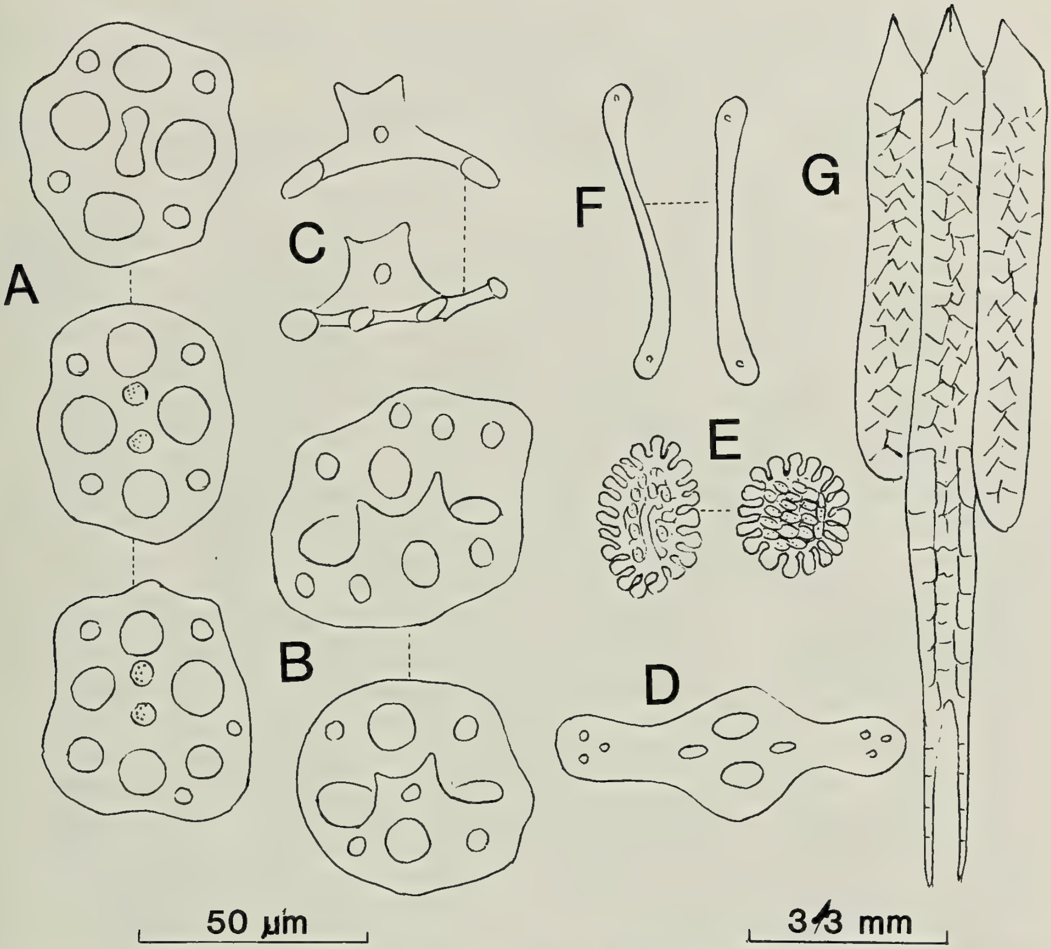

Fig. 16. *Thyone papuensis* Théel. A, tables from body wall; B, tables from body wall, oblique view; C, tables from body wall, lateral view; E, rosettes from introvert; F, rods from tentacles; G, radial and interradial pieces of calcareous ring.

about 16 mm near mid-body. Body spindle-shaped, more tapered posteriorly than anteriorly. Tentacles 10, ventral pair smaller. Tube feet delicate, numerous, scattered all over body, slightly more numerous ventrally than dorsally. Calcareous ring tubular, 10 mm long, composed of mosaic of small pieces; radials with short posterior projections (Fig. 17I). No obvious anal papillae. Color in alcohol grayish white, with numerous scattered purple spots. Body wall thick but not hard, with numerous ossicles. Polian vesicle and stone canal single.

Ossicles in body wall two-pillared tables (Fig. 17A–C), discs of variable outline with varying number of perforations, 60–170 µm long, 40–90 µm wide; spires 20–30 µm high, arched, ending in conical solid point (Fig. 17C). In tube feet endplate present, supporting tables (Fig. 17D, E) with elongated curved discs and high spires ending in solid point. Introvert with rosettes (Fig. 17G) and tables (Fig. 17F). Tentacles with rosettes and supporting rods of various sizes (Fig. 17H).

Remarks.—This species is distinctive in its color and in the form of the ossicles. It may be distinguished from *Thyone villosa* Semper from the Philippines, to which it bears some resemblance, in having fewer

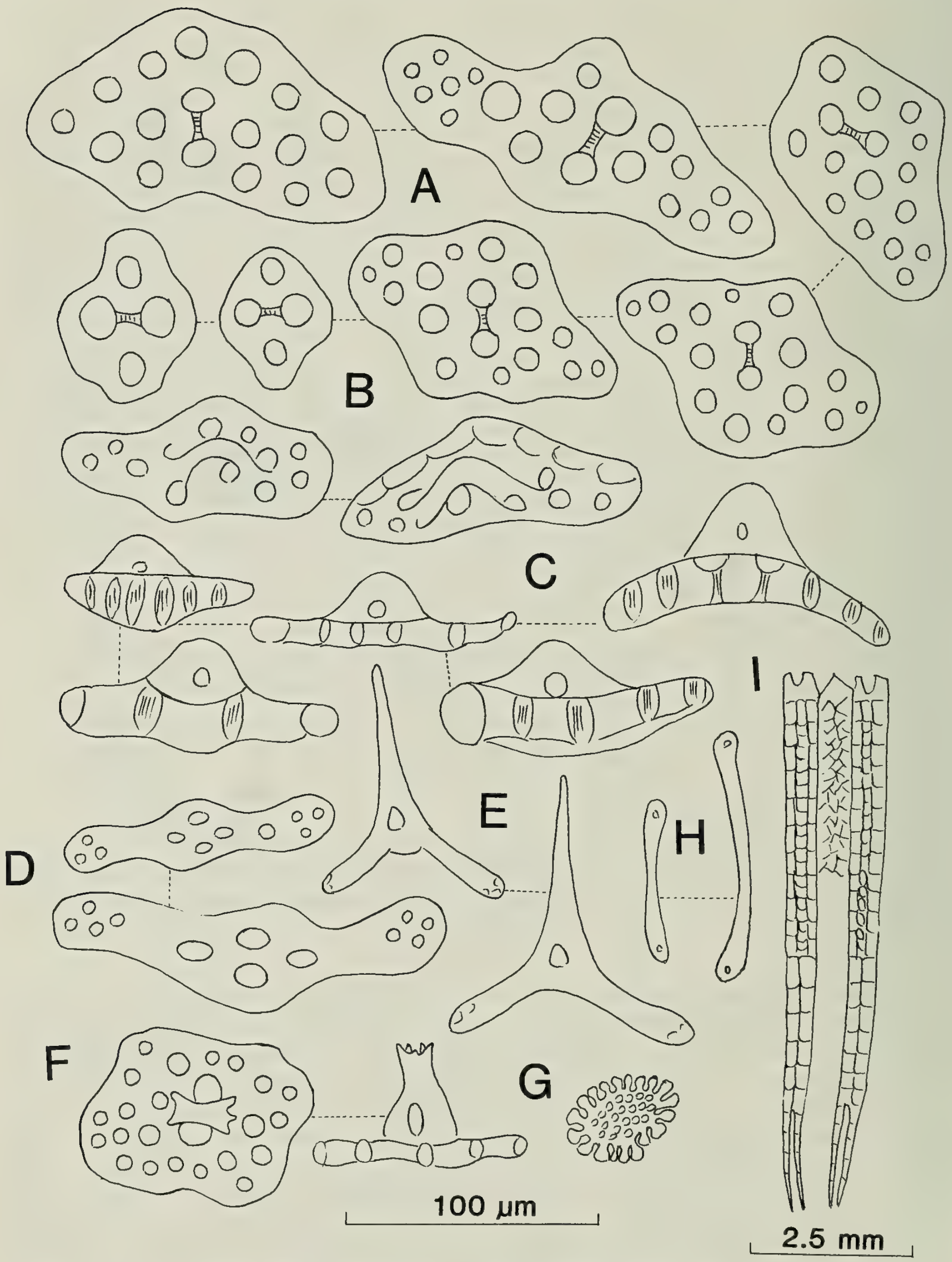

Fig. 17. *Thyone purpureopunctata* new species. A, tables from body wall; B, body wall tables, oblique view; C, tables from body wall, lateral view; D, discs of tables from tube feet; E, tables from tube feet, lateral view; F, tables from introvert; G, rosette from introvert; H, rods from tentacles; I, radial and interradial pieces of calcareous ring.

tube feet and tables with low arched spires ending in a single conical point.

Thyone sinensis, new species
Figs. 18, 20M

Material examined.—Holotype IOAS E1065, Dongshan, Fujian Province, 19 Dec 1981, 3.5 m, muddy bottom. Paratypes USNM E53143, same locality as holotype, 1 specimen; IOAS E1066, same locality as holotype, 2 specimens; IOAS E1078, Dongshan, Fujian province, 7 Mar 1963, 2 m, 2 specimens; IOAS E1079, Dongshan, Fujian province, 3 Jul 1981, 4 m, 2 specimens; IOAS E1079, Guangdong Province, 11 Dec 1954, intertidal zone, 1 specimen.

Diagnosis.—Small form, U-shaped, total length approximately 50 mm. Tentacles 10, ventral pair smaller. Body wall with numerous apparently nonretractile delicate tube feet, more numerous ventrally, with tendency to be arranged in bands on radii. Calcareous ring tubular, composed of relatively large pieces, with short posterior prolongations on radials. Ossicles in body wall two-pillared tables with irregular disc and low spire. Supporting tables in tube feet with high spires with 3–4 crossbeams.

Description.—Small species, body U-shaped, mouth and anus bent upwards. Largest dimension along ventral surface 50 mm, diameter at mid-body 15 mm. Ten tentacles, ventral pair smaller. Tubefeet numerous, delicate, nonretractile, more numerous ventrally, with tendency to be arranged in rows on radii. Anus surrounded by five groups of small papillae. Body wall thin, soft, with numerous ossicles. Color in alcohol white with yellowish tinge, especially ventrally, tube feet often orange in contrast. Calcareous ring tubular, 6 mm long, radials and interradials composed of large pieces; radials with short posterior projections; interradials about ⅔ length of radials (Fig. 18J). Polian vesicle and stone canal single.

Ossicles in body wall two-pillared tables with irregular disc and low spire with four apical teeth (Fig. 18A, B); disc diameter 65–100 μm, height of spire 30–50 μm. In tube feet supporting tables with elongate disc (Fig. 18C, D), 4 central perforations and usually single perforation at each end; spire high with 3–4 crossbeams, ending in 6 apical teeth; tables 100–130 μm long, 50–70 μm high (Fig. 18D). Tube feet with well-developed end plates (Fig. 18E). In introvert tables (Fig. 18G, H) and rosettes (Fig. 18I). Tentacles with supporting perforated plates of varying size (Fig. 18F).

Remarks.—A distinctive species, with tubular calcareous ring made up of large pieces, and tables with several holes. In most other species of *Thyone,* the discs of the tables have eight or fewer perforations. The discs of the tables in this new species resemble those of *T. pedata* Semper (Liao & Clark, 1995:505), but in this latter species the spires are much higher than those of the new species.

Family Placothuriidae Pawson & Fell, 1965

Placothuria Pawson & Fell, 1965
Placothuria molpadioides (Semper)

Ocnus molpadioides Semper, 1868:55, pl. 15 fig. 3; Théel, 1886:118.

Stolus molpadioides.—Panning, 1949:463; Clark & Rowe, 1971:182; Liao & Clark, 1995:497, fig. 302, pl. 23 fig. 2.

Placothuria molpadioides.—Liao, 1997: 224, fig. 134.

Material examined.—Off the Gulf of Tonkin to eastern Guangdong, 17–57 m, 78 specimens.

Diagnosis.—Body large, up to 135 mm in length, U-shaped, rigid. Ossicles in body wall overlapping thick plates usually exceeding 1 mm in diameter. Tube feet with table-like ossicles. Tentacles with delicate rods and rosettes.

Remarks.—This species has now been well characterized by Liao & Clark (1995) and Liao (1995). It differs from all other *Placothuria* species in having table-like supporting rods in the tube feet.

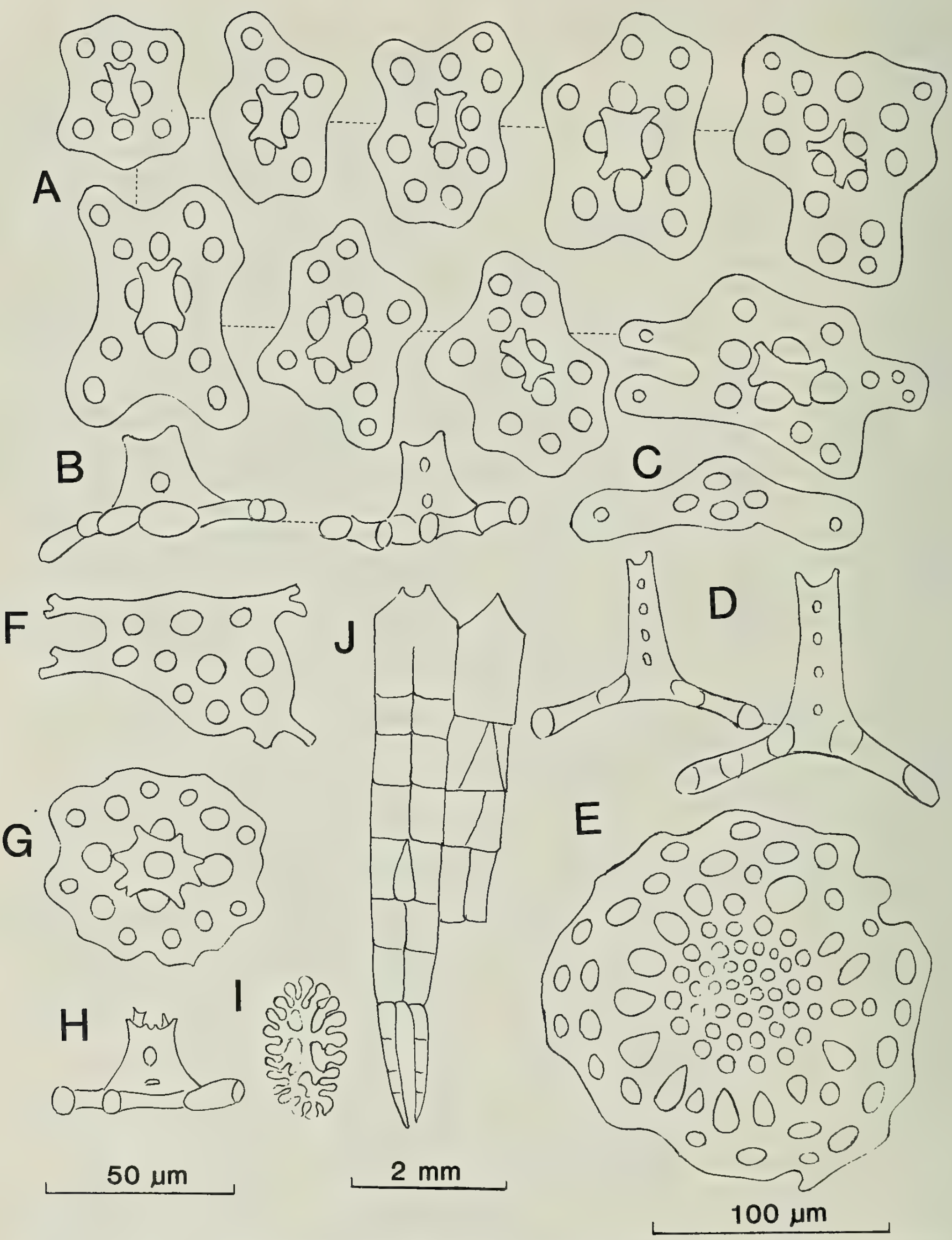

Fig. 18. *Thyone sinensis* new species. A, tables from body wall; B, tables from body wall, lateral view; C, disc of tables from tube feet; D, tables from tube feet, lateral view; E, endplate from tube foot; F, plate from tentacles; G, tables from introvert, lateral view; H, introvert table, lateral view; I, rosette from introvert; J, radial and interradial pieces of calcareous ring.

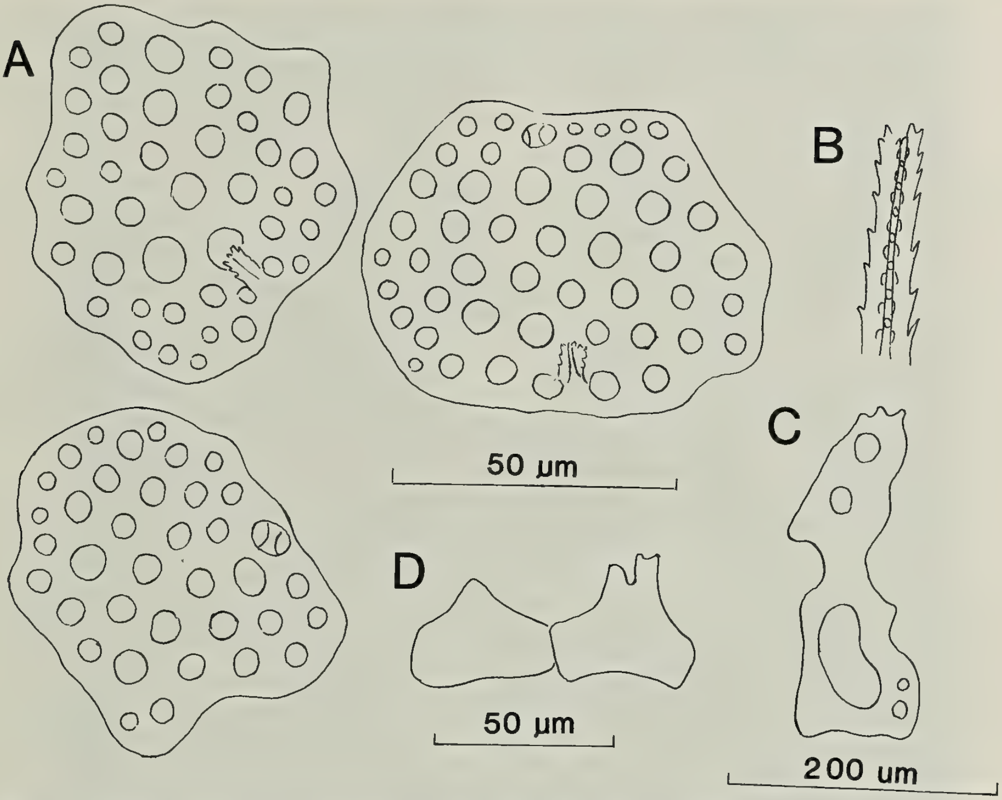

Fig. 19. *Vaneyella dactylica* (Ohshima). A, scales from body wall; B, lateral view of spire from body wall scale; C, perforated plate from tentacle; D, radial and interradial pieces of calcareous ring.

Placothuria ohshimai Liao

Cucumaria mosaica Ohshima, 1915:265; 1916:279, fig. 5, 6. (Objective junior homonym of *Cucumaria mosaica* Koehler & Vaney, 1910)
Pentamera mosaica Panning, 1949:465.
Placothuria ohshimai Liao, 1997:225, fig. 135.
Mitsukuriella squamulosa.—Liao, 1997: 229 (Non *Cucumaria squamulosa* Mitsukuri, 1912) Non: *Cucumaria mosaica* Koehler & Vaney, 1910

Material examined.—Off Yellow Sea, 33°N, 124°30′E, 64 m, 1 specimen; East China Sea, 30°30′N, 125°E, 65 m, 2 specimens.

Diagnosis.—Body medium-sized, up to 45 mm in length, U-shaped, rigid. Ossicles in body wall scales up to 0.5 mm diameter, associated with numerous knobbed tables and derivatives therefrom. Tube feet with tables; tentacles with rods.

Remarks.—A distinctive species, differing from the three other known species in this genus (*P. molpadioides* (Semper), *P. huttoni* (Dendy), *P. squamata* Pawson) in having knobbed tables in the body wall along with the scales. When Ohshima described and named this species in 1915, the species name was an objective junior homonym of *Cucumaria mosaica* Koehler & Vaney, 1910, and thus the name was not available, despite Panning's (1949) attempt to transfer the species to another genus. A new and very appropriate name was finally provided by Liao (1997, p. 225). The record of *Mitsukuriella squamulosa* (Mitsukuri) in Liao (1997) and in Lane et al. (2000) should be cancelled. Re-examination shows

Fig. 20. A, *Phyllophorus* (*Phyllophorella*) *dubius* Cherbonnier; B, *Phyllophorus* (*Phyllophorella*) *kohkutiensis* Heding & Panning; C, *Phyllophorus* (*Phyllothuria*) *donghaiensis* new species, Holotype; D, *Phyllophorus* (*Isophyllophorus*) *orientalis* new subgenus, new species, Holotype; E, The same, from anterior, showing 20 subequal tentacles; F, *Anthochirus loui* Chang; G, *Anthochirus loui* Chang; H, *Neothyonidium spiniferum* new species, Paratype; I, *Allothyone longicauda* (Östergren); J, *Stolus crassus* new species, Holotype; K, *Thyone crebrapodia* Cherbonnier; L, *Thyone purpureopunctata* new species. Holotype; M, *Thyone sinensis* new species, Paratype; N, *Ypsilothuria bitentaculata* (Ludwig); O, *Vaneyella dactylica* (Ohshima). All figures are approximately natural size; figure K is enlarged about 1.5 times.

that the two specimens previously referred to *Mitsukuriella squamulosa* are certainly *Placothuria ohshimai.*

Order Dactylochirotida

Family Vaneyellidae Pawson & Fell, 1965

Vaneyella dactylica (Ohshima)
Figs. 19, 20O

Pseudocucumis dactylicus Ohshima, 1915: 272; 1916–19:395, fig. 76.
Vaneyella dactylica.—Heding & Panning, 1954:45.

Material examined.—East China Sea, 29°45′N, 128°30′E, 850 m, 5 specimens; East China Sea, 27°45′N, 128°E, 900 m, 5 specimens.

Diagnosis.—Small form, up to 4 cm in length with spindle-shaped body, mouth and anus distinctly upturned. Tentacles 15, 7 larger and 8 smaller, digitiform. Calcareous ring simple, no posterior prolongations on radials (Fig. 19A). Ossicles in body wall imbricating scales, single-layered, with numerous perforations and excentric spiny spire near margin of scale (Fig. 19A, B). Tentacles with perforated plates.

Remarks.—This very interesting dactylochirote does not seem to have been collected since the *Albatross* obtained a single specimen in the East China Sea, off Koshiki Islands, Japan (31°9′N, 129°22′E), at a depth of 715 m. Our ten specimens were taken near the type locality. They are undoubtedly identical with the specimen originally described by Ohshima (1915).

Checklist of Dendrochirote and Dactylochirote Holothurians of China

New taxa are in bold. Species marked with an asterisk (*) are discussed in the text. Scientific names, authors and dates are followed by known distribution in China seas, and known depth ranges. Abbreviations: Y, Yellow Sea; E, East China Sea; S, South China Sea; m, metres.

Order Dendrochirotida

Family Cucumariidae

Subfamily Colochirinae

Cercodemas anceps (Selenka, 1867). E, S, 0–10 m.
Colochirus quadrangularis Troschel, 1846. E, S, 0–100 m.
Leptopentacta imbricata (Semper, 1868). E, S, 0–54 m.
Plesiocolochirus inornatus (Marenzeller, 1881). Y, E, 0–30 m.
Plesiocolochirus nipponensis (Clark, 1938). E, 0–30 m.
Pseudocolochirus violaceus (Théel, 1886). S, 20–67 m.

Subfamily Cucumariinae

Pseudocnus echinatus (Marenzeller, 1881). E, S, 0–50 m.

Subfamily Thyonidiinae

***Actinocucumis chinensis*, new species** S, 45 m.
Actinocucumis typicus Ludwig, 1875. E, S, 0–50 m.
Mensamaria intercedens (Lampert, 1885). E, S, 0–67 m.

Family Phyllophoridae

Subfamily Phyllophorinae

**Anthochirus loui* Chang, 1948. Y, 15–67 m.
**Phyllophorus* (*Phyllophorella*) *dubius* Cherbonnier, 1960. E, S, 43–125 m.
**Phyllophorus* (*Phyllophorella*) *kohkutiensis* Heding & Panning, 1954. S, 36–53 m.
Phyllophorus (*Phyllophorella*) *liuwutiensis* Yang, 1937. E, S, 0 m.
Phyllophorus (*Phyllophorella*) *spiculata* Chang, 1935. E, S, 0–30 m.
**Phyllophorus* (*Phyllothuria*) *cebuensis* (Semper, 1868). S, 42–125 m.
****Phyllophorus* (*Phyllothuria*) *donghaiensis*, new species.** E, 100 m.
Phyllophorus (*Phyllothuria*) *hypsipyrga* (Marenzeller, 1881). Y, E, 30–100 m.
Phyllophorus (*Phyllothuria*) *ordinatus* Chang, 1935. Y, 0 m.
****Phyllophorus* (*Isophyllophorus*) *orientalis*, new subgenus, new species.** Y, 41 m.

Subfamily Semperiellinae

**Neothyonidium inflatum* (Sluiter, 1901). S, 37–74 m.

**Neothyonidium minutum* (Ohshima, 1915). E, 116 m.

***Neothyonidium spiniferum*, new species.** S, 31–99 m.

Pentadactyla japonica (Marenzeller, 1881). E, 60–103 m.

Phyrella fragilis (Ohshima, 1912). S, 0 m.

Subfamily Thyoninae

**Allothyone longicauda* (Östergren, 1898). Y, 0–47 m.

**Allothyone mucronata* (Sluiter, 1901). S, 20–89 m.

Havelockia versicolor (Semper, 1868). S, 0–59 m.

**Pentamera constricta* (Ohshima, 1915). E, 55–150 m.

Stolus albescens Liao, 1995. S, 20–109 m.

Stolus buccalis (Stimpson, 1855). E, S, 0–54 m.

Stolus canescens (Semper, 1868). S, 74–89 m.

***Stolus crassus*, new species.** S, 74 m.

***Stolus micronodosus*, new species.** S, 92 m.

Thorsonia adversaria (Semper, 1868). E, S, 16–50 m.

Thyone anomala (Östergren, 1898). E, S, 0–103 m.

Thyone bicornis Ohshima, 1915. S, 23–61 m.

**Thyone crebrapodia* Cherbonnier, 1988. E, S, 47–73 m.

Thyone fusus chinensis Yang, 1937. E, 0 m.

**Thyone papuensis* Théel, 1886. Y, 25–58 m.

Thyone pedata Semper, 1868. S, 55 m.

Thyone pohaiensis Liao, 1986. Y, 0–8 m.

***Thyone purpureopunctata*, new species.** S, 30–60 m.

***Thyone sinensis*, new species.** E, S, 0–4 m.

Thyone spinifera Liao, 1995. S, 15–115 m.

Family Placothuriidae

**Placothuria molpadioides* (Semper, 1868). S, 17–57 m.

**Placothuria ohshimai* Liao, 1997. Y, E, 60–65 m.

Family Sclerodactylidae

Subfamily Cladolabinae

Afrocucumis africana (Semper, 1868). S, 0 m.

Cladolabes aciculus (Semper, 1868). S, 0 m.

Cladolabes crassus (Clark, 1938). S, ? m.

Cladolabes schmeltzii (Ludwig, 1875). S, 0 m.

Euthyonidiella tungshanensis (Yang, 1937). E, 0–80 m.

Ohshimella ehrenbergi (Selenka, 1867). S, 0 m.

Subfamily Sclerodaetylinae

Sclerodactyla multipes (Théel, 1886). Y, 0–50 m.

Order Dactylochirotida

Family Ypsilothuriidae

Ypsilothuria bitentaculata (Ludwig, 1894). E, S, 510–580 m.

Family Vaneyellidae

**Vaneyella dactylica* (Ohshima, 1915). E, 850–900 m.

Distribution Patterns of Dendrochirotes and Dactylochirotes of China

Of the 56 dendrochirote and dactylochirote holothurian species now known from China seas, approximately 40 species (71%) are more widely distributed, in the Indo-west-Pacific area generally, or in the China-Japan area. One species, *Ypsilothuria bitentaculata* (Ludwig), is more or less cosmopolitan. Sixteen species (28%), including the eight new species described here, are known only from China seas. In a detailed analysis of the echinoderm fauna of the South China Sea, Lane et al. (2000) found that when echinoderms as a whole are considered, endemism is lower (12%), while endemism in holothurians is 16%. For further discussion of distribution patterns, see Lane et al. (2000).

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Diplectroninae of Sri Lanka (Trichoptera: Hydropsychidae)

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Abstract.—The subfamily Diplectroninae of Sri Lanka is revised. The male genitalia of the lectotypes of the three described species, *Diplectrona papilionacea* (Hagen), *D. maligna* (Hagen) and *D. taprobanes* (Hagen), are figured and diagnostic notes and distributions given. Three new species, *D. malickyi, D. longistyla* and *D. ingens* are described, figured and distributions presented, and *D. kirimaduhela* Schmid is newly synonymized with *D. maligna.* The genus *Diplectronella* Ulmer, type species *D. taprobanes,* is synonymized with *Diplectrona* Westwood, type species *D. felix* McLachlan.

The Trichoptera, or caddisflies, of Sri Lanka (or Ceylon) have been relatively well studied in the latter half of the 1900's (Schmid 1958, Malicky 1973, Chantaramongkol & Malicky 1986). Yet new collections continue to produce new and undescribed species (Flint 2000). Recent routine curation of large numbers of unsorted Sinhalese caddisflies in the collection of the National Museum of Natural History (NMNH) has resulted in the discovery of undescribed species in many genera. Unless marked otherwise, all material listed in this paper is in the collection of the NMNH. This paper is another contribution to the understanding of the Sri Lankan fauna.

Hagen in 1858 and 1859 produced the seminal study on the "Neuropteroid" fauna of the island, in which he described or listed 32 species of Caddisflies out of a total of 143 species of "Neuropteroids." In this work he described four species of *Hydropsyche,* one of which, *H. mitis,* is a species of *Tinodes* in the family Psychomyiidae. Ulmer (1928) transferred the other three species, *H. taprobanes, H. papilionacea,* and *H. maligna* to the subfamily Diplectroninae, placing the first in *Diplectronella* and the other two in *Diplectrona.* Mosely (1931) gave a good redescription with figures of the male genitalia of *D. taprobanes.* In addition he proposed a suite of characters by which the genera *Diplectrona* and *Diplectronella* could be distinguished: the latter lacks fork 1 in the hindwing and the internal reticulate sacs in the male abdomen. He also stated that the male genitalia are "rather more simple than in *Diplectrona,* the intermediate appendages being apparently wanting." When I compare the male genitalia of *D. taprobanes* with the type species of *Diplectrona, D. felix* which has fork 1 and two pairs of reticulate sacs, I find a total concordance of genital structures in the two with only minor differences in their shapes. Considering the six Sinhalese species here treated, we find three correspond to *Diplectronella,* one (*D. maligna*) has fork 1 but no internal sacs, and two (*D. papilionacea* and *D. malickyi*) have fork 1 and one pair of internal sacs. The male genitalia of all six are so similar as to be barely separable. In the New World, the North American *D. modesta* has fork 1 but no internal sacs, while the Mexican *D. chiapensis* also has fork 1 and one pair of internal sacs and both have the Sinhalese type of male genitalia. A superficial survey of the southeast Asian species shows the genital structures to be identical to those of the above species, but nothing is mentioned concerning fork 1 or internal sacs. The species in South Africa, Australia, New Zealand, and some species in New Guinea, mostly have fork 1, and two pairs of internal sacs, but the genitalia are so different in structure that they can hardly be considered congeneric. Considering this assortment of characteristics I find no way to continue the recognition of *Diplectronella* based on the presence or absence of fork 1 and internal sacs and must place the genus in synonymy of *Diplectrona* (NEW SYNONYMY).

During a visit to the Natural History Museum, London in July 2000 while I was searching for the example that was the basis of Ulmer's 1906 description of *D. papilionacea,* I discovered "types" of three species Kimmins had designated in 1958. Further search revealed that these had never been published, perhaps because of the appearance of Schmid's study in that same year. These examples were borrowed and studied with the result that one of the species is found to be *D. maligna,* the second *D. malickyi,* and the third, including the Ulmer specimen, *D. ingens.* I have refrained from mentioning his MS names so as to avoid giving any status to them, but included the examples in material examined. In addition I borrowed the three examples mentioned by Schmid (1958) as *Diplectrona* spp. The cleared genitalia were carefully compared with those of the other species in the genus from the island. Although the female genitalia offer only subtle differences between the species, these seem to match closely those of *D. papilionacea.*

To aid in the recognition of the insular species, I have prepared new figures from the Hagen lectotypes as well as the undescribed species. The males of the six species may be distinguished by the following key. The females are easily separable into two groups based on the presence or absence of fork 1, with some species further distinguished by size or color.

Key to Sinhalese *Diplectrona* Species

1\. Fork 1 present in hind wing 2
Fork 1 absent in hind wing 7
2\. Males 3
Females 5
3\. With a single pair of reticulate sacs in abdomen; forewing either fuscous with white maculae or brown with stramineous maculae 4
Lacking internal abdominal sacs; forewing uniformly fuscous . . . . . *D. maligna*
4\. Eyes large, in frontal aspect, eye width greater than interocular distance; forewing fuscous with white maculae . . . . *D. malickyi*
Eyes normal, in frontal aspect width barely half that of interocular distance; forewing brown with stramineous maculae . . . . *D. papilionacea*
5\. Forewing fuscous, possibly with white maculae 6
Forewing brown with many stramineous spots . . . . *D. papilionacea*
6\. Forewing uniformly fuscous *D. maligna*
Forewing fuscous with scattered white maculae . . . . *D. malickyi*
7\. Males 8
Females 10
8\. Larger, forewing length 10.5–12 mm . . . . *D. ingens*
Smaller, forewing length 8–9 mm 9
9\. Apex of phallus with two pairs of small sclerites; lateral filament of fifth sternum reaching to anterior half of seventh sternum . . . . *D. taprobanes*
Apex of phallus with one pair of sclerites; filament of fifth sternum attaining the eighth to base of inferior appendages . . . . *D. longistyla*
10\. Size larger, 12–15 mm . . . . *D. ingens*
Size smaller, 8–10 mm . . . . *D. taprobanes and longistyla*

Diplectrona papilionacea (Hagen)
Figs. 1–6, 36

Hydropsyche papilionacea Hagen, 1859: 211.—Ross, 1952:33 [lectotype ♂].
Hydromanicus papilionaceus: Ulmer, 1906: 78 [description, venation ♀ paratype (BMNH); this specimen is *D. ingens,* q.v.].

Diplectrona papilionacea: Ulmer, 1928:316 [to *Diplectrona*].—Fischer, 1963:148; 1972:150 [bibliography].—Weaver, 1993: 41 [lectotype MCZ 11022, listed].

Diplectrona papillionacea [sic]: Schmid, 1958:118 [color, genitalia ♂ paratype].

Diplectrona spp.: Schmid, 1958:119 [three examples believed to be of 2 species].

A rather uncommon species that has been found in a wide range of elevations: 200 to 4000 ft. [ca. 60–1220 m.]. The three females mentioned by Schmid (1958) as *Diplectrona* spp. were studied. The female genitalia seem inseparable from those of *D. papilionacea,* although the differences between the species in this sex are minuscule. Even the venation and color pattern seem comparable although one example seems to have a deeper ground color of the forewing. However, the size of the forewing, 12–13 mm is strikingly larger than that in the other examples of the species (7–9 mm). In spite of their conformity in size, the genitalia and color pattern preclude them from being examples of *D. ingens.* It is possible that yet another species, closely related to *D. papilionacea* still exists in the highland of the island. Their data is included below.

The male genitalia of this species (Schmid 1958, pl. 21, figs. 5, 6) are hardly to be distinguished from those of its Sri Lankan congeners. It does have fork 1 in the hindwing, thus easily distinguishing it from the common *D. taprobanes* which it closely resembles in coloration. In addition to the long process of the fifth sternum it does have a pair of internal sacs attached between the seventh and eighth segments.

Material examined.—"Ceylon Nietner" [the original description states this is from Rambodde at 3500 to 4000 feet], "Hagen," "Type 11022," "Lectotype Hydropsyche papilionacea Hagen," ♂ lectotype, 2 paralectotypes ♂ (MCZ). Sri Lanka, Western Province, Colombo District, Padukka, 300′ [ca. 90 m.], 16 Nov 1970, O. S. Flint, Jr., 1♂, 2♀. Tunmodera, 200′ [ca. 60 m.], 17 Nov 1970, O. S. Flint, Jr., 1♀. Central Prov., Kandy Dist., Madugoda, 2600′ [ca. 790 m.], 24 Nov 1970, O. S. Flint, Jr., 1♀. 2.5 mi. [ca. 4.0 km.] NE Laksapana, 2700′ [ca. 825 m.], 16 Sep 1970, O. S. Flint, Jr., 1♀. Kiriwan Ellya, Sigira-Alle, 3000′ [ca. 910 m.], 28 Sep 1970, O. S. Flint, Jr., 1♀. Nuwara Eliya Dist., Nuwara Eliya, 24–27 Feb 1954, F. Schmid, 1♀; same, but 11 Mar 1954, 1♀; same, but 4 Apr 1954, 1♀ (CNC).

Diplectrona maligna (Hagen)
Figs. 7–12, 36

Hydropsyche maligna Hagen, 1859:211.—Ross, 1952:33 [lectotype ♂].

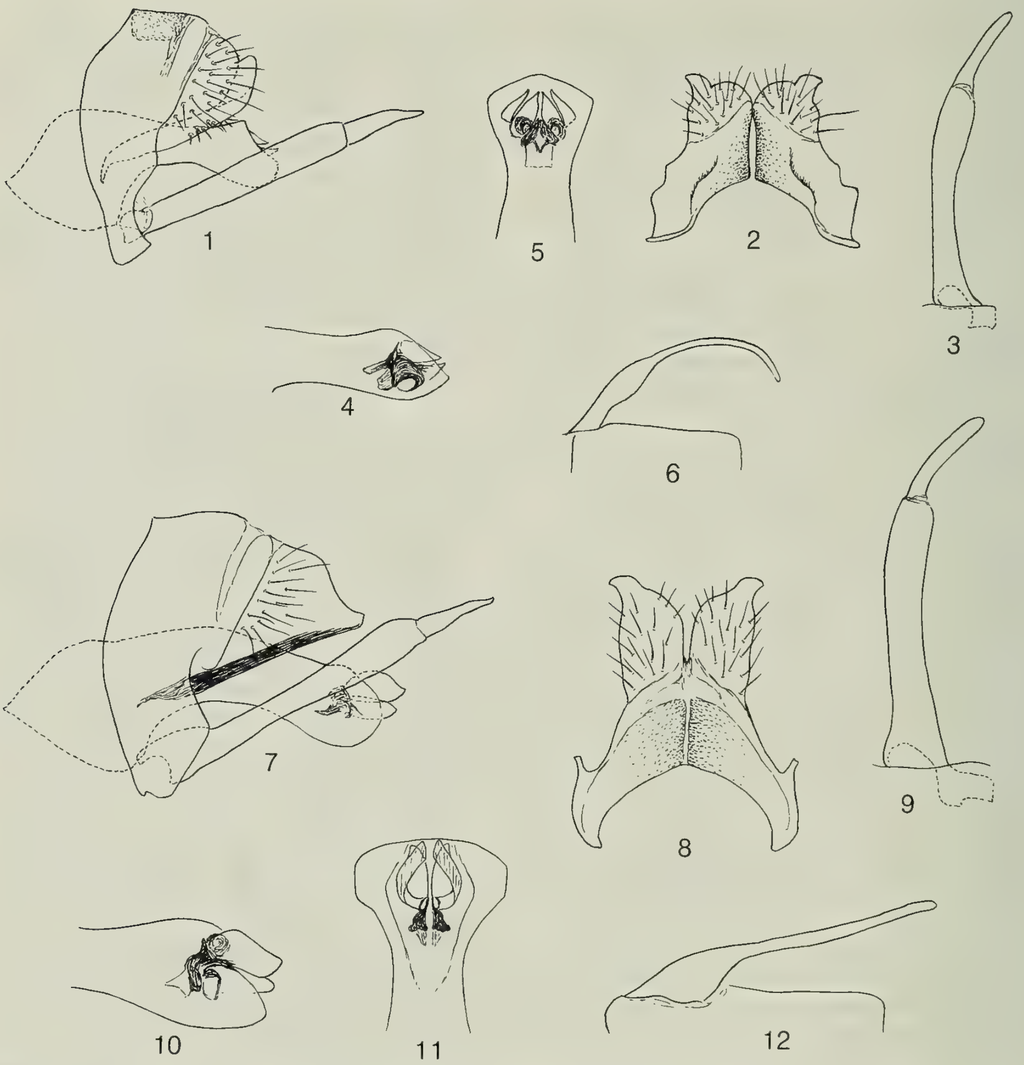
Diplectrona maligna: Ulmer, 1928:316 [to *Diplectrona*].—Schmid, 1958:118 [color ♀ paratype, identity unknown].—Fischer, 1963:146; 1972:150 [bibliography].—Weaver, 1993:41 [lectotype MCZ 11023, listed].

Diplectrona kirimaduhela Schmid, 1958: 117 [♂ genitalia].—Fischer, 1972:149 [bibliography]. NEW SYNONYMY.

This is a relatively uncommon species, found in the central highlands of the island from 1000 ft. [ca. 300 m] to 7000 ft [ca. 2135 m]. The collection of material of both sexes and comparison with the lectotype of *D. maligna* and holotype of *D. kirimaduhela* confirms the synonymy of these species. Kimmins had in 1958 set aside a pair of this species as the types of a new species which he never published. They are included in the material examined.

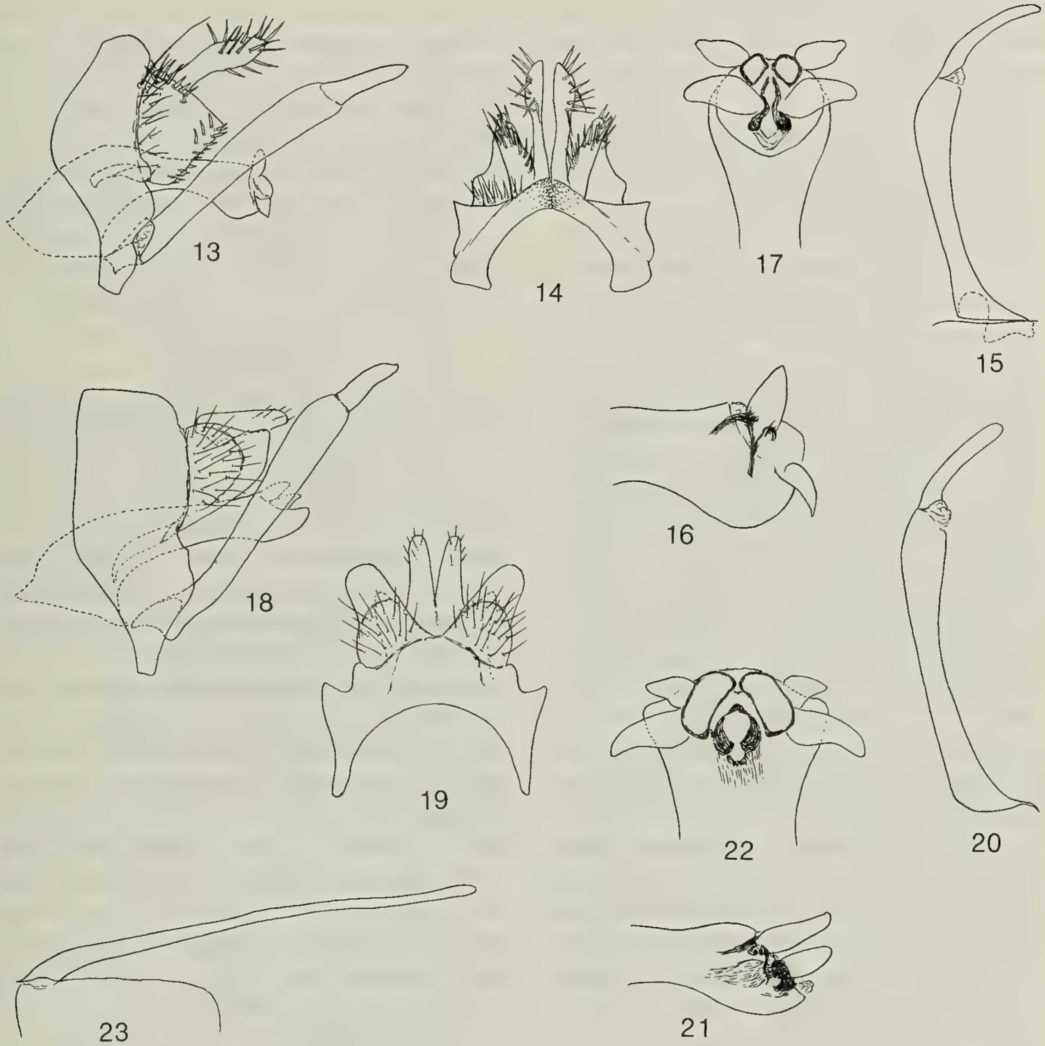
The male genitalia are shown by Schmid (1958, pl. 21, figs. 3, 4) under the name of *D. kirimaduhela.* Fork 1 is present in the hindwing of this species, but there are no internal reticulate sacs in the male abdomen only long processes from the anterolateral corners of the fifth sternum. These processes are quite variable in length, being almost twice as long as the fifth sternum in the lectotype and some other specimens, to being only slightly longer than the fifth sternum in the series from Deniyaya.

Material examined.—"Ceylon Nietner"



Figs. 1–12. Male terminalia. *D. papilionacea*: 1, lateral; 2, ninth and tenth terga, dorsal; 3, inferior appendage, posteroventral; 4, tip of phallus, lateral; 5, tip of phallus, dorsal; 6, dorsolateral margin of fifth sternum with appendage, lateral. *D. maligna*: 7, lateral; 8, ninth and tenth terga, dorsal; 9, inferior appendage, posteroventral; 10, tip of phallus, lateral; 11, tip of phallus, dorsal; 12, dorsolateral margin of fifth sternum with appendage, lateral.

[the original description states this is from Rambodde at 3500 to 4000 feet], "Hagen," "Type 11023," "Lectotype Hydropsyche maligna Hagen," 1♂ (MCZ). "Ceylan (C.P.) [Central Province, Nuwara Eliya District], Horton Plains, 7–8 III 1954, F. Schmid," "holotype ♂ Diplectrona kirimaduhela F. Schmid 1956," "Type No 71899 USNM"; same, but 23 Apr 1980, W. N. Mathis, T. Wijesinhe & L. Jayawickrema, 1♀; same, but 7000′ [2135 m], 3–4 Oct 1970, O. S. Flint, Jr., 1♂. N'Eliya [Nuwara Eliya], 6500′ [1980 m], 23-IV-23 [23 Apr 1923], 1♂, 1♀ (BMNH). 2.4 mi. [3.85 km] S. Pattipola, roadside pool, 20 Feb 1970, Davis & Rowe, 4♂, 1♀, 1 without abdomen. Lovers Leap Creek, 7000 ft. [2135 m], 15 Mar 1973, Baumann & Cross, 1♂, 1♀.



Figs. 13–23. Male terminalia. *D. malickyi*: 13, lateral; 14, ninth and tenth terga, dorsal; 15, inferior appendage, posteroventral; 16, tip of phallus, lateral; 17, tip of phallus, dorsal. *D. ingens*: 18, lateral; 19, ninth and tenth terga, dorsal; 20, inferior appendage, posteroventral; 21, tip of phallus, lateral; 22, tip of phallus, dorsal; 23, dorsolateral margin of fifth sternum with appendage, lateral.

Kandy District, Kabaragala, Nillomalai, 22–23 Mar 1975, S. & P. B. Karunaratne, 1♂, 1♀. Southern Prov., Matara District, Deniyaya, near 1000 feet elevation [ca. 305 m], 19–20 Oct 1976, Hevel et al., 8♂.

Diplectrona malickyi, new species

Figs. 13–17, 36

Diplectrona sp. (*maligna?*) Hagen.—Chantaramongkol & Malicky, 1986:528 [♂, misidentification].

This is closely related to *D. maligna* (Hagen) on the basis of size, and presence of fork 1 in the hindwing. It is easily recognized in both sexes by its coloration, being fuscous with the forewings bearing many silvery-white spots. In addition the male has its eyes much enlarged, the abdomen has a pair of small internal sacs, and its tenth tergum divided into 2 pairs of separate lobes, both bearing notably enlarged setae.

A male and female of this species were

discovered in the BMNH as types of a new species Kimmins intended to describe, but never did. This pair are included as paratypes herein.

Adult.—Length forewing, male 7–8 mm, female 9–10. Color fuscous; forewing fuscous with many small silvery-white maculae. Hind tibia of male and female bearing long, silky hair from all sides. Fifth sternum of male with anterodorsal filament, tapering apicad, directed posteriad, and almost attaining apex of sixth segment. With a pair of small internal sacs between seventh and eighth segments. Male genitalia: Ninth segment annular; anterior margin convex, posterior margin not produced ventrally. Tenth segment divided into paired inner and outer lobes; inner lobes separated mesally to base, in lateral aspect narrow and semierect and projecting beyond outer lobes half the length of these lobes, bearing many enlarged setae from apical half; outer lobes trianguloid in lateral aspect, with basal row of setae and dorsal and ventral rows of short, enlarged setae. Inferior appendages long, terete, apical segment almost half as long as basal segment in posterior aspect. Phallus tubular, elongate, angled near base; apex inflated ventrally, with a pair of dorsolateral, elongate lobes and a pair of smaller apicolateral lobes; phallotremal sclerites complex, with a pair of strongly sclerotized, ventral, rounded lobes.

Material examined.—Holotype, male: Sri Lanka, Central Province, Kandy District, Hasalaka, 1000′ [ca. 305 m], 30–31 Mar 1973, Baumann & Cross, at black light (NMNH). Paratypes: Same data, 1♀. Kandy, 22–29 Mar 1971, P. & P. Spangler, collected at black light, 1♂. Peredeniya, Hantana Hill, 2000′ [ca. 610 m], 29 Mar 1973, Baumann & Cross, 1♂. Madugoda, ca. 2600 ft. [ca. 790 m], 1 Apr 1973, Baumann & Cross, at black light, 1♀. Matale District, Elkaduwa, Hunas Falls, 3000′ [ca. 915 m], 5 Apr 1973, Baumann & Cross, 1♂, 2♀. Sabaragamuwa Province, Ratnapura District, Kalu Ganga, Indurawa Jungle, 1000 ft. [ca. 305 m], 23 Mar 1973, Baumann & Cross, collected at black light, 1♀. Uggalkaltota, Irrigation Bungalow, 350 ft. [ca. 105 m], 31 Jan–8 Feb 1970, Davis & Rowe, 1♀. Rakwana, 3-V-29 [3 May 1929], 1♂ (BMNH). North Central Province, Polonnaruwa Province, Polonnaruwa District, Polonnaruwa, 6 May 1974, Gans & Prasanna, 1♂. [Uva Prov., Monaragala Dist.], Bibile, 17-VII-29 [17 Jul 1929], 1♀ (BMNH).

Diplectrona ingens, new species
Figs. 18–23, 37

Hydromanicus papilionaceus: Ulmer, 1906: 78 [description, venation ♀ paratype (BMNH); mixed type series].

This species is very closely related to both *D. taprobanes* and *D. longistyla,* but immediately recognized by its much larger size and pair of dark, chevron-shaped marks on the posterior border of the forewing. Like the two aforementioned species, this one lacks fork 1 in the hindwing (several of the largest females have a small fork 1, and in 1 specimen it is lacking on one side and present on the other). The male genitalia of the three species are virtually identical, both *D. ingens* and *D. taprobanes* have 2 pairs of sclerites at the apex of the phallus, whereas *D. longistyla* has only 1 pair. Other aspects of the genitalia do not offer any clear-cut distinguishing characteristics for *D. ingens.*

The specimen that was the basis for the Ulmer (1906) reference was located in the BMNH. It and another example were part of the original type series of *D. papilionacea,* but are not conspecific with the lecto- and paralectotypes found in the MCZ. The male of the BMNH pair is labelled in Hagen's hand as "Hydropsyche papillionacea," and the female in Ulmer's hand as "Hydromanicus papilionaceus." Both these two and another 4 examples were set aside by Kimmins in 1958 as the types of one of his new species, but never published. They are included in the paratype series below.

Adult.—Length forewing, male 10.5–12 mm, female 12–15 mm. Color light brown;

forewings light brown marked with darker spots, posterior margin stramineous with 2 brown chevron-like marks ⅓ and ⅔ of length (females usually darker and less contrasting in marks). Hind tibia of male bearing long, silky hair from all sides. Fifth sternum of male with anterodorsal filament, tapering apicad, directed posteriad, and attaining seventh to middle of eighth segment. Male genitalia: Ninth segment annular; anterior margin slightly convex, posterior margin angled over base of inferior appendage, ventral bridge very narrow. Tenth segment divided into paired inner and outer lobes; inner lobes separated mesally for more than half length, in lateral aspect barely surpassing outer lobes; outer lobes with large, bulging, setate wart basally, distal margin thin and angulate. Inferior appendages long, terete, apical segment a third as long as basal segment in posterior aspect. Phallus tubular, elongate, curved from base; apex slightly inflated, with 2 pairs of elongate dorsolateral lobes (lateralmost pair in holotype, figured, are larger than in most paratypes) and a ventral scoop-like structure; phallotremal sclerites complex, with a pair of strongly sclerotized, ventral, bean-like lobes.

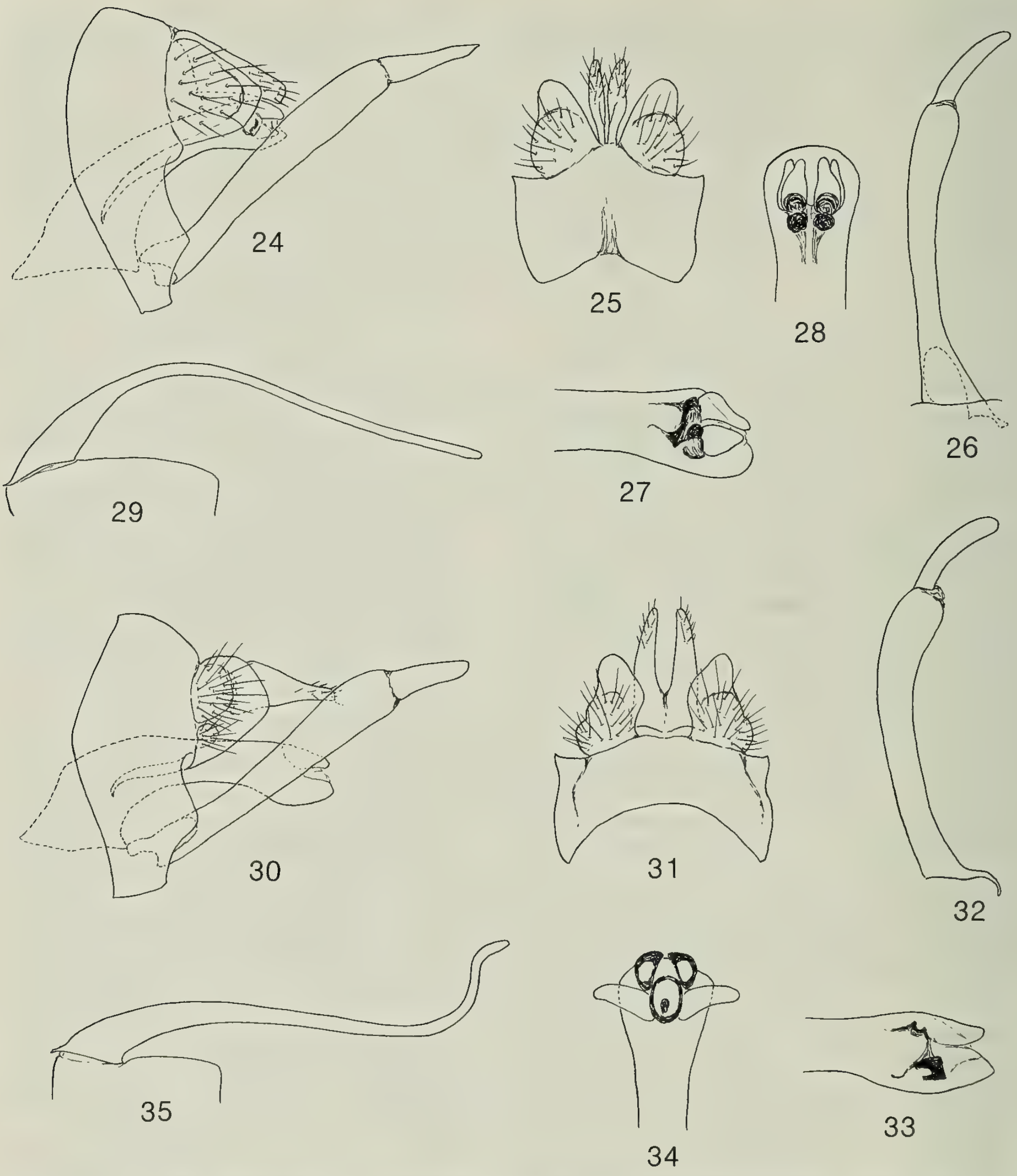
Material examined.—Holotype, male: Sri Lanka, Central Province, Nuwara Eliya District, Pattipola, 6100′ [ca. 1860 m], 3–6 Oct 1970, O. S. Flint, Jr. (NMNH). Paratypes: Same data, 3♀. Horton Plains, 7000′ [ca. 2130 m], 3–4 Oct 1970, O. S. Flint, Jr., 1♀. Agrapatana Rd., Horton Plains, 6600′ [ca. 2010 m], 4 Oct 1970, O. S. Flint, Jr., 3♀. Ohiya, 17 Apr, 1♂; same, but 21 Apr, 1♂, same, but 28 Apr, 1♂, 1♀ (BMNH). High Forest, Kurundu Oya, 5000 ft. [ca. 1525 m], 18 Mar 1973, Baumann & Cross, 1♂, 2♀. Ambawela, 5000 ft. [ca. 1525 m], 14 Mar 1973, Baumann & Cross, 3♂. Hakgala Botanic Garden, 1650 mtrs., 23–25 Feb 1977, K. V. Krombein et al., blacklight, 3♂; same data, but 6–8 Oct 1976, 1♀; same, but 6 Oct 1970, O. S. Flint, Jr., 1♂. Hakgala Botanic Garden, Circuit Bungalow, 5–8 Feb 1979, K. V. Krombein et al., blacklight, 2♂. Uva Province, Badulla District, Kande-Ela Reservoir, 6200′ [ca. 1890 m], 1–5 Oct 1970, O. S. Flint, Jr., 1♂. Ceylon [only data], 1♂ labelled by Hagen "Hydropsyche papillionacea," 1♀ labelled by Ulmer "Hydromanicus papilionaceus" (BMNH).

Diplectrona taprobanes (Hagen), new combination
Figs. 24–29, 38

Hydropsyche taprobanes Hagen, 1858: 487.—Ross, 1952:33 [lectotype ♂].
Hydromanicus taprobanes: Ulmer, 1905:98 [in key only, to *Hydromanicus*].
Diplectronella taprobanes: Ulmer, 1928: 317 [to *Diplectronella*].—Mosely, 1931: 197 [venation, genitalia ♂].—Schmid, 1958:119 [variation, distribution].—Fischer, 1963:151; 1972:153 [bibliography].—Weaver, 1993:41 [lectotype MCZ 11021, listed].

This is the commonest and most widespread species on the island of Ceylon. It is known from low to high elevations, but seems commonest at elevations in the range of 300 to 3000 meters. The genitalia have been well illustrated by Mosely (1931), but are figured here, especially for comparative purposes. There seems to be considerable variation in the appearance of the tenth tergum, as already noted by Schmid (1958). Fork 1 is lacking in the hindwing of the species, as it is in *D. ingens* and *D. longistyla.* For specific differences between these three species see their diagnoses.

Material examined.—"Ceylon Nietner" [the original description states this is from Rambodde at 3500 to 4000 feet], "Hagen," "Type 11021," "Lectotype Hydropsyche taprobanes Hagen," ♂ lectotype (MCZ). The NMNH has over 650 specimens, from about 75 localities in the following provinces and districts: Central Province—Kandy District, Matale District, Nuwara Eliya District; Eastern Province—Ampari District; North Central Province—Anuradhapura District; Sabaragamuwa Province—Ke-



Figs. 24–35. Male terminalia. *D. taprobanes*: 24, lateral; 25, ninth and tenth terga, dorsal; 26, inferior appendage, posteroventral; 27, tip of phallus, lateral; 28, tip of phallus, dorsal; 29, dorsolateral margin of fifth sternum with appendage, lateral. *D. longistyla*: 30, lateral; 31, ninth and tenth terga, dorsal; 32, inferior appendage, posteroventral; 33, tip of phallus, lateral; 34, tip of phallus, dorsal; 35, dorsolateral margin of fifth sternum with appendage, lateral.

galle District, Ratnapura District; Southern Province—Galle District, Hambantota District, Matara District; Uva Province—Badulla District; Western Province—Colombo District, Kalutara District.

Diplectrona longistyla, new species
Figs. 30–35, 37

This is clearly the sister species of *D. taprobanes,* not only the coloration but the

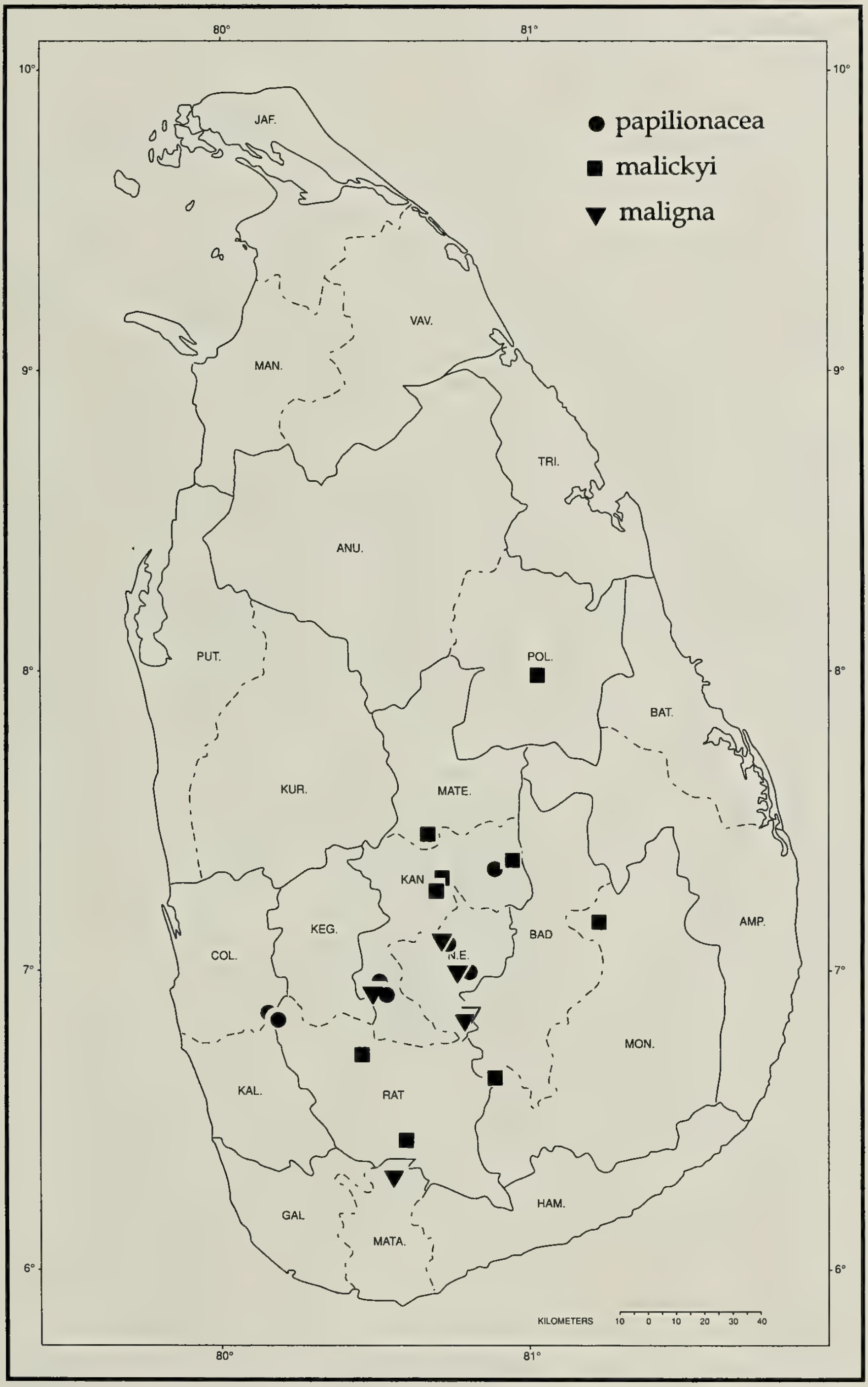


Fig. 36. Distribution on Sri Lanka of *D. papilionacea, D. malickyi,* and *D. maligna.* Two to four letter abbreviations are of names of Districts.

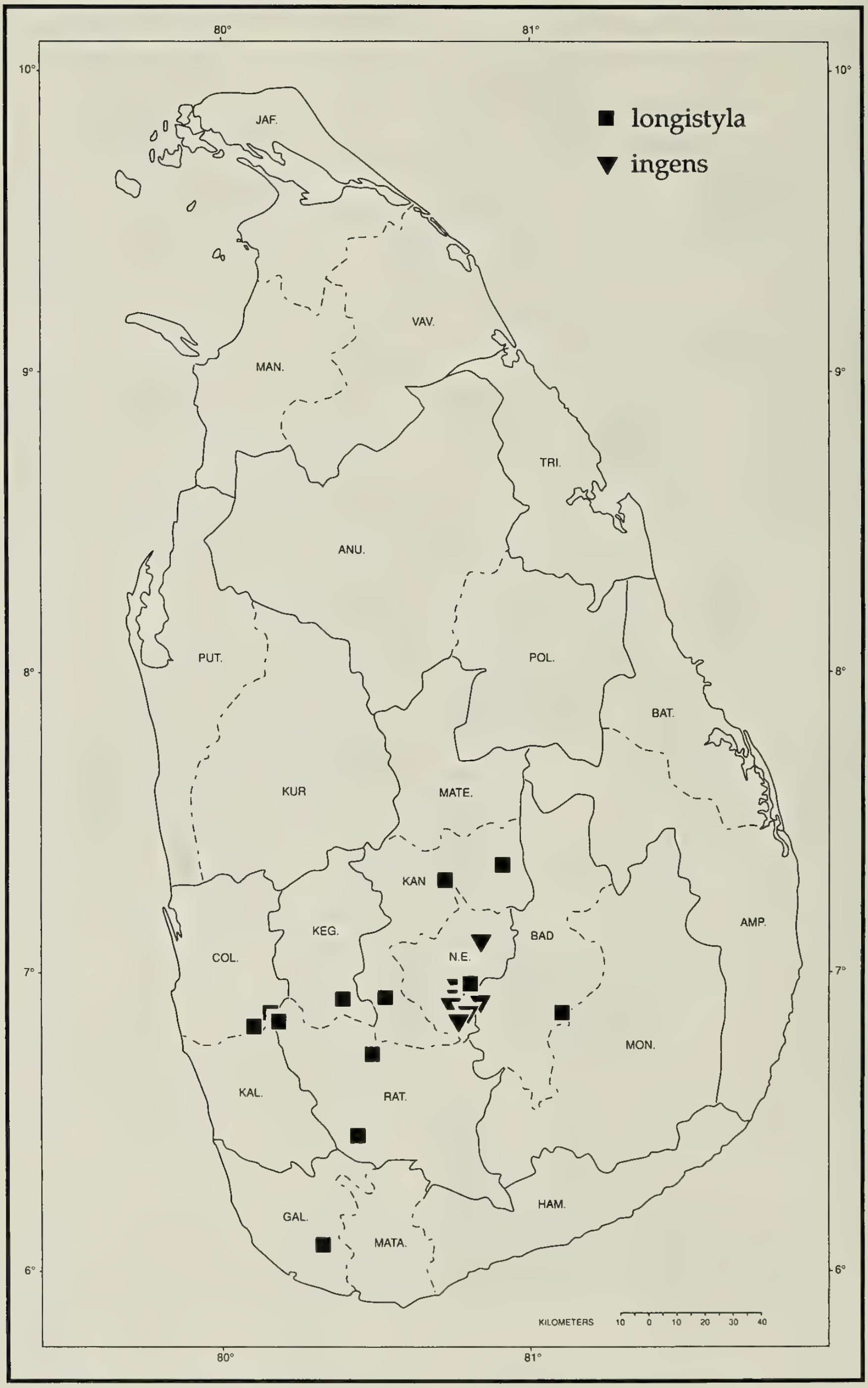


Fig. 37. Distribution on Sri Lanka of *D. longistyla* and *D. ingens.* Two to four letter abbreviations are of names of Districts.

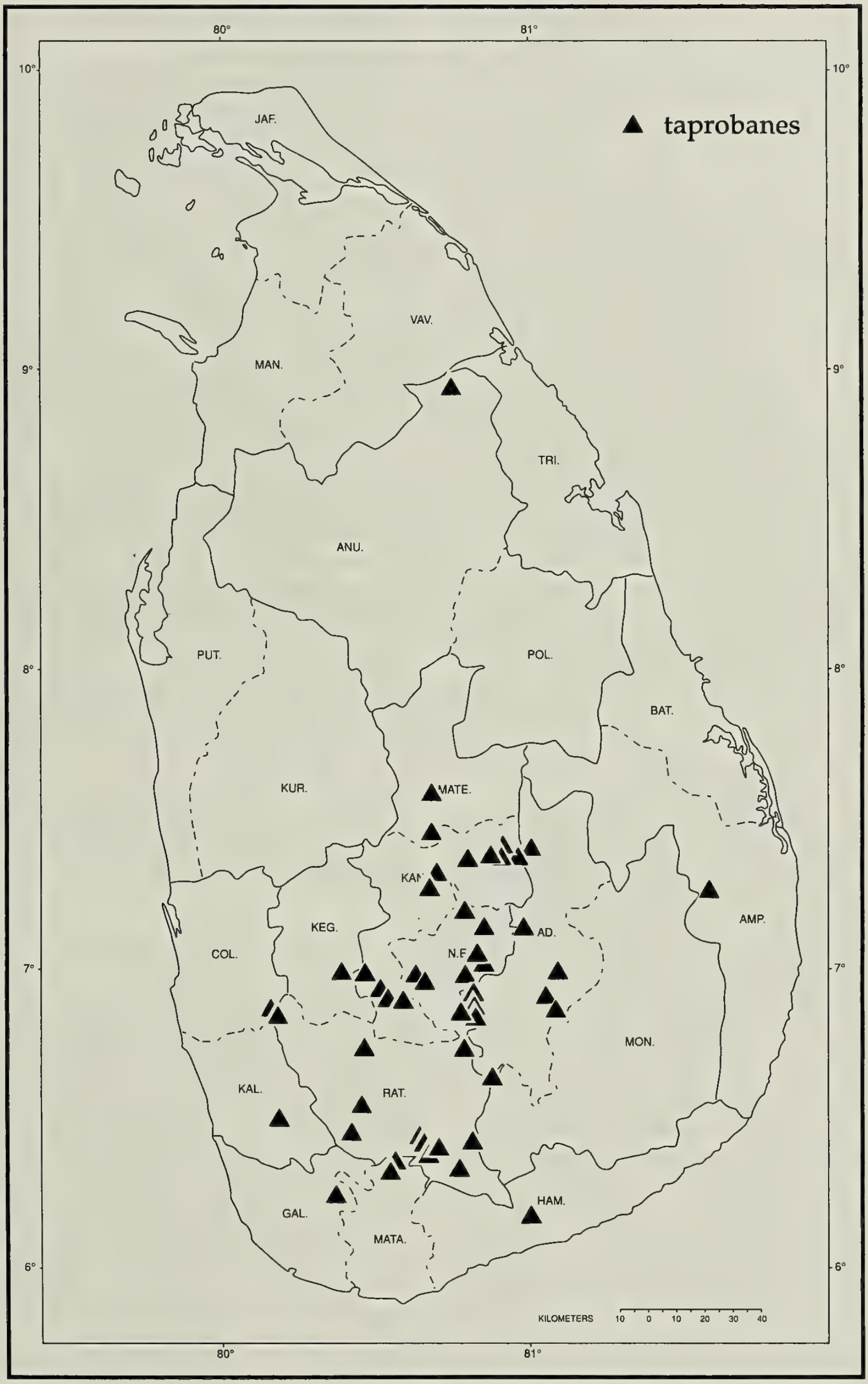


Fig. 38. Distribution on Sri Lanka of *D. taprobanes.* Two to four letter abbreviations are of names of Districts.

overall male genitalia are nearly identical and both lack fork 1 in the hindwing. The lateral style of the fifth sternum is longer in this species, reaching at least into the eighth segment or more often to the inferior appendages (depending on the degree the body segments are telescoped), but only into the seventh segment in *D. taprobanes.* It is further distinguished by the presence of only a single pair of apical processes at the tip of the phallus instead of two as in *D. taprobanes.* The shapes of the inner and outer lobes of the tenth tergum are quite variable in both species and overlap to some degree, but *D. taprobanes* only rarely has an elongate, rather narrow inner lobe as seen in lateral aspect as is typical of *D. longistyla* and shown here.

Adult.—Length forewing 8–9 mm. Color brown; a band of stramineous hair posteriad from head, thorax and along posterior margins of forewings; forewings brown marked with stramineous spots, posterior margin stramineous with brown incursion from front at one and two thirds of length (sometimes this stramineous band is not developed and the area is simply spotted with stramineous hair). Hind tibia of male bearing long, silky hair from all sides. Fifth sternum of male with anterodorsal filament, tapering apicad, directed posteriad, and attaining middle of eighth segment up to bases of inferior appendages. Male genitalia: Ninth segment annular; anterior margin slightly convex, posterior margin produced over base of inferior appendage. Tenth segment divided into paired inner and outer lobes; inner lobes separated mesally almost to base, in lateral aspect usually narrowed apically and projecting beyond outer lobes the length of these lobes; outer lobes with large, bulging, setate warts basally, distal margin thin and angulate. Inferior appendages long, terete, apical segment a third as long as basal segment in posterior aspect. Phallus tubular, elongate, angled near base; apex slightly inflated, with a pair of dorsolateral, elongate lobes and a ventral scoop-like structure; phallotremal sclerites complex, with a pair of strongly sclerotized, ventral, bean-like lobes.

Material examined.—Holotype, male: Sri Lanka, Western Province, Colombo District, Tunmodera, 200′ [ca. 60 m], 17 Nov 1970, O. S. Flint, Jr. (NMNH). Paratypes: Same, data 9♂. Labugama, 400 feet [ca. 120 m], 24 Aug 1973, G. Ekis, 1♂. Padukka, 300′ [ca. 90 m], 16 Nov 1970, O. S. Flint, Jr., 2♂. Central Province, Kandy District, Kandy, 21 Feb 1971, Piyadasa & Somapala, 2♂. Madugoda, 2600′ [ca. 800 m], 24 Nov 1970, O. S. Flint, Jr., 2♂. 2.5 mi. [ca. 4.0 km] NE Laksapana, 2700′ [ca. 820 m], 26 Nov 1970, O. S. Flint, Jr., 3♂. Nuwara Eliya District, Hakgala Botanic Garden Circuit Bungalow, 5–8 Feb 1979, Krombein et al., 1♂. Uva Province, Badulla District, Koslanda, Diyaluma Falls, 3000 ft [ca. 915 m], 19 Mar 1973, Baumann & Cross, 1♂. Sabaragamuwa Province, Ratnapura District, Gilimale Lumber Mill, 115 ft [ca. 35 m], 20–25 Oct 1976, Hevel et al., 2♂. 2 mi. [ca. 3.2 km] S of Weddagala, Sinharaja Jungle, 6–12 Feb 1977, Krombein et al., 4♂. Southern Province, Galle District, Kottawa Forest Reserve, 10–11 Jan 1975, Krombein et al., 1♂.

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A new geryonid crab from the Amirante Basin, western Indian Ocean (Crustacea: Decapoda: Brachyura)

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Abstract.—Two deep water geryonid crabs, *Chaceon crosnieri* Manning & Holthuis, and *C. goreni,* a new species, are reported from the Amirante Basin. *Chaceon goreni,* the seventh species of the genus to be recognized from the western Indian Ocean, is described from material collected in 1400 m off Alphonse Island. It most closely resembles *C. collettei* Manning, in having a spine externally on the carpus of the cheliped; but it is distinguished in having longer, more slender frontal and anterolateral spines, and proportionately longer, more slender pereopods.

Six species of the deep water geryonid genus *Chaceon* Manning & Holthuis, 1989 have been described from the western Indian Ocean thus far. *Chaceon paulensis* (Chun, 1903) is known from Amsterdam and St. Paul Islands, and *C. collettei* Manning, 1992 from Walters Shoals, both in the southernmost reaches of the Indian Ocean; *C. macphersoni* (Manning & Holthuis, 1988) was collected off South Africa, Mozambique and Madagascar, *C. crosnieri* Manning & Holthuis, 1989 off Madagascar, *C. alcocki* Ghosh & Manning, 1993 was found off Travancore, India, and *C. somaliensis* Manning, 1993 off Somalia. Recently, several geryonid crabs were collected by an ichthyological expedition to the Amirante Basin. The specimens, here identified as belonging to *C. crosnieri* and a new species, described here, constitute the first geryonid records for the islands.

The type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), and in the National Collections, Tel Aviv University (TAU). The following abbreviations are used: cl, carapace length, measured on the midline; coll, collector; ovig, ovigerous; mm, millimeters.

Chaceon crosnieri Manning & Holthuis, 1989
Fig. 1

Material examined.—Indian Ocean: Amirante Basin, Alphonse I., 1000 m, trammel net 100 m, 20 Dec 1998, coll M. Goren: 1 ♂ 102.6 mm, 1 ♀ 107.3 mm, USNM 307241; 5 ♂♂ 74.8–123.5 mm, 2 ♀♀ 98.8, 102.4 mm, 6 ♀♀ ovig 90.6–123.2 mm, TAU AR 27778. Between Alphonse and Bijoutier Is., 1400 m, trammel net 100 m, 17 Dec 1998, coll M. Goren: 1 ♂ 134.3 mm, TAU AR 27779.

Chaceon goreni, new species
Figs. 2, 3

Material examined.—Indian Ocean: Amirante Basin, Between Alphonse and Bijoutier Is., 1400 m, trammel net 100 m, 17 Dec 1998, coll M. Goren: 1 ♂ 86.3 mm, holotype, TAU AR 27780; 1 ♂ 80.0 mm, paratype, USNM 309740.

Description.—Carapace transversely ovate, 1.15–1.20 times as wide as long; sur-

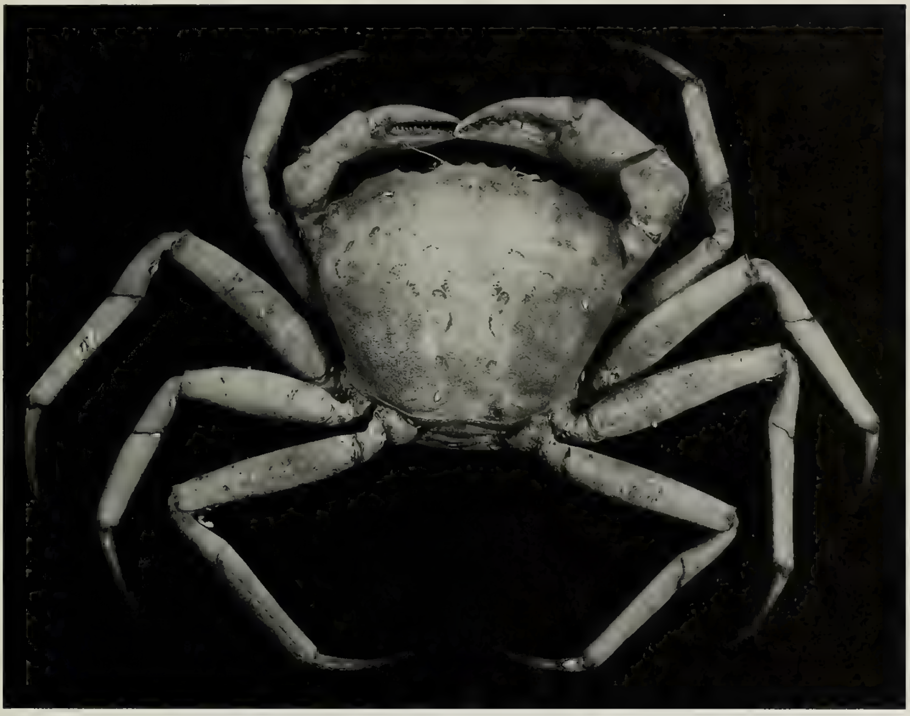

Fig. 1. *Chaceon crosnieri* Manning & Holthuis, 1989, male, cl 134.3 mm, dorsal view, TAU AR 27779.

Fig. 2. *Chaceon goreni,* new species, male holotype, cl 86.3 mm, dorsal view, TAU AR 27780.

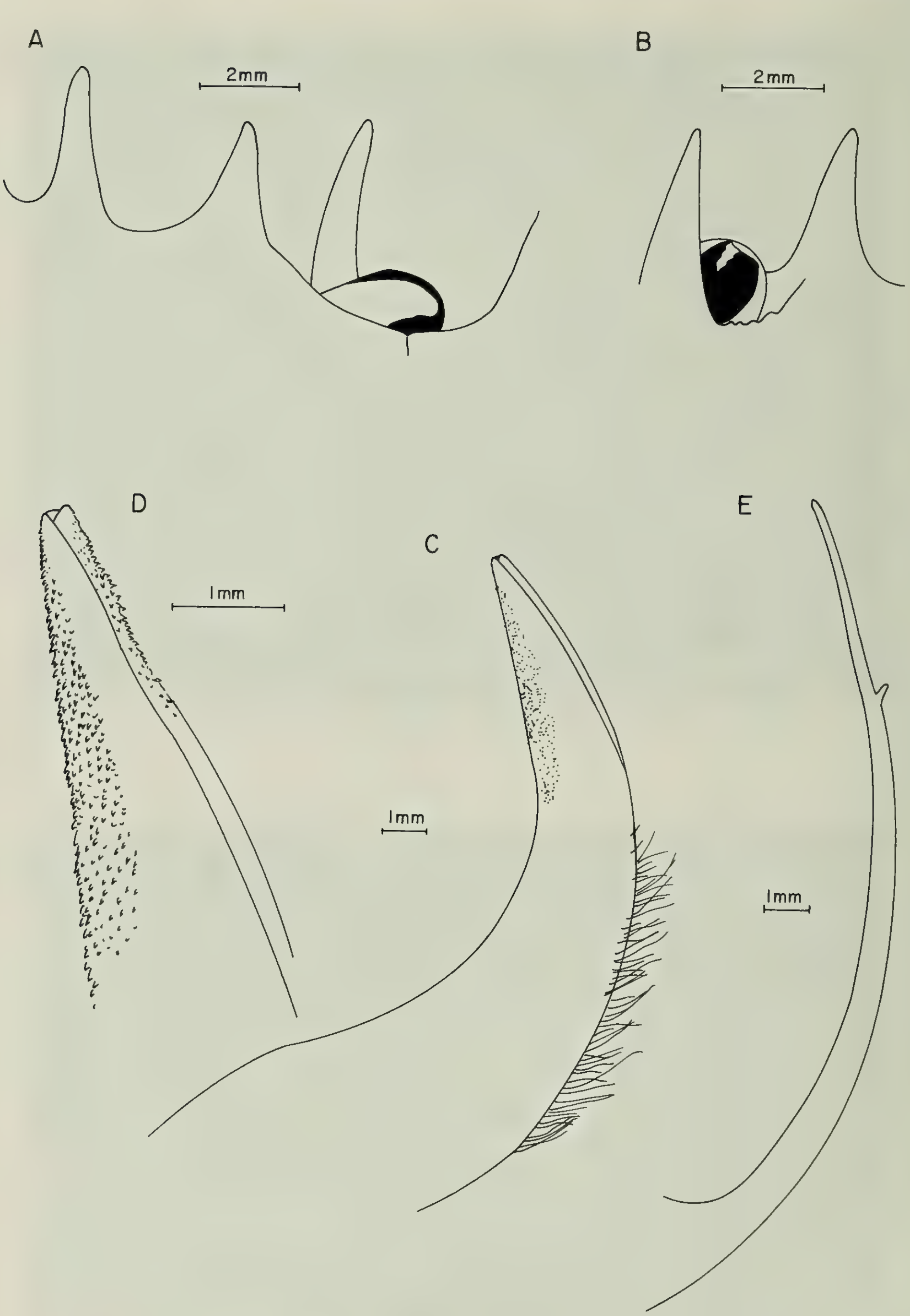

Fig. 3. *Chaceon goreni,* new species, male holotype, cl 86.3 mm, TAU AR 27780. a, front; b, ventral view of orbit; c, male first pleopod; d, apex of male first pleopod; e, male second pleopod.

face pitted; gastric region inflated; branchial regions well demarcated, slightly swollen, rugose. Front quadridentate, frontal teeth acuminate, elongate, submedian teeth extending further forward than lateral teeth; distance between submedian teeth smaller than distance between submedian and lateral teeth. Supraorbital margin obscurely granulate, submedially fissured; infraorbital margin medially granulate, inner angle bearing elongate, acuminate spine, extending beyond apices of lateral frontal teeth. Anterolateral margin convex, with 5 equidistant prominent spines. Posterolateral margin indistinctly convex. Posterior margin subcristate, sinuous, medially concave. Merus of third maxilliped subquadrate; external angle rounded. Ischium subrectangular, with oblique sulcus submedially. Exopod columnar, triangular denticle distally on inner margin. Chelipeds robust, subequal. Cheliped merus bearing prominent subdistal and distal spines on upper margin, Carpus with conical granules dorsally, with prominent spine on outer margin, another present on inner margin. Outer surface of palm rugose, granulose, granules more prominent on upper margin. Fingers longer than palm, cutting edges of fingers of larger chela with molariform teeth proximally. Pereopods long, slender, laterally compressed; fifth pereopodal merus nearly 6 times as long as wide, 0.75 times as long as carapace. Pereopodal meri, carpi, dorsally spinulose, spinules larger distally; pereopodal propodi dorsally spinulose, spinules smaller distally. Posterior 3 pereopodal meri bearing spine distally on upper margin. Dactyli laterally compressed, bearing longitudinal groove on upper margin. Surface of thoracic sternum pitted. Male abdomen triangular, telson broadly triangular, anteriorly rounded. Male first pleopod stout, tapering distally, curved distad; subdistally spinulose. Male second pleopod nearly as long as first, filiform, digitate process subdistally on inner margin.

Color.—Carapace pale brown, legs pinkish-orange.

Etymology.—Named for Dr. Menachem Goren, who collected the crabs, savoured some, but preserved most for the benefit of science.

Remarks.—*Chaceon goreni* is the seventh species of the genus described from the western Indian Ocean. It differs from the other species in the region, viz. from *C. alcocki* Ghosh & Manning, 1993, *C. crosnieri* Manning & Holthuis, 1989, *C. macphersoni* (Manning & Holthuis, 1988), *C. paulensis* (Chun, 1903), and *C. somaliensis* Manning, 1993, in having a spine on the outer margin of the carpus of the cheliped. *Chaceon goreni* resembles *C. collettei* Manning, 1992 from Walters Shoals at the southwestern Indian Ocean, but differs in having longer, more slender frontal and anterolateral spines, as well as longer and proportionately more slender pereopods. In the males of *Chaceon collettei* the fifth pereopodal merus is 4.9–5.2 times as long as wide, whereas in *C. goreni* it is nearly six times as long as wide. Fifth pereopodal dactylus 0.83 times as long as propodus in *C. collettei,* 0.92 times as long as propodus in *C. goreni.*

The haul off Alphonse Island yielded nearly one hundred *Chaceon* crabs, most were served for dinner to the gustatory gratification of the ichthyologists.

Acknowledgments

Dr. A. Baranes organized the Israeli ichthyological expedition to the Amirante Basin, Dr. A. Diamant supplied the color description, A. Shoob took the photographs, H. Bernard inked the drawings—we thank them all. Sincere thanks to P. Ng for his valuable comments.

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Description of two new species of *Polyonyx* Stimpson, 1858 from the Indo-West Pacific, with a key to the species of the *Polyonyx sinensis* group (Crustacea: Decapoda: Porcellanidae)

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Abstract.—Two new species of the genus *Polyonyx* Stimpson, 1858, *P. tulearis* and *P. thai* are described. The new species belong to the *P. sinensis* group, which currently contains 11 species from the Indo-West Pacific, three from the eastern Atlantic, and three from American waters. A key for all species in this group is included.

The *Polyonyx sinensis* species group was defined by Johnson (1958: 97) for taxa characterized by him as follows: "Lateral margins of carapace without spines. Carapace broader than long, transversely ovate, or rectangular with rounded corners. Front rather narrow, trilobate with the median lobe broad and rounded and projecting little beyond the lateral lobes, which are often scarcely developed so that the front is almost straight. Chelipeds with the anterior margins of the carpus and merus unarmed; a more or less marked development of hairs on their outer, and often also on their inner surfaces. Legs hairy dorsally, and often the carapace also more or less hairy. Dactyl of the walking legs with the dorsal claw much smaller than the ventral claw, and bearing two or three accessory spinules." Most of the species are definitely known to live as commensals of tube dwelling polychaetes. The species of the group are widespread in the Indo-West Pacific where it is represented now by 11 species. Three additional species are known from the tropical eastern Atlantic and three from American waters.

When Johnson (1958) revised the Indo-West Pacific species of the genus *Polyonyx,* the genus comprised 14 species, some of which were assigned to other genera by later workers (Ng & Sasekumar 1993). Of the Indo-West Pacific species attributed to the *P. sinensis* group by Johnson (1958), *P. sinensis* Stimpson, 1858, *P. utinomii* Miyake, 1943, *P. pedalis* Nobili, 1905, and *P. transversus* (Haswell, 1882), are currently considered as valid. In addition, *P. loimicola* Sankolli, 1965, *P. maccullochi* Haig, 1965, *P. haigae* McNeil, 1968, *P. vermicola* Ng & Sasekumar, 1993, and *P. bella* Hsueh & Huang, 1998, have been described since then and adescribed to the *P. sinensis* group by the original authors. *P. bella* is considered a junior synonym of *P. sinensis* (see Discussion). The position of *P. plumatus* Yang & Xu, 1994 was not discussed at all in the original description, it seems to be identical with *P. haigae* and is considered a junior synonym of that species. *P. cometes* Walker, 1887 which was included in the *P. sinensis* group by Johnson (1958) was placed in a new genus by Ng & Nakasone (1993) but is considered a member of the *P. sinensis* group in this paper since it fits in all respects with Johnson's definition. The three *Polyonyx* species from western Africa (Chace 1959) correspond with the basic morphological features of the *P. sinensis* group and have to be included here. The same is true for three species from the Americas which were recognized by Haig (1960) as clearly belonging to Johnson's *P. sinensis* group. The type species of the genus, *P. gibbesi,* is the only

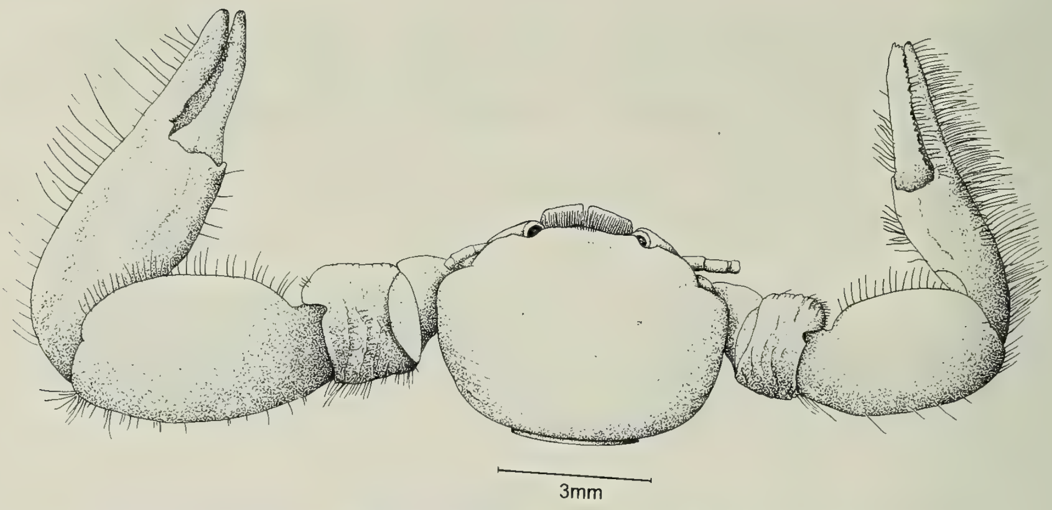

Fig. 1. *Polyonyx tulearis,* new species. Male holotype, Tulear, Madagascar, USNM 296465: dorsal view of body and chelipeds.

species from the western Atlantic and a common commensal in the tubes of the annelid *Chaetopterus variopedatus* (Renier).

Study of collections in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), revealed the presence of two undescribed species of the *P. sinensis* group from the Indo West Pacific. The measurements given refer to maximum carapace length (CL) and carapace width (CW).

Family Porcellanidae

Polyonyx tulearis, new species

Figs. 1, 2

Material.—Holotype: male, CL 4.1 mm, CW 5.2 mm, Madagascar, Tulear, shore, RV *Anton Bruun,* hand-collected, 11 Aug 1964, USNM 296465. Paratype: ovigerous female, CL 5.4 mm, CW 7.3 mm, same data as holotype, USNM 296466.

Description.—Carapace (Fig. 1) subovate, about 1.3 times as wide as long, broadest at epibranchial level; moderately convex longitudinally. Cervical and gastric grooves distinct, epigastric elevations prominent; anterolateral margin depressed at beginning of cervical groove to receive basal part of antennae; surface smooth anteriorly, slightly rugose with oblique striae near postero-lateral margins; devoid of setae except with scattered plumose setae near lateral margins and with forward-directed setae fringing frontal margin. Front broad, slightly trilobed in dorsal view, distinctly trilobate in frontal view (Fig. 2A), median lobe bluntly rounded, extending somewhat beyond lateral lobes. Orbits well defined; eyes large, partly visible from above.

Basal antennal segment with transverse crest; ventral face partly bent upward, visible from above. Segments of peduncle smooth.

Third thoracic sternite slender, without median lobe. Ischium of third maxilliped (Fig. 2D) about as long as broad, with scattered long setae on outer face.

Merus of chelipeds (Fig. 1) with well developed, anteriorly crenulate rounded lobe, laterally setose, with transverse, setose rugae on upper surface; outer distal angle of smaller cheliped with several conical tubercles. Carpus about 1.6 times as long as wide, surface smooth except for some low transverse striae near outer border; inner shelf evenly convex throughout length, finely denticulate on proximal half of mar-

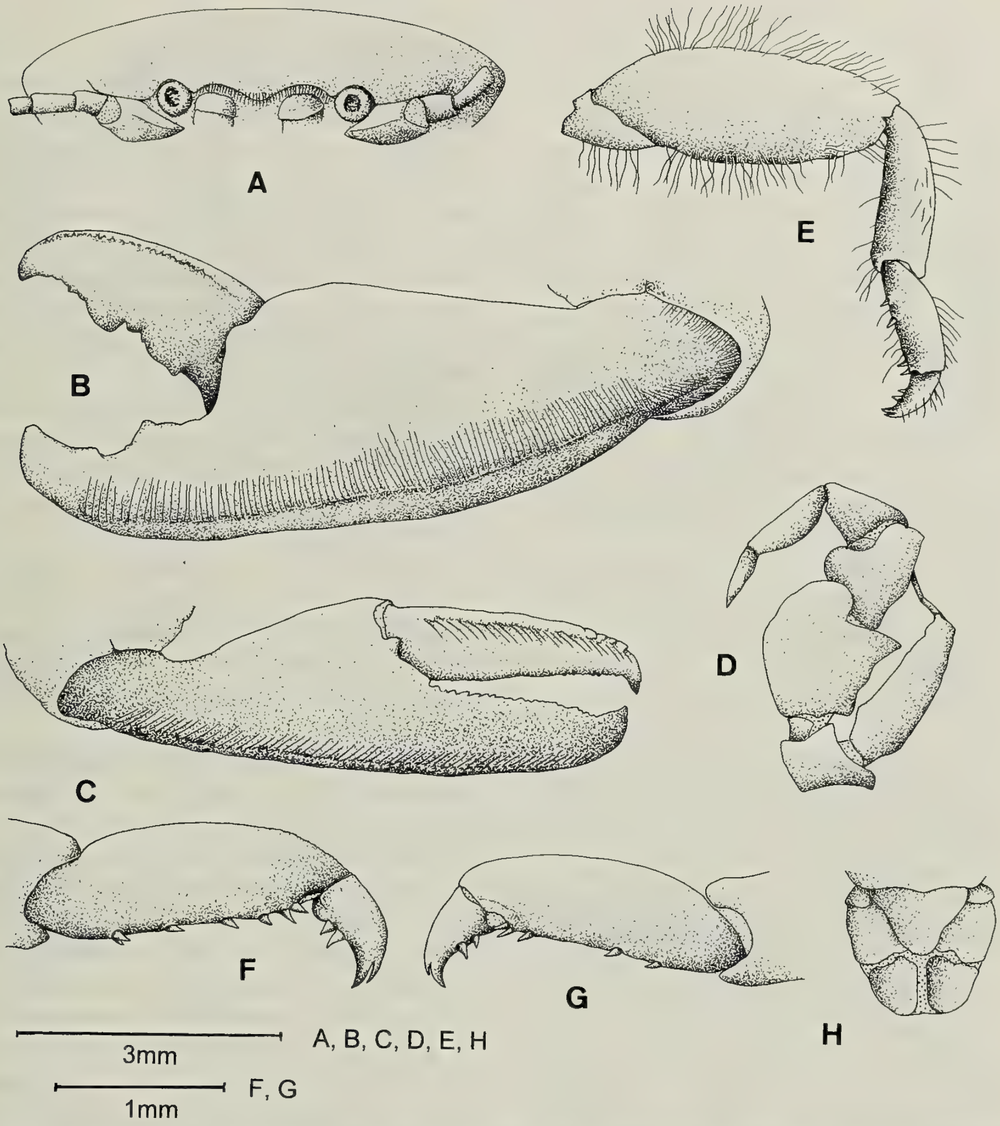

Fig. 2. *Polyonyx tulearis,* new species. Male holotype, Tulear, Madagascar, USNM 296465: A. front, anterior view; B. left (greater) chela, dorsal view; C. right (smaller) chela, ventral view; D. third left maxilliped, outer view; E. first left ambulatory leg, ventral view; F. propodus and dactylus of second right ambulatory leg, dorsal view; G. first left ambulatory leg, propodus and dactylus, dorsal view; H. telson, dorsal view.

gin, fringed with widely-set plumose setae. Chelae (Figs. 1, 2B, C) swollen, smooth, except for faint longitudinal ridge starting from dorsal articulation of movable finger; external margin with tuberculate ridge visible only in lateral view, fringed with row of simple setae. Fingers slightly curved outward. Fingers of mayor cheliped somewhat gaping near tip, movable finger with denticulate ridge throughout length starting from outer articulation. Cutting edge of pollex with strong tubercle-like tooth proximally and smaller tooth distally; dactylus with 2 large tooth, first near base and second median; fingers of smaller cheliped closing completely, movable finger with accentuated longitudinal ridge formed by row of tubercle-like teeth accompanied by dense fringe of setae; cutting edge of both fingers denticulate.

Ambulatory legs (Figs. 2E–G) decreasing in size from first to third pair, moderately setose. Merus and carpus unarmed; propodus about 3 times as long as wide, armed on lower margin with 5–7 stout, movable spinules including pair at distal end, proximal spines sometimes paired. Dactylus hooked, with bifid tip and 2 strong conical spinules on lower margin, distal one usually largest.

Uropods and telson (Fig. 2H) fringed with long plumose setae; males with pair of pleopods.

Habitat.—The only known specimens were collected by hand from the shore, but no commensalism was reported.

Etymology.—The specific name is derived from the type locality, Tulear, Madagascar.

Remarks.—Polyonyx tulearis is most similar to congeners that have a prominent crested lobe on the merus of the chelipeds, more than three terminal spines on the propodus of the walking legs, and lack spinulation on the inner side of all walking legs. *Polyonyx quadratus* is distinct because of the tubercles on the outer side of the chelae. The remaining species, *P. maccullochi, P. senegalensis, P. vermicola,* and the second new species described here, *P. thai,* have the fingers of the larger cheliped strongly curved outward, a character that easily distinguishes them from *P. tulearis.*

Polyonyx thai, new species
Figs. 3, 4

Material.—Holotype: male, CL 2.7 mm, CW 4.0 mm, Thailand; Chorburi Province, Bang Saen Beach, Gulf of Thailand, 13°20′N 100°55′E, 15 Jan 1959; exposed sand beach, commensal with polychaete worms (Chaetopteridae), leg. Dr. G. M. Moore, USNM 296463. Paratype: ovigerous female, CL 3.4 mm, CW 4, 9 mm, same data as holotype, USNM 296464.

Description.—Carapace (Fig. 3) subrectangular, 1.4–1.5 times wider than long, broadest at epibranchial level; moderately convex from front to back; anterolateral margin somewhat depressed to receive basal portions of antennae; carapace regions faintly indicated, surface punctate, without setae except on posterolateral margins and lateral walls. Front broad, sinuously trilobate in dorsal and frontal view (Fig. 4A), lobes obtuse, median lobe scarcely extending beyond lateral lobes; frontal margin with row of upwardly directed short setae. Orbits shallow; eyes large, completely visible from above.

Basal segments of antennae triangular, with transverse crest, partly visible from above; segments of peduncle cylindrical, smooth, flagellum large, reaching nearly twice length of carapace, with short stiff setae throughout length.

Third thoracic sternite narrow, trilobate anteriorly; median lobe broadly triangular, lateral lobes with rounded tip. Ischium of third maxilliped (Fig. 4C) about as long as broad with scattered long setae on outer face.

Chelipeds (Fig. 3) unequal, merus with well developed cristate lobe extending distally beyond proximal border of merus, upper surface with some rugae, lateral borders fringed with plumose setae. Carpus about 1.5 times longer than wide, upper surface evenly rounded, smooth; inner border tapering proximally, broadening to large rounded lobe fringed with line of large plumose setae; external portion of carpus with scattered setae. Larger chela (Fig. 4F) swollen, surface smooth, thickly setose near external margin; similar setation on internal margin extending into gape of fingers. Fingers curved outward, gaping, dactylus considerably shorter than pollex; cutting edge of pollex with large conical tooth proximally, dactylus with large rounded tooth near base and a smaller tuberculate one submedially. Chela of smaller cheliped (Figs.

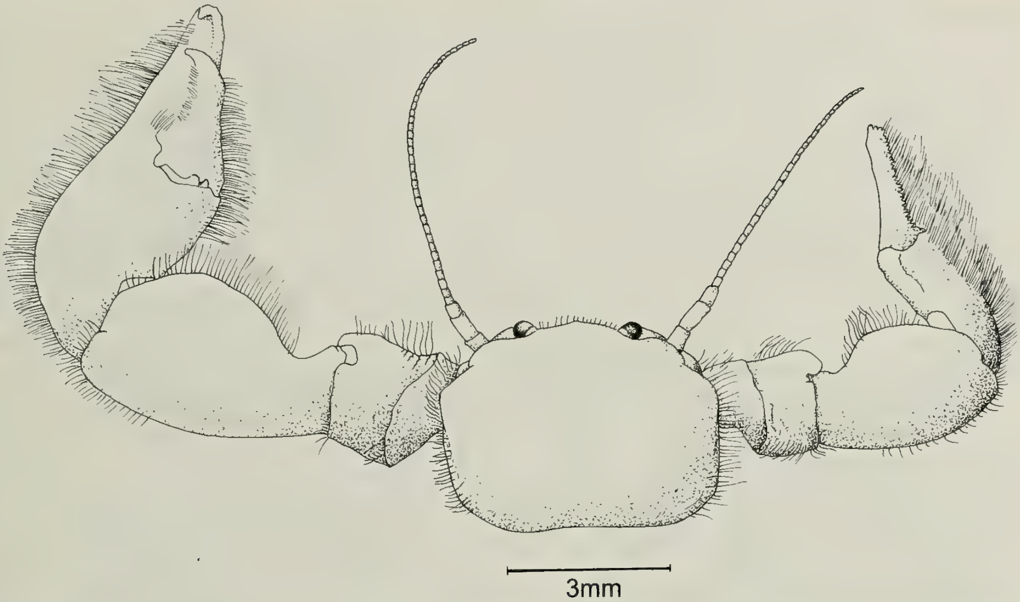

Fig. 3. *Polyonyx thai,* new species. Male holotype, Bang Saen Beach, Chorburi Province, Gulf of Thailand, USNM 296463: dorsal view of body and chelipeds.

4D, E) slender, fingers slightly curved outward; palm with faint ridge starting from articulation of movable finger; outer border of palm and fingers covered with long, plumose setae, movable finger with long elevated ridge along outer margin formed by row of flattened rounded tubercles; fingers closing completely, cutting edges with fine denticulation.

Ambulatory legs (Figs. 4G–I, K) decreasing in size from first to third pair, thickly setose. Merus and carpus unarmed; propodus 2 times as long as wide, armed on lower margin with three to five conical spines in addition to three terminal spines. Dactylus compact, on lower margin with bifid curved tip and two strong conical spinules, distal one largest.

Uropods and telson fringed with long plumose setae; first pair of pleopods present in males.

Variations.—The setation of the frontal margin of the female paratype is denser and not confined in a row as in the male holotype. In contrast to the smooth surface of the larger chela of the male, that of the female paratype bears a faint dorsal ridge which joins the dorsal articulation of the dactylus and which continues, more pronounced, on the dorsal margin of the dactylus, and becomes tuberculate towards the tip of the finger. The three left walking legs of the paratype female also have more spines on the lower margin of the propodus than the holotype, numbering eight, five and seven respectively in addition to the three terminal spines, from first to third leg, versus five, three and four respectively for the male holotype.

Habitat.—The new species was collected from chaetopterid worm tubes together with a series of *P. sinensis* (three males and two females).

Etymology.—The species name is derived from the country of the type locality, Thailand, used as a noun in apposition.

Remarks.—*Polyonyx thai* has the fingers of the larger cheliped strongly curved outward, a character shared only with three other species of the group. From *P. vermicola,* it is most easily distinguished by the form of the carpus of the larger cheliped,

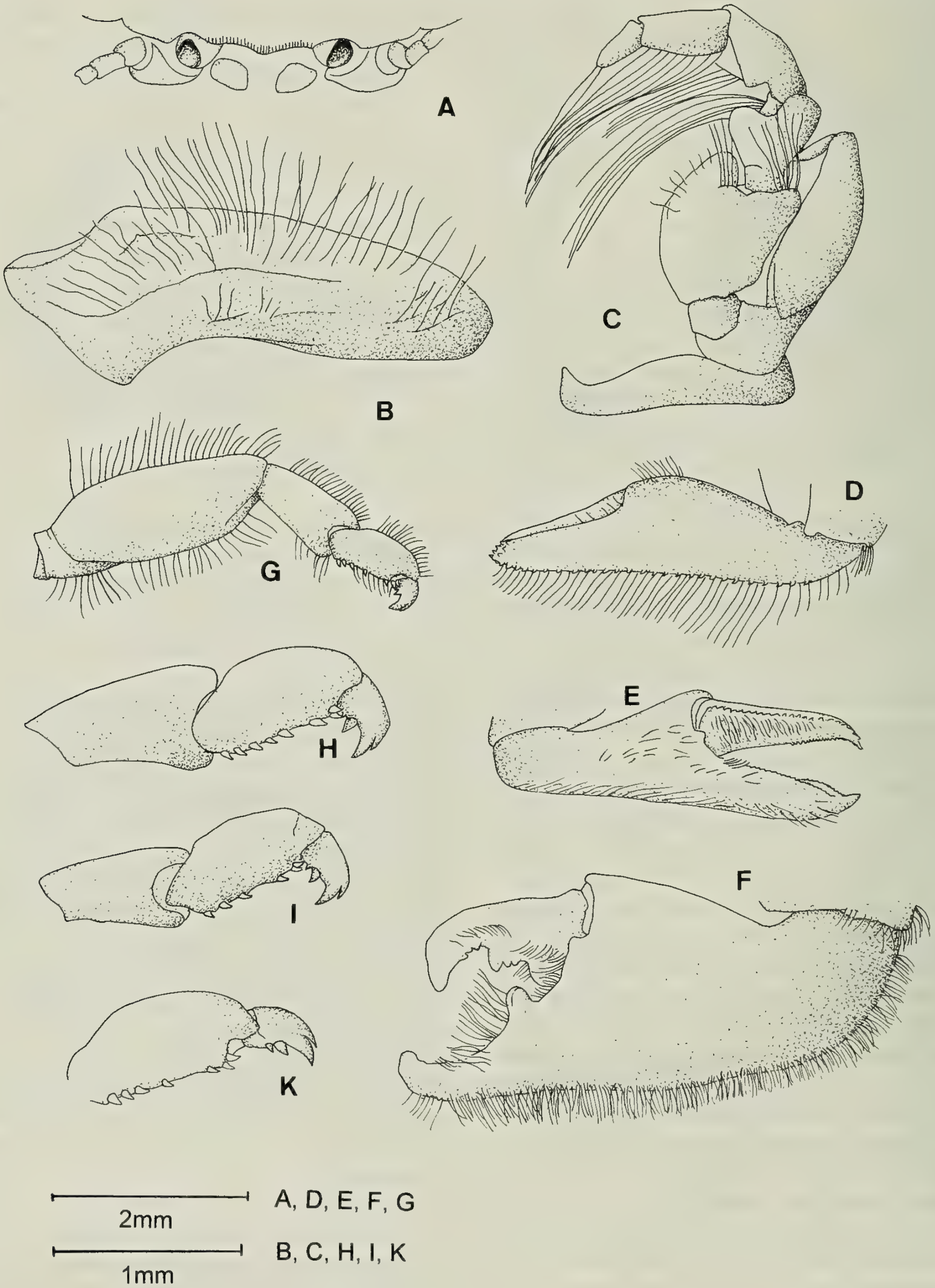

Fig. 4. *Polyonyx thai*, new species. Male holotype Bang Saen Beach, Chorburi Province, Gulf of Thailand: A. front, anterior view; B. left lateral wall of carapace; C. third left maxilliped, outer view; D. right (smaller) chela, ventral view; E. same, dorsal view; F. left (greater) chela, dorsal view; G. first right ambulatory leg; H. same, detail of propodus and dactylus; I. second right ambulatory leg, detail of spinulation of propodus and dactylus; K. third right ambulatory leg, detail of spinulation of propodus and dactylus.

the inner margin being concave over the proximal half in that species, whereas *P. thai* has only a short concavity on the much shorter carpus of both chelipeds. The cutting edge of the pollex of the larger chela is entire in *P. vermicola,* whereas there is a very prominent rounded tooth in *P. thai. Polyonyx senegalensis* can be distinguished by the convex frontal carpal lobe of the chelipeds, and the absence of prominent teeth on the cutting edges of the larger chela. *Polyonyx maccullochi* differs in the subovate carapace which is only slightly broader than long, the narrow front with a strong median lobe and the lack of a concavity on the proximal inner margin of the carpus of the chelipeds. The new species and the specimens of *P. sinensis* included in the same sample represent the first finding of members of the *P. sinensis* group in Thailand and increase the number of species reported for Thailand by Yang & Naiyanetr (1997) to 17.

Discussion

When Johnson (1958) divided the genus *Polyonyx* he characterized the *P. biunguiculatus* group as ". . . the central and largest group of the genus" and assigned *P. biunguiculatus* (Dana, 1852), *P. obesulus* Miers, 1884, *P. parvidens* Nobili, 1905, *P. triunguiculatus* Zehntner, 1894 and, with some doubts, *P. hendersoni* Southwell, 1909 to that group. Later, Haig (1979) included *P. parvidens* in the synonymy of *P. obesulus.* Actually, the differences discussed by Johnson (1958), and some other morphological features which can be seen in the description of *P. hendersoni* by Tirmizi et al. (1989), and additional ones which were revealed in a recent study of Hendersons material from the London Museum set this species apart from typical *Polyonyx. Polyonyx hendersoni* does not fit at all with any group of *Polyonyx* and will be assigned to a separate genus in a forthcoming paper, together with *P. splendidus* Sankolli, 1963 which was placed in the *P. biunguiculatus* group by Sankolli (1965).

As a result, the *P. biunguiculatus* group now comprises just three species that are restricted to the Indo-West Pacific. All of those three species are free living, and while they are sometimes associated with corals and sponges, they are never found in worm tubes, as are most of the remaining *Polyonyx* species.

By far the largest *Polyonyx* species group is the *P. sinensis* group. Johnson (1958) considered only the species from the Indo-West Pacific, and subsequent workers (e.g., Sankolli 1965, Ng & Sasekumar 1993, Hsueh & Huang 1998) never compared all species in a worldwide context. For the eastern Pacific, Haig (1960) recognized *P. nitidus* Lockington, 1878 and *P. quadriungulatus* Glassell, 1935. Haig (1960) considered the warm temperate outer Baja California population of *P. quadriungulatus* different from the Gulf of California *P. nitidus.* The range of *P. nitidus* was later extended southward to Panama (Haig 1962) and Isla Gorgona, Colombia (Werding & Haig 1982). The discovery of *P. quadriungulatus* by Kudenow & Haig (1974) in the Gulf of California led those authors to admit that both taxa might be conspecific. Comparison of the basic characters used by Haig (1960) to separate the two species (spinulation of the propodi and dactyli of the walking legs) indicate that these characters are not constant. Therefore, *P. quadriungulatus* is considered a junior synonym of *P. nitidus.* Additionally, a second species *P. confinis* Haig, 1960 is present in the eastern Pacific. This species has been found only once, and an association with a host species was not observed. The description of *P. bella* by Hsueh & Huang (1998) and a pair of paratypes from the USNM was compared with a series of *P. sinensis* from Thailand, found together with the type series of *P. thai,* new species, in the USNM. *Polyonyx bella* is not distinguishable from *P. sinensis,* and is therefore considered a junior synonym of that species.

Polyonyx cometes is here considered a member of the *P. sinensis* group since the characters revealed by Ng & Nakasone (1993) for the genus *Eulenaios* Ng & Nakasone, 1993, do not withstand a critical review on a worldwide level. The authors consider the setal pattern as perhaps the "most distinctive feature of the species". However, the setation is a character which exhibits a wide variation in the different species, and seems to be inadequate for the establishment of a separate genus. The same is true for the shape of the carapace and the form of the front and the carapace regions. The ridge of granules observed on the dactylus of the smaller cheliped is used by Ng & Nakasone (1993) as an additional character defining *Eulenaios*. But similar ridges are present in *P. senegalensis* and in both new species described herein. Further, the authors mention the membranous articulation between cheliped carpus, merus and propodus as "seeming more extensive than in other species". This obviously quantitative feature appears in a very similar degree in *P. gibbesi* where it was checked for comparison. Another argument is the size of the species which is described as "larger than any other known *Polyonyx* species". But the largest *P. cometes* dealt with is 11.2 × 8.2 mm. The holotype of *P. quadriungulatus* (= *P. nitidus*) measures 13.5 × 9.1 mm and that of *P. nitidus* 10 × 7 mm (Haig 1960), and Williams (1984) indicates for *P. gibbesi* a maximum breadth of 16 mm. For the australian *P. transversus,* Baker (1905) and Haig (1965) record a size of 11 × 8 mm. As a distinguishing larval property Ng & Nakasone (1993) mention the form of the telson of zoea I "being more proportionally elongate than in any other known species". Probably, the authors were not aware of the larval descriptions given by Shenoy & Sankolli (1973) for *P. loimicola* and those from Shepherd (1979) for *P. transversus.* As all other known *Polyonyx* larvae, the two species exhibit an elongate telson in Zoea I. Shepherd records a broads : length ration of 1 : 1.75 for the larvae of *P. transversus* and the respective value given by Ng & Nakasone for *P. cometes* is "about 1 : 1.8". Finally, the insertion of the telson setae of the first zoea as appears in Fig. 5, I in the paper of Ng & Nakasone (1993) shows apparently an incompletely developed telson as it is typically present in prezoeae. On the other hand, the *P. sinensis* group including *P. cometes* exhibit some key characters which make advisable to maintain the group as a systematic category. The common features are in the unique form of the chelipeds and the dactyls of the walking legs. An even more significant feature may be seen in the adaptation of living in tubes of annelid worms which is developed only in the members of the *P. sinensis* group.

Key to species of the *Polyonyx sinensis* group

1. Walking legs with merus unarmed ventrally 2
– At least third pair of walking legs armed with spines ventrally on merus 14
2. Frontal and lateral parts of carapace and chelipeds densely coated with setae which obscure the outline of the structure (Singapore) .... *Polyonyx cometes* Walker, 1887
– Setation of carapace and chelipeds different 3
3. Propodus of walking legs without spines except for terminal triplet 4
– Propodus of walking legs with at least one spine in addition to terminal triplet 6
4. Frontal lobe acute in frontal view, extending well beyond obtuse lateral angles (western Africa) .... *P. bouvieri* Saint-Joseph, 1900
– Frontal lobe scarcely produced, not extending beyond lateral angles 5
5. Carapace margins with thickly matted setae; meral lobe of chelipeds slightly produced (western coast of India) .... *P. loimicola* Sankolli, 1965
– Carapace margins not setose; meral lobe of chelipeds largely produced (Japan) .... *P. utinomii* Miyake, 1943
6. Outer surface of chelae with scattered

tubercles (western Africa) . . . . *P. quadratus* Chace, 1959

– Outer surface of chelae without tubercles 7

7\. Dorsal surface of carapace with scattered long setae; Propodus of walking legs with numerous (>60) minute spinules at lower margin (western Pacific) . . . . *P. haigae* McNeil, 1968 (Syn. *P. plumatus* Yang & Xu. 1994)

– Dorsal surface of carapace not setose; propodus of walking legs without numerous minute spinules (<20) at lower margin 8

8\. Inner margin of carpus of both chelipeds evenly convex 9

– Inner margin of at least mayor cheliped convcave proximally, convex distally 12

9\. Propodus of walking legs with more than 12 spinules on lower margin (Australia) . . . . *P. transversus* (Haswell, 1882)

– Propodus of walking legs with less than 10 spinules on lower margin 10

10\. Chelipeds slender, fingers of both chelae straight (Madagascar) . . . . *P. tulearis,* new species

– Chelipeds stout, fingers of larger chela bent outward distally 11

11\. Front narrow, forming a prominent acute median lobe; proximal inner angle of carpus of chelipeds softly rounded (Australia) *P. maccullochi* Haig, 1965

– Front broadly obtuse, median lobe blunt; proximal inner angle of carpus of chelipeds forming a rounded nearly rectangular angle (western Africa) . . . . *P. senegalensis* Chace, 1959

12\. Inner border of carpus of chelipeds tapering proximally forming a deep short concavity; carpus of larger cheliped about 1.5 times broader than long (Gulf of Thailand) . . . . *P. thai* new species

– Inner border of carpus of larger cheliped concave over the proximal half; carpus of larger cheliped about 2 times broader than long 13

13\. Pollex of larger cheliped with large blunt subproximal tooth on cutting edge (western Pacific) . . . . *P. sinensis* Stimpson, 1858 (Syn. *P. bella* Hsue & Huang, 1998)

– Pollex of larger cheliped entire on cutting edge (peninsular Malaysia) . . . . *P. vermicola* Ng & Sasekumar, 1993

14\. Proximal angle of carpal lobe of chelipeds obtuse (Indian Ocean) . . . . *P. pedalis* Nobili, 1905

– Proximal angle of carpal lobe of chelipeds strongly pronounced, subrectangular (American species) 15

15\. Longitudinal crest on the manus of the mayor cheliped (eastern Pacific—Nicaragua) . . . . *P. confinis* Haig, 1960

– Manus of chelipeds without longitudinal crest 16

16\. Propodus of walking legs without movable spinules additional to the posterodistal triplet, manus of minor cheliped markedly outcurved (western Atlantic) . . . . *P. gibbesi* Haig, 1956

– Propodus of walking legs with one or two movable spinules additional to the posterodistal triplet, manus of minor cheliped not markedly outcurved (eastern Pacific) . . *P. nitidus* Lockington, 1878

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Larval development of *Epialtus bituberculatus* H. Milne Edwards, 1834 (Crustacea: Decapoda: Brachyura: Majidae) with comments on majid larvae from the southwestern Atlantic

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Abstract.—The larval development of the spider crab *Epialtus bituberculatus* H. Milne Edwards which lives on rocky shores with algae such as *Sargassum* and *Hypneia,* is described. Larvae were obtained from ovigerous females collected in Ubatuba, State of São Paulo, Brazil. Rearing was carried out at 24 ± 1°C, with an average salinity of 35‰. Larval development consists of two zoeal stages and one megalopa. Zoeal development was completed in 9.5 days. Analysis indicated that zoeae of *E. bituberculatus* are very similar to those of *E. brasiliensis* Dana and *Acanthonyx scutiformis* (Dana). Differences noted between these species pertain to the setation of the carapace, maxillule and second maxilliped. The main morphological features useful for identification are presented together with a summary of features that characterize larvae of majid subfamilies in Brazil. A key for the identification of southwestern Atlantic majid zoeae to the family level is provided.

The understanding of evolutionary relationships amongst crabs is largely based on adult morphology. Unlike benthic adults, crustacean larvae are planktonic and therefore not subject to the same selection pressures as later stages. Therefore, larvae contain a much neglected source of characters that may help solve relationships obscured in adults. For example, larval characters have been shown to be useful as phylogenetic evidence to group subfamilies (Marques & Pohle 1998). However, while improvements in laboratory rearing techniques since the middle of this century have increased the knowledge on larvae, developmental stages are still unknown for the majority of brachyurans and decapods.

In the southwestern Atlantic, along the coast of Brazil, Uruguay and Argentina, brachyurans are represented by 329 species in 170 genera and 24 families (Boschi et al. 1992, Melo 1996, Pohle et al. 1999). According to Melo (1996), the Brazilian fauna is composed of 302 brachyuran species but larval development is known for less than one third of these taxa (Pohle et al. 1999).

The Majidae is one of the most diverse brachyuran families, with approximately 900 species worldwide. In the Southwest Atlantic this group is represented by 83 species among the subfamilies Epialtinae, Inachinae, Inachoidinae, Mithracinae, Pisinae and Tychinae (Melo 1996). Details on larval development is known for only 19 of these species: *Libinia spinosa* H. Milne Edwards, 1834 (Boschi & Scelzo 1968, Clark et al. 1998); *Libidoclaea granaria* H. Milne Edwards & Lucas, 1843 (Fagetti 1969); *Taliepus dentatus* (H. Milne Edwards, 1834) (Fagetti & Campodonico 1971); *Anasimus latus* Rathbun, 1894 (Sandifer & Van Engel 1972); *Eurypodius latreillei* Guérin-Méneville, 1828 (Campodonico & Guzmán 1972); *Stenorhynchus seticornis* (Herbst, 1788) (Yang 1976); *Mithraculus forceps* (A. Milne-Edwards, 1875) (Wilson et al. 1979 as *Mithrax* (*Mithraculus*) *forceps*); *Mithraculus coryphe* (Herbst, 1801) (Scotto & Gore 1980 as *Mithrax* (*Mithraculus*) *coryphe*); *Mithrax verrucosus* H. Milne Edwards, 1832 (Bolaños & Scelzo 1981); *Microphrys bicornutus* (Latreille, 1825) (Gore et al. 1982); *Mithrax hispidus* (Herbst, 1790) (Goy et al. 1981 as *M. pleuracanthus* Stimpson, 1871 and cf. Fransozo & Hebling, 1982); *Mithrax caribbaeus* Rathbun, 1920 (Bolaños et al. 1990); *Libinia ferreirae* Brito Capello, 1871 (Bakker et al. 1990); *Epialtus brasiliensis* Dana, 1852 (Negreiros-Fransozo & Fransozo 1991); *Acanthonyx scutiformis* (Dana, 1851) (Hiyodo et al. 1994 as *A. petiverii* H. Milne Edwards, 1834); *Pitho lherminieri* (Schramm, 1867) (Bolaños et al. 1996); and *Pyromaia tuberculata* (Lockington, 1876) (Fransozo & Negreiros-Fransozo 1997).

According to Melo (1996), the species subject of this study *Epialtus bituberculatus* H. Milne Edwards 1834, is found on the coasts of Florida, Gulf of Mexico, Antilles, Colombia, Venezuela, and in Brazil from Ceará to São Paulo States. In the present study all larval stages of *E. bituberculatus*, reared under laboratory conditions, are described and compared with other majid larvae from the southwestern Atlantic.

Material and Methods

Three ovigerous females of *E. bituberculatus* were hand-collected intertidally along rocky shores of Ubatuba (23°28′00″S, 45°03′33″W), on the northern Coast of São Paulo State, where they are associated with algae of the genera *Sargassum* and *Hypneia.* The crabs were transported from the collection sites to the laboratory using insulated 20 liters containers with one liter of sea water.

In the laboratory, ovigerous females were maintained at constant temperature (24 ± 1°C) in a 10 liters aquarium filled with sea water (35‰), and provided with continuous aeration until larvae hatched. Crabs were fed with a continuous supply of living algae, supplemented by fresh fish muscle tissue offered twice a week. Ovigerous females were inspected daily for hatched larvae or pre-zoeae. The larvae were reared following the techniques described by Negreiros-Fransozo & Fransozo (1991). Two hundred freshly hatched zoeae from a single female were transferred to an acrylic vessel with 50 ml filtered and aerated sea water at 35‰ and 24 ± 1°C, one larva per container. A light regime of 12 hours dark/light was maintained. Seawater was changed daily after examining the condition of larvae, followed by feeding with about 20 newly hatched *Artemia* nauplii per larva. Larvae were preserved in a 1:1 mixture of 96% ethyl alcohol and glycerin, whereas exuviae were kept in pure glycerin. Illustrations by light microscopy and the aid of *camera lucida* were made from live and preserved larvae, and from exuviae. For morphological descriptions, the setation is given from proximal to distal segments. Ten specimens were examined for the description and measurements of each larval stage. The descriptive terminology of Bookhout & Costlow (1974), and Pohle & Telford (1981) was used here. Specimens of each larval stage are deposited in the collection of Departamento de Zoologia, Instituto de Biociências, UNESP, Botucatu, SP, Brazil under #NEBECC 000026.

Results

The larval development of *E. bituberculatus* consists of two zoeal stages followed by the megalopa. The zoeal phase lasted 9.5 ± 0.3 days. The duration of the complete larval development was not determined because none of the megalopae moulted to the first crab instar.

Description of *E. bituberculatus* larvae
Zoea I (Fig. 1I; 2 a–g; 4I)

Size.—carapace length: 0.61 ± 0.02 mm

Carapace (Fig. 1I).—With rostral and dorsal spine, but lacking lateral spines. With 2 postorbital plumose setae. Posterolateral margin bearing 7 plumose setae. Eyes sessile.

Abdomen (Fig. 4I).—Five cylindrical somites, somite 6 fused to telson. Only somite 2 has pair of knobs laterally. First somite with 3 simple setae dorsally. Posterodorsal margin of somites 2–5 with 2 small setae.

Telson (Fig. 4I).—Bifurcated, each furcal shaft covered with spinules and bearing lateral spine. Furcal arch bears 3 pairs of plumodenticulate processes.

Antennule (Fig. 2a).—Conical, unsegmented, with 3 terminal aesthetascs and 1 simple seta.

Antenna (Fig. 2b).—Protopod an elongate tapering process with rows of spinules distally; exopod shorter than protopod, with 2 short simple setae apically; endopod as a bud medially on protopod.

Mandible (Fig. 2c).—With asymmetric small teeth on incisor and molar processes. No palp.

Maxillule (Fig. 2d).—Coxal endite with 6 (7) setae. Basial endites with 8 setal processes. Two-segmented endopod bearing 2 subterminal and 4 terminal plumodenticulate setae on distal segment.

Maxilla (Fig. 2e).—Coxal endite unilobed, 4 plumose subterminal setae and 2 plumose terminal setae. Basial endite with 4 and 5 (6) setae on proximal and distal lobe, respectively. Unsegmented endopod bears 4 terminal and 2 subterminal setae. Scaphognathite with 12 marginal plumose setae and narrow posterior apical process.

First maxilliped (Fig. 2f).—Coxopodite naked. Basipodite bearing 2, 2, 3, 3 posterior marginal setae. Endopod 5-segmented, with 3, 2, 1, 2, 5 (6) setae. Exopod 2-segmented, with 4 terminal natatory setae.

Second maxilliped (Fig. 2g).—Coxopodite naked. Basipodite bearing 2 posterior marginal setae. Endopod 3-segmented, with 0, 1 and 4 setae, respectively. Exopod 2-segmented, with 4 natatory setae on distal segment.

Third maxilliped and developing pereiopods.—Present as buds under the carapace.

Zoea II (Figs. 1II; 3 a–g; 4II)

Size.—carapace length: 0.73 ± 0.04 mm

Carapace.—With 9 plumose setae on postero-lateral margin. Eyes stalked (Fig. 1II). Sixth abdominal somite (Fig. 4II) separated from telson. Somites 2–5 bearing 2 simple setae on posterior margin and somite 6 without setae. Knobs on somite 2 reduced. Somites 2–5 with biramous pleopod buds (Fig. 1II).

Antennule (Fig. 3a).—With 5 terminal aesthetascs and 1 simple seta.

Antenna (Fig. 3b).—With endopod enlarged.

Mandible (Fig. 3c).—With anterodorsal palp bud.

Maxillule (Fig. 3d).—Coxal endite with 8 plumose and 2 simple setae. Basial endite with 11 setal processes. Endopod with 1 plumose seta on proximal and 2 + 4 on the distal segment.

Maxilla (Fig. 3e).—Coxal endite unilobed with 2 plumose subterminal and 4 plumose terminal setae. Basial endite with 5 setae on each lobe. Endopod with 3 (4) terminal and 2 subterminal setae. With 20 (21) + 3 marginal plumose setae on scaphognathite.

First maxilliped (Fig. 3f).—Basipod with 2, 2, 3, 3 plumose setae. Exopod with 6 natatory setae.

Second maxilliped (Fig. 3g).—Exopod with 6 natatory setae.

Third maxilliped and *pereiopods* present as rudimentary buds.

Megalopa (Figs. 4M; 5; 6 a–h; 7 a–j)

Size.—Carapace length: 1.17 ± 0.04 mm; carapace width: 0.72 ± 0.04 mm.

Carapace.—Smooth, longer than wide, sub-rectangular posteriorly to orbits (Fig. 5). Short rostrum deflected ventrally. Covered by few setae as shown.

Abdomen. (Fig. 4M).—Shorter than carapace and covered by few setae.

Telson. Smooth, with posterior convex margin bearing 4 setae.

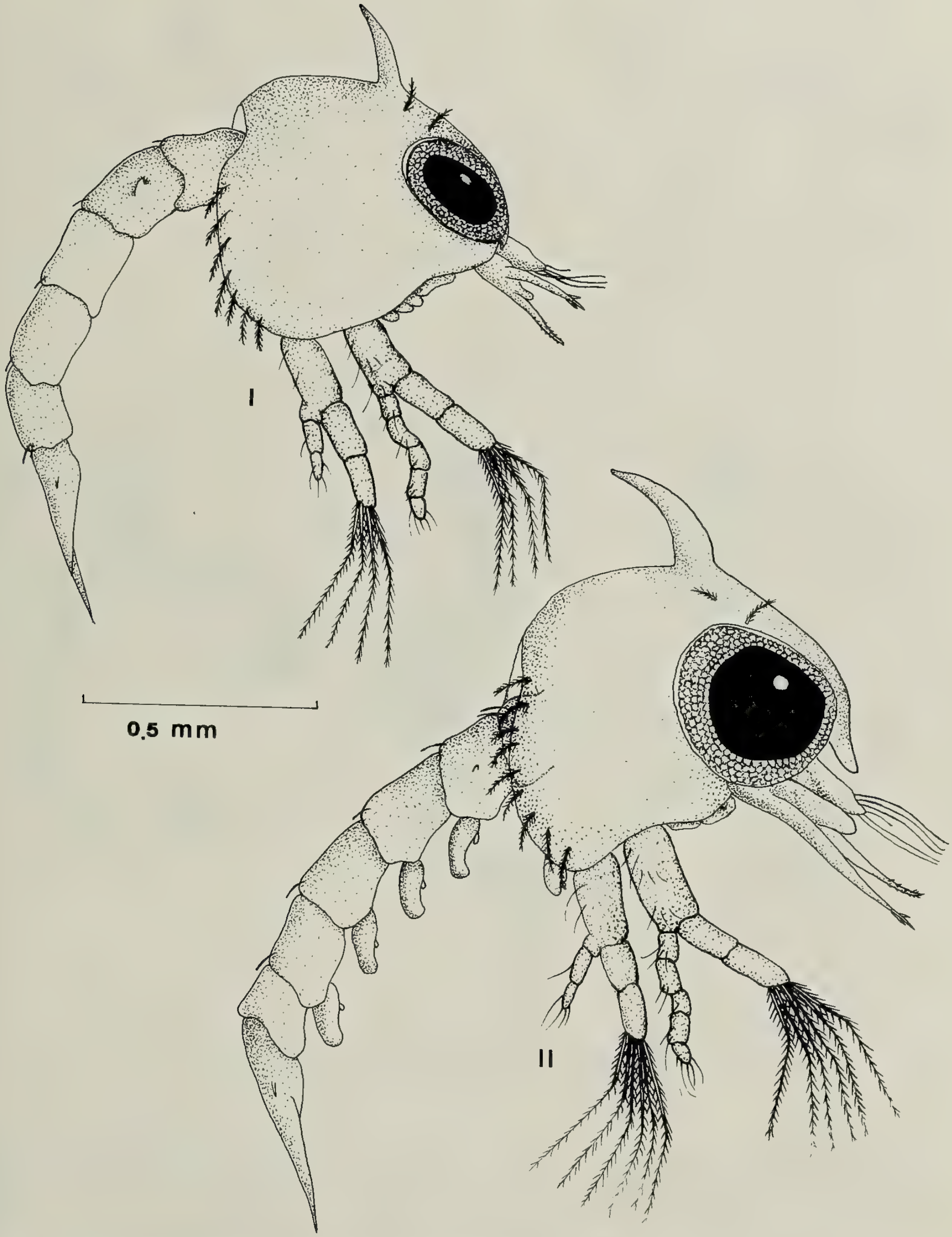

Fig. 1. *Epialtus bituberculatus* H. Milne Edwards, 1834. Lateral view of first (I) and second (II) zoea.

Antennule (Fig. 6a).—Peduncle 3-segmented. One-segmented endopod with 3 apical setae and 1 subterminal simple seta. Exopod 4-segmented, bearing 0, 6, 6, 2 aesthetascs and 1 simple seta on segment 2.

Antenna (Fig. 6b).—Peduncle 3-segmented, with 0, 1 and 1 simple setae. Flagellum 5-segmented, bearing 2 simple setae on each distal segment.

Mandible (Fig. 6c).—Flat, with dentate

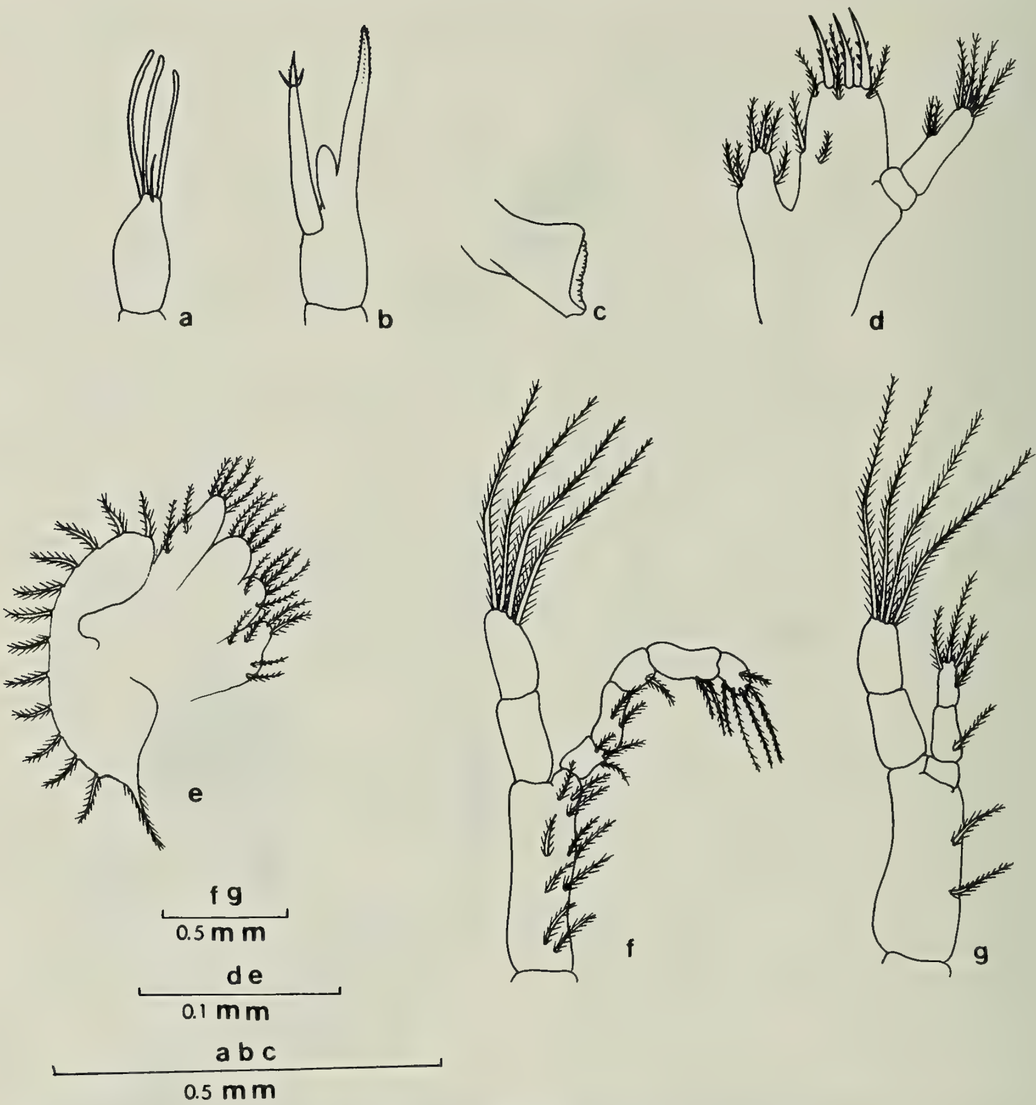

Fig. 2. *Epialtus bituberculatus* H. Milne Edwards, 1834. Appendages of the first zoea: a, antennule; b, antenna; c, mandible; d, maxillule; e, maxilla; f, first maxilliped; g, second maxilliped.

inner margin. Palp 2-segmented, with 6 simple setae on terminal segment.

Maxillule (Fig. 6d).—Coxal endite with 7 and basial endite with 11 setae. Protopod with 1 seta. Endopod unsegmented and naked.

Maxilla (Fig. 6e).—Coxal endite unilobed with 6 setae. Basial endite unilobed bearing 10 setae. Endopod naked. Scaphognathite with 30 marginal plumose setae and 2 small plumose setae on the blade surface.

First maxilliped (Fig. 6f).—Coxal endite has about 3 plumose setae and basial endite 6 setae; both endites have additional setae. Two-segmented endopodite distally with 6 setae. Exopod 2-segmented, with 1 simple seta on proximal and 2 plumose setae on terminal segment. Epipod with 5 long setae.

Second maxilliped (Fig. 6g).—Endopod 4-segmented with 0, 1, 3 and 5 setae. Exopod 2–segmented with 0 and 4 plumose setae. Epipod absent.

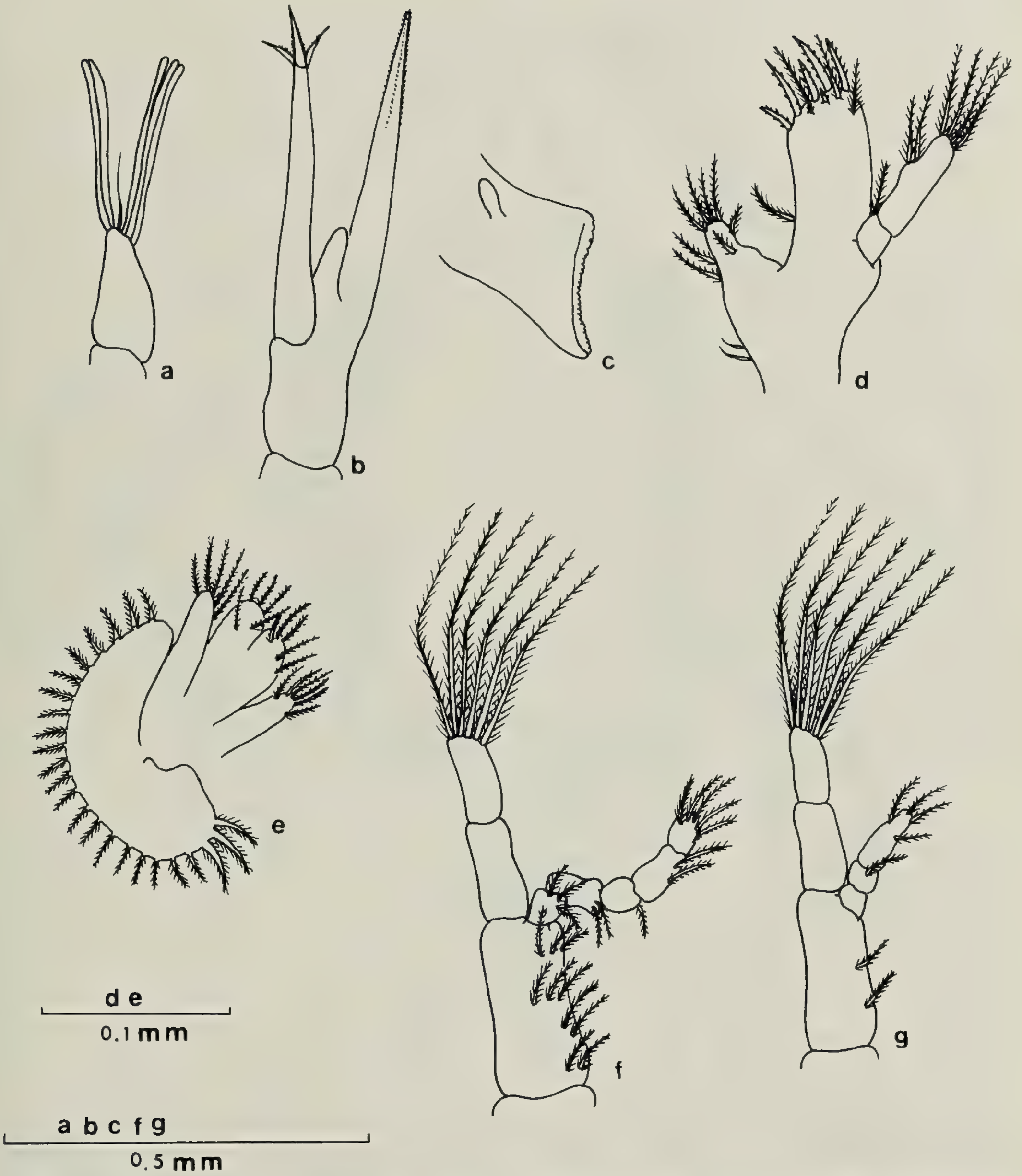

Fig. 3. *Epialtus bituberculatus* H. Milne Edwards, 1834. Appendages of the second zoea: a, antennule; b, antenna; c, mandible; d, maxillule; e, maxilla; f, first maxilliped; g, second maxilliped.

Third maxilliped (Fig. 6h).—Endopod 5-segmented, bearing several simple and plumose setae on all segments. Ischiopodite with 5 spines. Exopod 2-segmented with 1, 2 setae. Epipod with 5 plumose setae and one simple seta.

Pereiopods (Fig. 7a–e).—Chelipeds symmetrical. Second pair of pereiopods with spine on basi-ischium. The second, third, fourth and fifth pairs of pereiopods carry 5 spine-like process on the inferior border of the dactylus. Other segments are covered by setae as shown.

Pleopods (Fig. 7f–i).—Fully developed

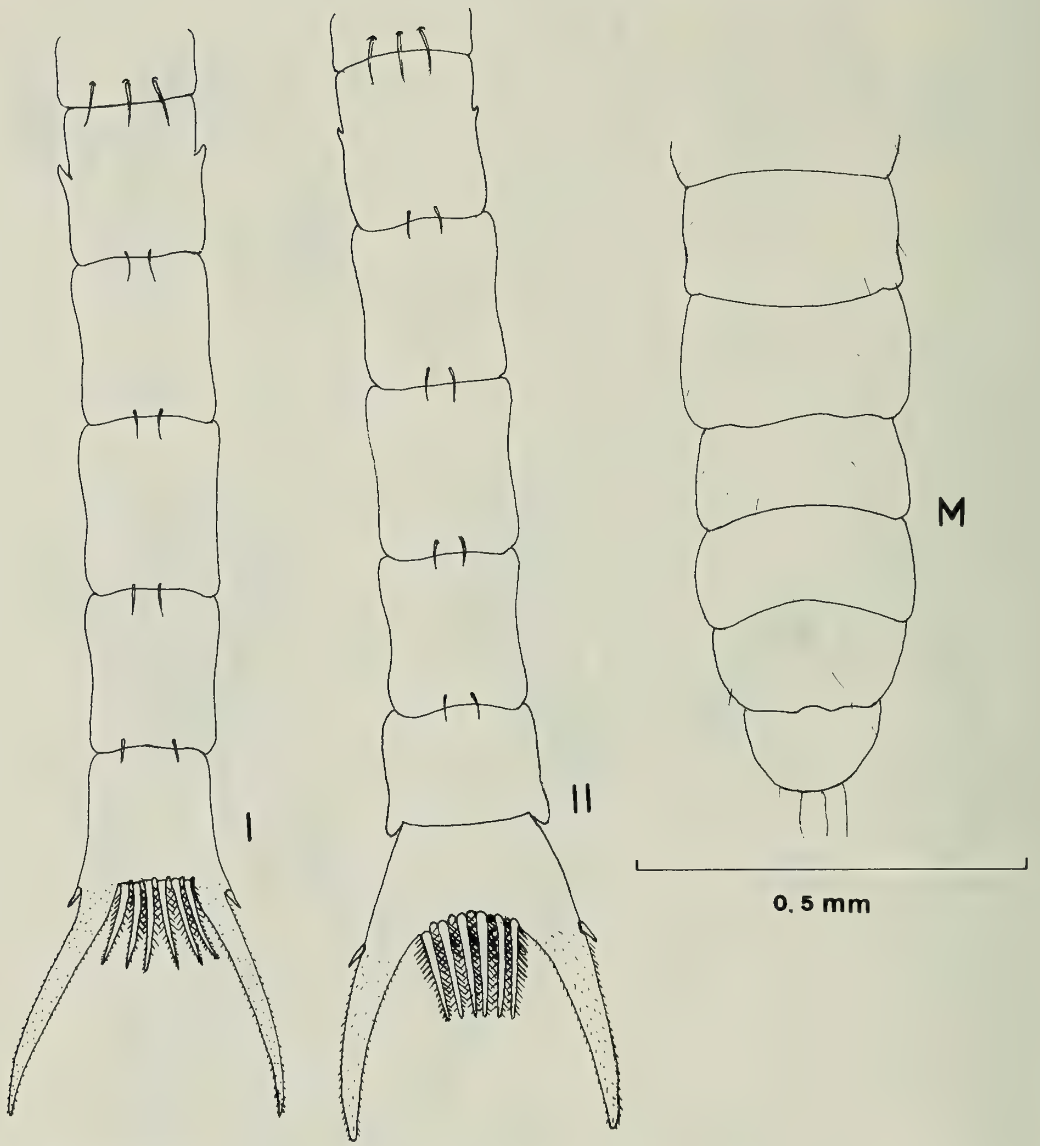

Fig. 4. *Epialtus bituberculatus* H. Milne Edwards, 1834. Dorsal view of telson: first zoea (I); second zoea (II), and megalopa (M).

biramous setose pleopods on abdominal somites 2–5. Exopods of somites 2–5 with 10, 10, 10, 8 plumose natatory setae, respectively. Endopods with 2 hooks each.

Uropod (Fig. 7j).—Uniramous and 2-segmented, with 4 terminal plumose setae.

Discussion

The larval development in the Majidae is distinct from other brachyuran families in that it consists of only two zoeal stages and one megalopa. According to Gore (1985), this brachyuran family is characterized by advanced development, in which the young hatch as zoeae, but in a state more developed than in other families. This is characterized by fewer stages as well as shorter duration of stages.

Among Majidae of the Southwest Atlantic, the time required to reach the megalopa

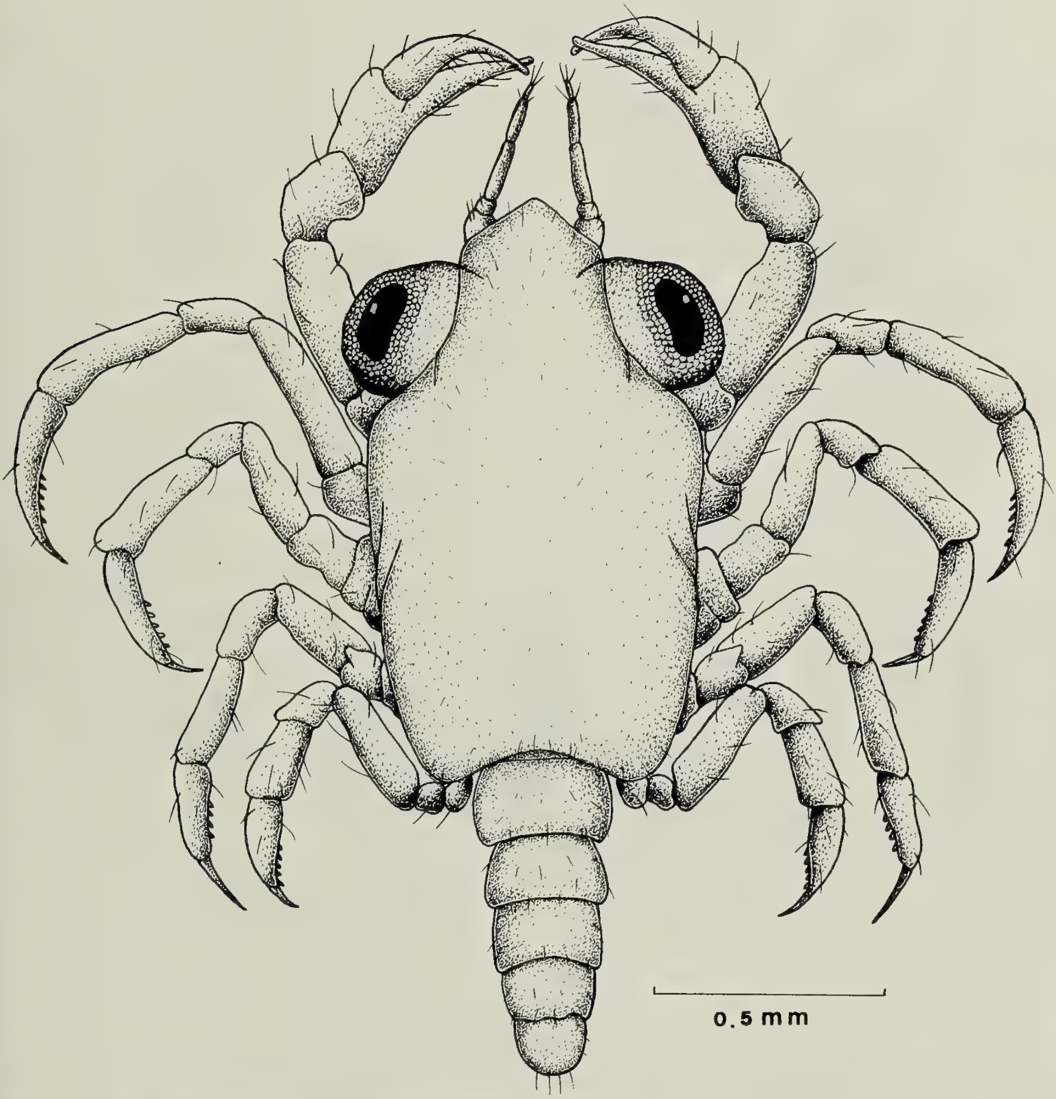

Fig. 5. *Epialtus bituberculatus* H. Milne Edwards, 1834. Dorsal view of megalopa.

is relatively short compared to other brachyuran species (Fransozo & Hebling 1982). The shortest larval development of majids might represent a specialization that may be linked to the existing large species diversity of this group.

Unlike other brachyurans, such as Xanthidae that shows great variation in antennal morphology; Majidae larvae from the southwestern Atlantic coast are morphologically conservative, for example, in antenna and telson.

Rice (1980) identified the diagnostic morphological features for majid zoeae as: telson with well developed furcae that are often covered with minute spinules, maxillary scaphognathite with at least nine marginal setae, and well developed pleopods on the second zoeal stage. Negreiros-Fransozo & Fransozo (1991) summarized the main features that can be used for identification at the subfamily level for species occurring along the south and southeastern Brazilian coast.

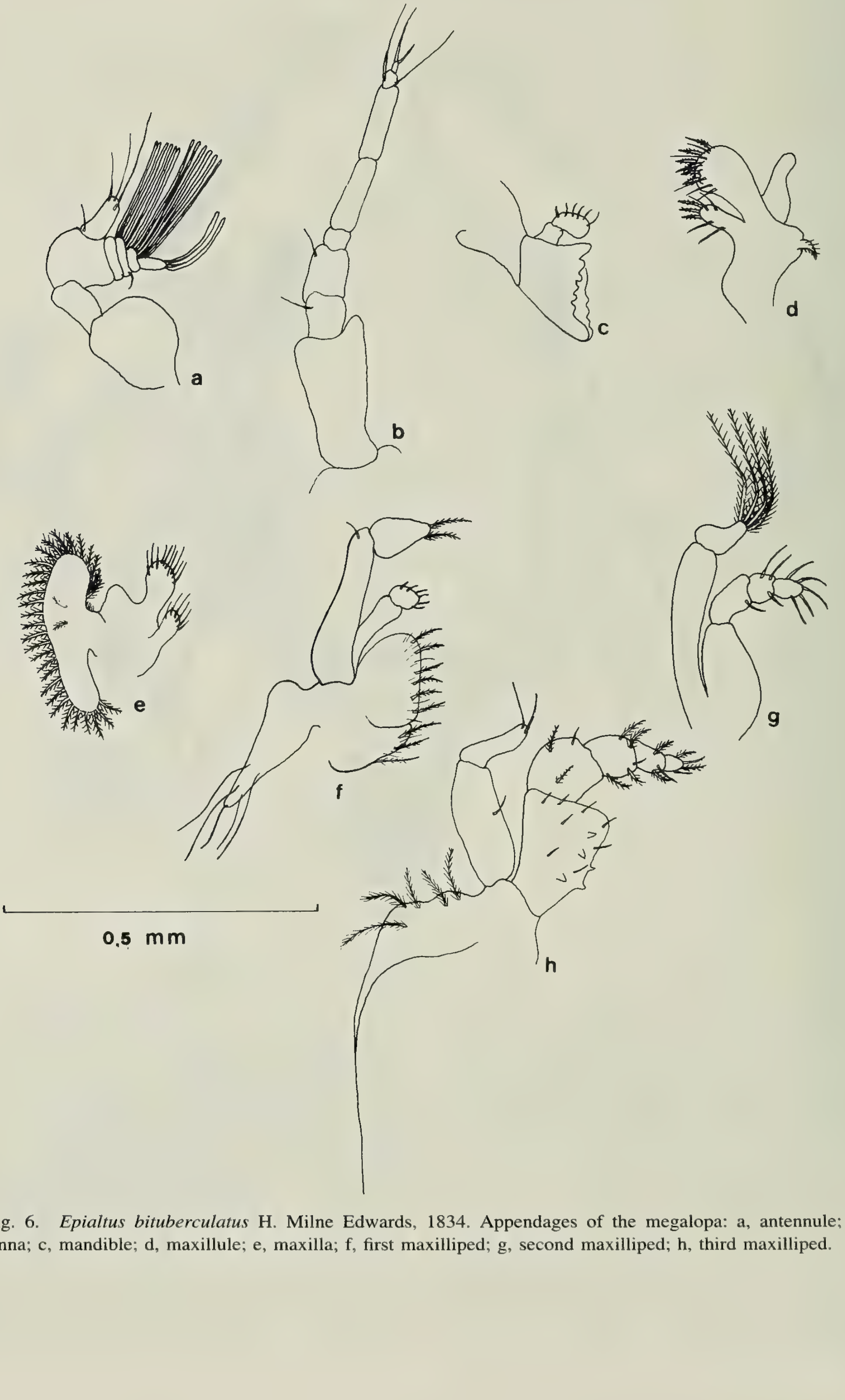

Fig. 6. *Epialtus bituberculatus* H. Milne Edwards, 1834. Appendages of the megalopa: a, antennule; b, antenna; c, mandible; d, maxillule; e, maxilla; f, first maxilliped; g, second maxilliped; h, third maxilliped.

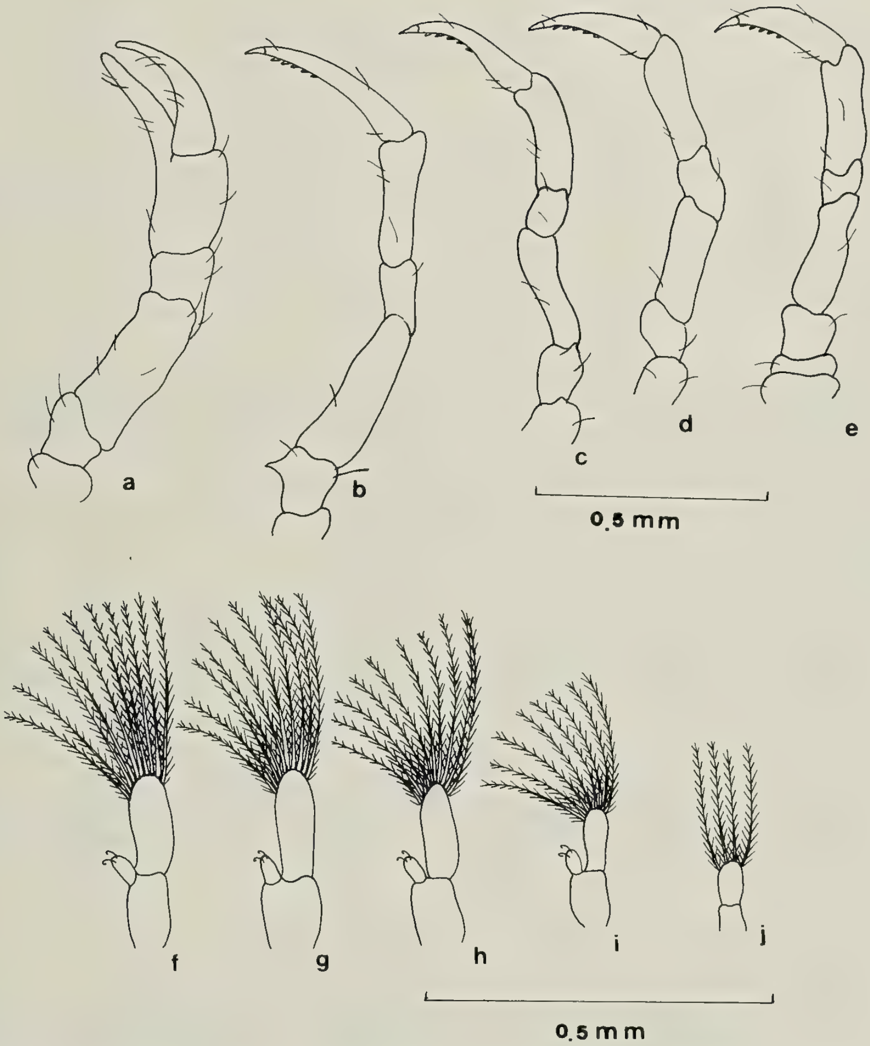

Fig. 7. *Epialtus bituberculatus* H. Milne Edwards, 1834. Appendages of the megalopa: a, cheliped; b, c, d, e, second to fifth pereiopods; f, g, h, i, second to fifth pleopods and j, uropod.

Tables 1 to 3 summarize the main features that characterize the larvae of the Majidae subfamilies from the southwestern Atlantic, and the following key will aid in their identification.

Subfamily level identification key for zoea I and II of Majidae occuring along the southwestern Atlantic coast

1. Carapace with forehead protuberance between the dorsal and rostral spines .... Inachinae
– Carapace without forehead protuberance 2
2. Carapace with only dorsal spine .... Inachoidinae
– Carapace with rostral and dorsal spine 3
3. Abdominal somites with postero-lateral process 4
– Abdominal somites without postero-lateral process .... Epialtinae
4. Maxillary scaphognathite with 12 or 13 plumose setae in zoea I, and 23 to 26 setae in zoea II 5

Table 1.—Comparison of the first zoeal stage of Majidae from southwestern Atlantic region.

		Characteristics							
Subfamilies	Species	Spines and setae on the carapace	Knobs on lateral side of the abdomen	Postero-lateral process on abdomen	Maxillule endopod setation	Scaphognathite (marginal plumose setae + apical process)	Maxilla endopod setation	Setae on basis of the 1st maxilliped	Setae on the endopod of 2nd maxilliped
Pisinae	*Libinia spinosa*	1 rostral 1 dorsal + 7 setae	2nd somite	on 3rd to 5th somites	1+5	10+1	4	2, 2, 3, 3	0, 1, 4
	Libidoclaea granaria	1 rostral 1 dorsal + 5 setae	2nd somite	on 3rd to 5th somites	1+5	14+1	6	2, 2, 3, 3	0, 1, 5
	Libinia ferreirae	1 rostral 1 dorsal + 6(7) setae	2nd somite	on 3rd to 5th somites	1+5	10+1	5	2, 2, 3, 3	0, 1, 5
Mithracinae	*Mithraculus forceps*	1 rostral 1 dorsal + 6 setae	2nd somite	on 3rd to 5th somites	1+6	13	5	2, 2, 3, 3	0, 1, 5
	Mithraculus coryphe	1 rostral 1 dorsal + 6 setae	2nd somite	on 3rd to 5th somites	1+6	12+1	5	2, 2, 3, 3	0, 1, 5
	Mithrax verrucosus	1 rostral 1 dorsal + 3 setae	2nd somite	on 3rd to 5th somites	—	12+1	—	—	0, 1, 5
	Mithrax caribbeaus	1 rostral 1 dorsal + 7 setae	2nd somite	on 3rd to 5th somites	1+6	12+1	5	2, 2, 3, 3	0, 1, 5
	Mithrax hispidus	1 rostral 1 dorsal + 6 setae	2nd somite	on 3rd to 5th somites	1+6	12+1	5	2, 2, 3, 3	0, 1, 5
	Microphrys bicornutus	1 rostral 1 dorsal + 6 setae	2nd somite	on 3rd to 5th somites	1+6	12 (13)+1	5	2, 2, 3, 3	0, 1, 5
Inachinae	*Eurypodius latreillei*	1 rostral 1 dorsal 2 laterals + 4 setae	2nd and 3rd somites	on 3rd and 4th somites	1+6	10	6	2, 2, 3, 3	0, 1, 5

Table 1.—Continued.

Subfamilies	Species	Characteristics							
		Spines and setae on the carapace	Knobs on lateral side of the abdomen	Postero-lateral process on abdomen	Maxillule endopod setation	Scaphognathite (marginal plumose setae + apical process)	Maxilla endopod setation	Setae on basis of the 1st maxilliped	Setae on the endopod of 2nd maxilliped
	Stenorhynchus seticornis	1 dorsal 1 anterolateral projections + 3(4) setae	2nd and 3rd somites	on 3rd to 5th somites	4	10+1	5	2, 2, 2, 3	0, 1, 5
Inachoidinae	*Anasimus latus*	1 dorsal 1 pair of ocular and several setae	2nd somite	on 3rd to 5th somites	3	10+1	5	2, 2, 2, 3	0, 1, 4
	Pyromaia tuberculata	1 dorsal	2nd somite	absent	4	10+1	3	2, 2, 2, 2	0, 1, 4
Tychinae	*Pitho llerminieri*	1 rostral 1 dorsal + 7 setae + 2 post-orbital	2nd somite	on 3rd to 5th somites	1+5	13+1	5	2, 2, 3, 3	0, 1, 5
Epialtinae	*Taliepus dentatus*	1 rostral 1 dorsal + 4 setae	2nd somite	absent	1+5	10+1	4	2, 2, 2, 3	0, 1, 4
	Epialtus brasiliensis	1 rostral 1 dorsal + 4(5) setae + 2 post-orbital	2nd somite	absent	6	12+1	5	2, 2, 2, 3	0, 1, 4
	Acanthonyx scutiformis	1 rostral 1 dorsal smooth	2nd somite	absent	4	11+1	5	2, 2, 3, 3	0, 1, 4
	Epialtus bituberculatus	1 rostral 1 dorsal + 7 setae + 2 post-orbital	2nd somite	absent	6	12+1	6	2, 2, 3, 3	0, 1, 4

L. spinosa, L. granaria, L. ferreirae, M. forceps, M. coryphe, M. verrucosus, M. caribbeaus, M. hispidus, M. bicornutus, E. latreillei, S. seticornis, A. latus, P. tuberculata, P. llerminieri, T. dentatus, E. brasiliensis, A. scutiformis respectively described by Clark et al. (1998), Fagetti (1969), Bakker et al. (1990), Wilson et al. (1979), Scotto & Gore (1980), Bolaños & Scelzo (1981), Bolaños et al. (1990), Goy et al. (1981) and Fransozo & Hebling (1982), Gore et al. (1982), Campodónico & Guzmán (1972), Yang (1976), Sandifer & van Engel (1972), Fransozo & Negreiros-Fransozo (1997), Bolaños et al. (1996), Fagetti & Campodónico (1971), Negreiros-Fransozo & Fransozo (1991), Hiyodo et al. (1994).

Table 2.—Comparison of the second zoeal stage of Majidae from southwestern Atlantic region.

		Characteristics							
Subfamilies	Species	Spines and setae on the carapace	Knobs on lateral side of the abdomen	Postero-lateral process on abdomen	Maxillule endopod setation	Scaphognathite (marginal + apical)	Maxilla endopod setation	Setae on basis of the 1st maxilliped	Setae on the endopod of 2nd maxilliped
Pisinae	*Libinia spinosa*	1 rostral 1 dorsal + 8 setae	2nd somite	on 3rd to 5th somites	1+5	20	5	2, 2, 3, 3	0, 1, 4
	Libidoclaea granaria	1 rostral 1 dorsal + 7 setae	2nd somite	on 3rd to 5th somites	1+5	29	5	2, 2, 3, 3	0, 1, 5
	Libinia ferreirae	1 rostral 1 dorsal + 8 setae	2nd somite	on 3rd to 5th somites	1+5	20	5	2, 2, 3, 3	0, 1, 5
Mithracinae	*Mithraculus forceps*	1 rostral 1 dorsal + 7 setae	2nd somite	on 3rd to 5th somites	1+6	24	5	2, 2, 3, 3	0, 1, 5
	Mithraculus coryphe	1 rostral 1 dorsal + 6 setae	2nd somite	on 3rd to 5th somites	1+6	25	5	2, 2, 3, 3	0, 1, 5
	Mithrax verrucosus	1 rostral 1 dorsal + 6 setae	—	on 3rd to 5th somites	—	26	—	—	0, 1, 5
	Mithrax caribbeaus	1 rostral 1 dorsal + 8 setae	2nd somite	on 3rd to 5th somites	1+6	24	5	2, 2, 3, 3	0, 1, 5
	Mithrax hispidus	1 rostral 1 dorsal + 8 setae	2nd somite	on 3rd to 5th somites	1+6	24 (25)	5	2, 2, 3, 3	0, 1, 4
	Microphrys bicornutus	1 rostral 1 dorsal + 10 setae	2nd somite	on 3rd to 5th somites	1+6	23 (25)	5	2, 2, 3, 3	0, 1, 5
Inachinae	*Europodius latreillei*	forehead protuberances 1 rostral 1 dorsal 2 laterals + 4 setae	2nd and 3rd somites	on 3rd and 4th somites	1+6	20 (21) plumose setae	6	2, 2, 3, 3	0, 1, 5
	Stenorhynchus seticornis	forehead protuberances 1 dorsal	2nd and 3rd somites	on 3rd and 5th somites	4	19 (20) plumose setae	4(5)	2, 2, 2, 3	0, 1, 4
Inachoidinae	*Anasimus latus*	1 dorsal 1 pair of ocular	2nd somite	on 3rd and 5th somites	3	20 plumose setae	5	2, 2, 2, 3	0, 1, 4
	Pyromaia tuberculata	1 dorsal 3 setae	2nd somite	absent	4	20 plumose setae	4	2, 2, 2, 2	0, 1, 4

Table 2.—Continued.

		Characteristics							
Subfamilies	Species	Spines and setae on the carapace	Knobs on lateral side of the abdomen	Postero-lateral process on abdomen	Maxillule endopod setation	Scaphognathite (marginal + apical)	Maxilla endopod setation	Setae on basis of the 1st maxilliped	Setae on the endopod of 2nd maxilliped
Tychinae	*Pitho llerminieri*	1 rostral 1 dorsal 7 marginal setae + 4 setae	2nd somite	on 3rd and 5th somites	1+5	26 plumose setae	5	2, 2, 3, 3	1, 1, 5
Epialtinae	*Taliepus dentatus*	1 rostral 1 dorsal 4 setae	2nd and 3rd somites	absent	1+5	20 plumose setae	4	2, 2, 2, 3	0, 1, 4
	Epialtus brasiliensis	1 rostral 1 dorsal 7 setae + post-orbital	2nd somite	absent	6	19+1 plumose setae	6	2, 2, 2, 3	0, 1, 4
	Acanthonyx scutiformis	1 rostral 1 dorsal smooth	2nd somite	absent	4	22 plumose setae	5	2, 2, 3, 3	0, 1, 4
	Epialtus bituberculatus	1 rostral 1 dorsal 9 marginal setae + 2 post-orbital	2nd somite	absent	1, 6	20 (21) plumose setae	5 (6)	2, 2, 3, 3	0, 1, 4

L. spinosa, L. granaria, L. ferreirae, M. forceps, M. coryphe, M. verrucosus, M. caribbeaus, M. hispidus, M. bicornutus, E. latreillei, S. seticornis, A. latus, P. tuberculata, P. llerminieri, T. dentatus, E. brasiliensis, A. scutiformis respectively described by Clark et al. (1998), Fagetti (1969), Bakker et al. (1990), Wilson et al. (1979), Scotto & Gore (1980), Bolaños & Scelzo (1981), Bolaños et al. (1990), Goy et al. (1981) and Fransozo & Hebling (1982), Gore et al. (1982), Campodónico & Guzmán (1972), Yang (1976), Sandifer & van Engel (1972), Fransozo & Negreiros-Fransozo (1997), Bolaños et al. (1996), Fagetti & Campodónico (1971), Negreiros-Fransozo & Fransozo (1991), Hiyodo et al. (1994).

Table 3.—Comparison of the megalopa stage of Majidae from southwestern Atlantic region.

Subfamilies	Species	Characteristics				
		Expopod of antennule	Palp of mandible	Scaphognathite setae (marginal + superficial)	Setae on epipod of 3rd maxilliped	Uropod setae
Pisinae	*Libinia spinosa*	4-segmented 14 aesthetascs + 1 seta	3-segmented 0, 0, 5 setae	36	8	5
	Libidoclaea granaria	4-segmented 13 aesthetascs	3-segmented 0, 0, 5 setae	51	14	9
	Libinia ferreirae	3-segmented 10 setae	3-segmented 0, 0, 5 setae	38	6	5
Mithracinae	*Mithraculus forceps*	2-segmented 12 aesthetascs + 1 seta	unsegmented 5 setae	26 (30)	5	5
	Mithraculus coryphe	2-segmented 14 aesthetascs	2-segmented 0, 5 setae	32	6	4
	Mithrax verrucosus	2-segmented 13 aesthetascs	unsegmented 5 setae	31	4	5
	Mithrax caribbeaus	2-segmented 15 aesthetascs	unsegmented 5 setae	32	5	5
	Mithrax hispidus	3-segmented 12 aesthetascs + 1 seta	unsegmented 5 setae	28 (31)	6	5
	Microphrys bicornutus	2-segmented 13 aesthetascs	2-segmented 0, 5 (6) setae	28 (39)	5	4 (5)
Inachinae	*Europodius latreillei*	5-segmented 9 aesthetascs + 3 setae	—	39 (40)	12	5
	Stenorhynchus seticornis	3-segmented 13 (14) aesthetascs	2-segmented 0, 6 setae	32	6	2
Inachoidinae	*Anasimus latus*	3-segmented 10 aesthetascs + 2 setae	3-segmented 0, 0, 6 setae	28 to 30	3	4
	Pyromaia tuberculata	4-segmented 9 aesthetascs	2-segmented 0, 4 setae	32 (35) + 3	4	2

Table 3.—Continued.

		Characteristics				
Subfamilies	Species	Expopod of antennule	Palp of mandible	Scaphognathite setae (marginal + superficial)	Setae on epipod of 3rd maxilliped	Uropod setae
Tychinae	*Pitho llerminieri*	2-segmented 9 aesthetascs + 2 setae	2-segmented 0, 5 setae	31 (32) + 2	6	5
Epialtinae	*Taliepus dentatus*	4-segmented 15 aesthetascs + 4 setae	2-segmented 0, 5 setae	40	9	5
	Epialtus brasiliensis	4-segmented 13 aesthetascs + 3 setae	3-segmented 0, 0, 5 setae	38	10	5
	Acanthonyx scutiformis	4-segmented 12 aesthetascs	2-segmented 0, 5 setae	42	3	5
	Epialtus bituberculatus	4-segmented 14 aesthetascs + 1 simple seta	2-segmented 0, 6 setae	30	6	4

L. spinosa, L. granaria, L. ferreirae, M. forceps, M. coryphe, M. verrucosus, M. caribbeaus, M. hispidus, M. bicornutus, E. latreillei, S. seticornis, A. latus, P. tuberculata, P. llerminieri, T. dentatus, E. brasiliensis, A. scutiformis respectively described by Clark et al. (1998), Fagetti (1969), Bakker et al. (1990), Wilson et al. (1979), Scotto & Gore (1980), Bolaños & Scelzo (1981), Bolaños et al. (1990), Goy et al. (1981) and Fransozo & Hebling (1982), Gore et al. (1982), Campodónico & Guzmán (1972), Yang (1976), Sandifer & van Engel (1972), Fransozo & Negreiros-Fransozo (1997), Bolaños et al. (1996), Fagetti & Campodónico (1971), Negreiros-Fransozo & Fransozo (1991), Hiyodo et al. (1994).

- Maxillary scaphognathite with 10 or 14 plumose setae in zoea I and 20 or 29 plumose setae in zoea II .... Pisinae
5. Endopod of the maxillule with 1, 1 + 4 plumose setae .... Tychinae
- Endopod of the maxillule with 1, 2 + 4 plumose setae .... Mithracinae

This key can also be used in conjunction with the comparative features for each larval stage given in Tables 1–3.

Information in Tables 1–3 shows that larvae of *Epialtus bituberculatus* are very similar to those of *E. brasiliensis* and *Acanthonyx scutiformis,* with only slight setal differences on the carapace, maxillule and second maxilliped. These epialtinids species share an unilobed coxal endite of the maxilla, which is also present in *E. dilatatus* studied by Yang (1968). Although reduction of maxillary endites in larval Anomura and Brachyura has been discussed by van Dover (1982), she did not mention the single reduction of the coxal endite in such majids.

Overall, we agree with Marques & Pohle (1998), that larval descriptions of other epialtinids are needed to improve our understanding of phylogenetic relationships among majids.

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A new species of *Thor* Kingsley, 1878 (Crustacea: Decapoda: Caridea: Hippolytidae) from the tropical eastern Pacific

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Abstract.—A new caridean shrimp, *Thor cocoensis*, from the eastern Pacific, is described based on specimens from from Isla del Coco, Costa Rica and Islas Marchena and Santa Fé, Galápagos. This very small shrimp resembles *T. cordelli* Wicksten, but lacks a supraorbital spine and has one or two, not three, dorsal spines on the rostrum. There are three or four pairs of dorsolateral spines on the telson and one meral spine each on the third and fourth pereopods. The species is subtidal and is not known to have specific associations with other organisms.

While examining specimens of carideans taken in Costa Rica, we discovered a species of *Thor* Kingsley, 1878 that could not be identified as any known species. We compared the specimens with older material from the Galápagos Islands among the collections of the National Museum of Natural History (USNM) and Natural History Museum of Los Angeles County (LACM), and found eight additional specimens of this new species, described herein. Carapace lengths (CL) are given in millimeters. The holotype and some paratypes are deposited in the collections of the University of Costa Rica (UCR). We thank Michael Hodnett, Texas A&M University, and Richard Heard, Gulf Coast Research Laboratory, for assisting us in preparing the illustrations.

Thor cocoensis, new species
Figs. 1–4

Material.—Holotype female, ovigerous, CL 2.3. Bajo Alcyone, Isla del Coco, Costa Rica (Pacific), 35 m, 2 Apr 1992, UCR 1760-02. Paratypes: female, ov. CL 2.6, female, ov., CL 2.2, female, ov., CL 1.7, female, ov., CL 2.4, same data as holotype, UCR 1760-02. Female, ov., CL 1.6, Isla Santa Fé, Galápagos, 7–18 m, rock, 2 Feb 1933, *Velero III* sta. 46-33, USNM 260979. Male, CL 1.2, female, CL 1.0, female, CL 1.1, female, CL 1.2. Isla Santa Fé, Galápagos, 4 m, 2 Feb 1933, *Velero III* sta. 47-33, USNM 260980. Female, ov., CL 1.8, female, CL 1.1, SW side of Marchena Island, Galapágos, near mouth of tide pool; sand, rock and rubble, 17–26 m, 19 May 1984, LACM sta. GAL-84-36, CR19845158.

Description.—Small, stout-bodied hippolytid shrimp. Rostrum shorter than eyes or first segment of antennular peduncle, apex acute, with 1or 2 dorsal teeth, and unarmed or with 1 ventral tooth. Carapace without supraorbital spine, weak ridge in area of supraorbital spine; antennal spine prominent (Figs. 2A, B).

Abdominal somites smooth. Second with broad pleura; third with posterior margin produced dorsally in adult female. Fourth and fifth abdominal pleura with posteroventral margin acutely pointed, sixth with posterior ventral and lateral angles pointed (Fig. 1). Telson with 3 or 4 pairs dorsolat-

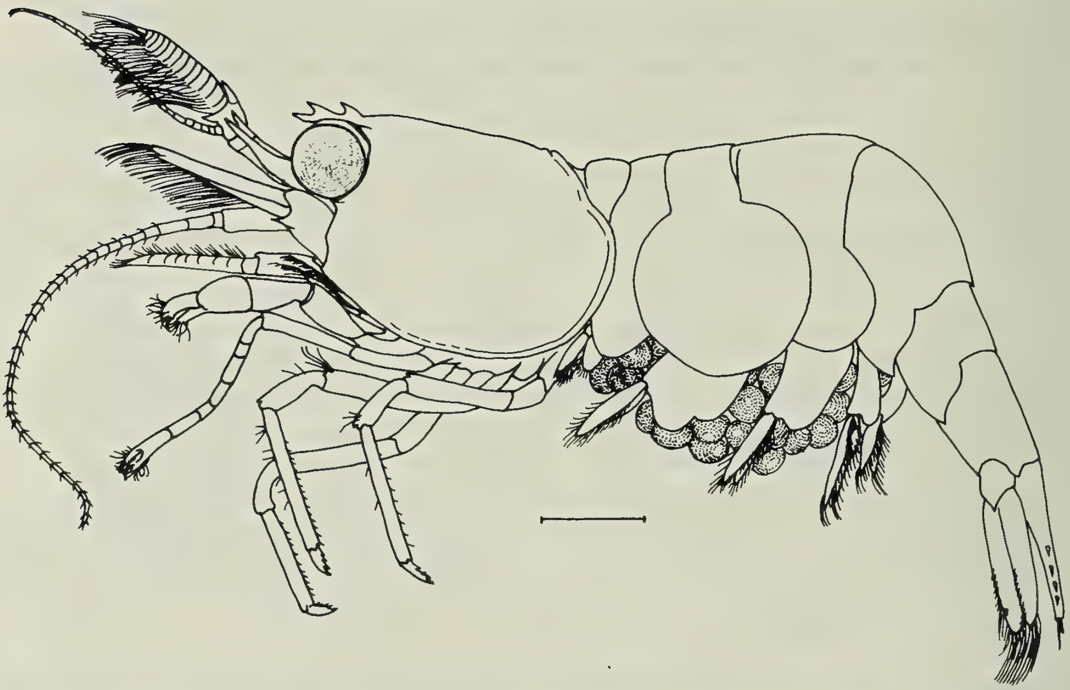

Fig. 1. *Thor cocoensis,* new species. Paratype female UCR-1760-02. Scale = 1 mm.

eral spines; posterior margin with 3 pairs spines, outer the shortest, next longest, mesial spines intermediate in length. Telson longer than uropods (Fig. 2C).

Eyes very large, pigmented.

Stylocerite acute, longer than first segment of antennular peduncle, with spine at base. First segment of antennular peduncle broad, with tooth on mesial surface; second segment short, with prominent lateral spine; third segment short. Upper antennular flagellum with stout proximal portion with dense sensory setae, ending in short lash. Lower flagellum slender, whip-like (Fig. 1).

Basicerite with small ventrolateral tooth. Carpocerite short, overreaching first segment of antennular peduncle. Scaphocerite longer than antennular peduncle, broad, rounded distally, blade of scaphocerite longer than its spine (Fig. 1).

Mandible without palp. Molar process stout, ending in spines; incisor process with 5 low spinules (Fig. 3A). First maxilla with bilobed palp, ending in long setae; upper lacinia broad, ending in row of stiff spines; lower lacinia slender, curved, ending in long setae (Fig. 3B). Second maxilla with short palp bearing terminal seta, distal endite deeply lobed, proximal endite small, scaphognathite 3 times as long as broad, anterior lobe large and rounded, posterior lobe small (Fig. 3C). First maxilliped with robust, 2-segmented palp; basal endite broad, with setose medial margin; coxal endite broad, sparsely setose; exopod with flagellum well developed; caridean lobe reduced to knob; epipod large and bilobed (Fig. 3D). Second maxilliped with distal segment narrow and set with brush of stiff setae; propodus broad, twice length of ultimate segment, with long setae; flagellum well developed; epipod triangular with small podobranch (Fig. 3E). Third maxilliped setose, extending beyond antennular peduncle when extended; with rounded epipod; exopod reaching past middle of antepenulti-

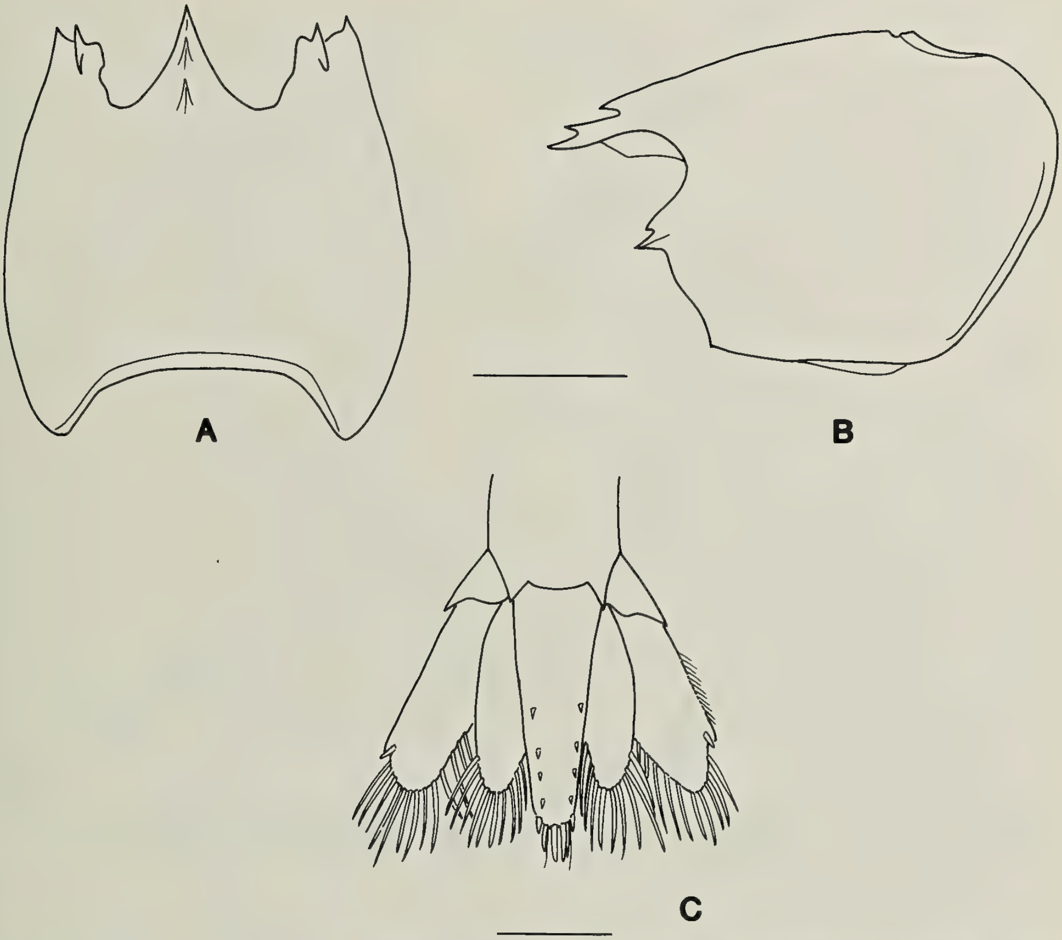

Fig. 2. *Thor cocoensis,* new species. Paratype female UCR-1760-02. A, carapace, dorsal view. B, carapace, lateral view. C, telson and uropods, dorsal view. Scale = 1 mm.

mate segment; antepenultimate segment longest, convex along lower surface, with distodorsal tooth and small distolateral spine; penultimate segment shortest; terminal segment setose, ending in sharp claws (Fig. 3F).

Pereopods without epipods. First pereopod stout and chelate. Fingers of chela about 0.5 length of palm, cutting edges without teeth; carpus about 2.5 longer than wide; merus slightly longer than carpus; ischium shorter than merus, with small preterminal ventral spines (Fig. 4A). Second pereopod slender and chelate, fingers of chela simple; carpus with 6 articles, relative proportions from most distal to proximal article 10:5:8:9:5:7 (Fig. 4B). Third pereopod of female with biunguiculate dactyl lined with 4 spinules along flexor margin; propodus with 9 or 10 spinules along flexor margin; carpus unarmed; merus with 1 spine (Fig. 4C). Fourth pereopod similar to third, with 1 meral spine; fifth without meral spines (Figs. 4D, E). Third pereopod of male unknown (missing from male specimen examined).

Second pleopod with appendix interna in both sexes; male with appendix masculina.

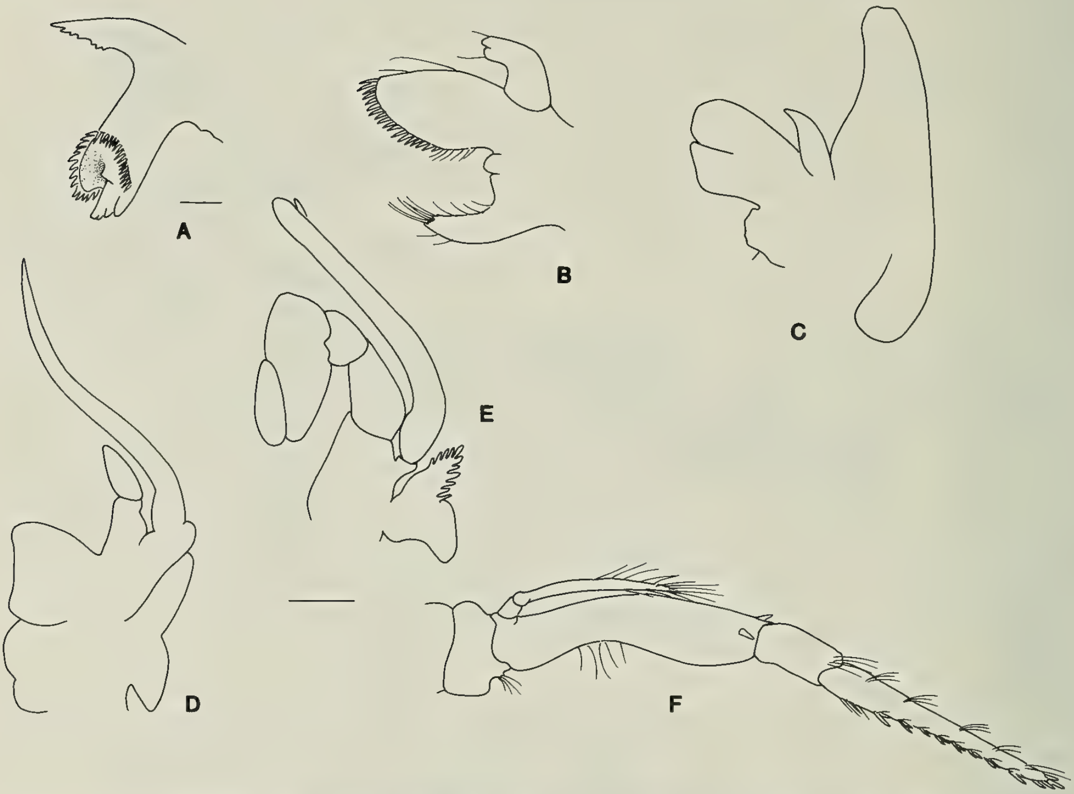

Fig. 3. *Thor cocoensis,* new species. Paratype female UCR-1760-02, mouthparts of right side. A, mandible. B, first maxilla. C, second maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped. Scales for A–B = 0.1 mm, for C–F, = 0.5 mm.

Outer uropod with fixed tooth and movable spine along suture.

Color in life not recorded.

Etymology.—The name is derived from the type locality, Isla del Coco (also known as Cocos Island).

Remarks.—This new species closely resembles *Thor cordelli* Wicksten, 1996, in size and body form. However, that species has a prominent supraorbital spine. The rostrum has three dorsal teeth, not one or two. The dactyls of *T. cordelli* are short and strongly spined, not elongate as in *T. cocoensis.*

Two other species of *Thor* occur in the eastern Pacific. *Thor algicola* Wicksten, 1987 grows to be larger than *T. cocoensis.* It has a camouflaged color pattern of lines and blotches, and a rostrum with four to six dorsal spines. The rostrum of the female is somewhat convex over the eye and has a bifid tip. It is intertidal or in shallow areas among algae, rocks or corals. *Thor amboinensis* (de Man 1888) is an associate of corals and other cnidarians. It has three to five dorsal teeth and one ventral tooth on the rostrum, short and stout dactyls of the female pereopods and a color pattern of large white dots on a dark background.

Both *Thor floridanus* Kingsley, 1878 and *T. manningi* Chace, 1972 of the Caribbean and western Atlantic are similar in size and shape to *T. cocoensis,* but each has a small supraorbital spine and a rostrum with four or more teeth. *Thor dobkini* Chace, 1972 of the western Atlantic has three to five rostral teeth and one or two spines on the merus of the first pereopod.

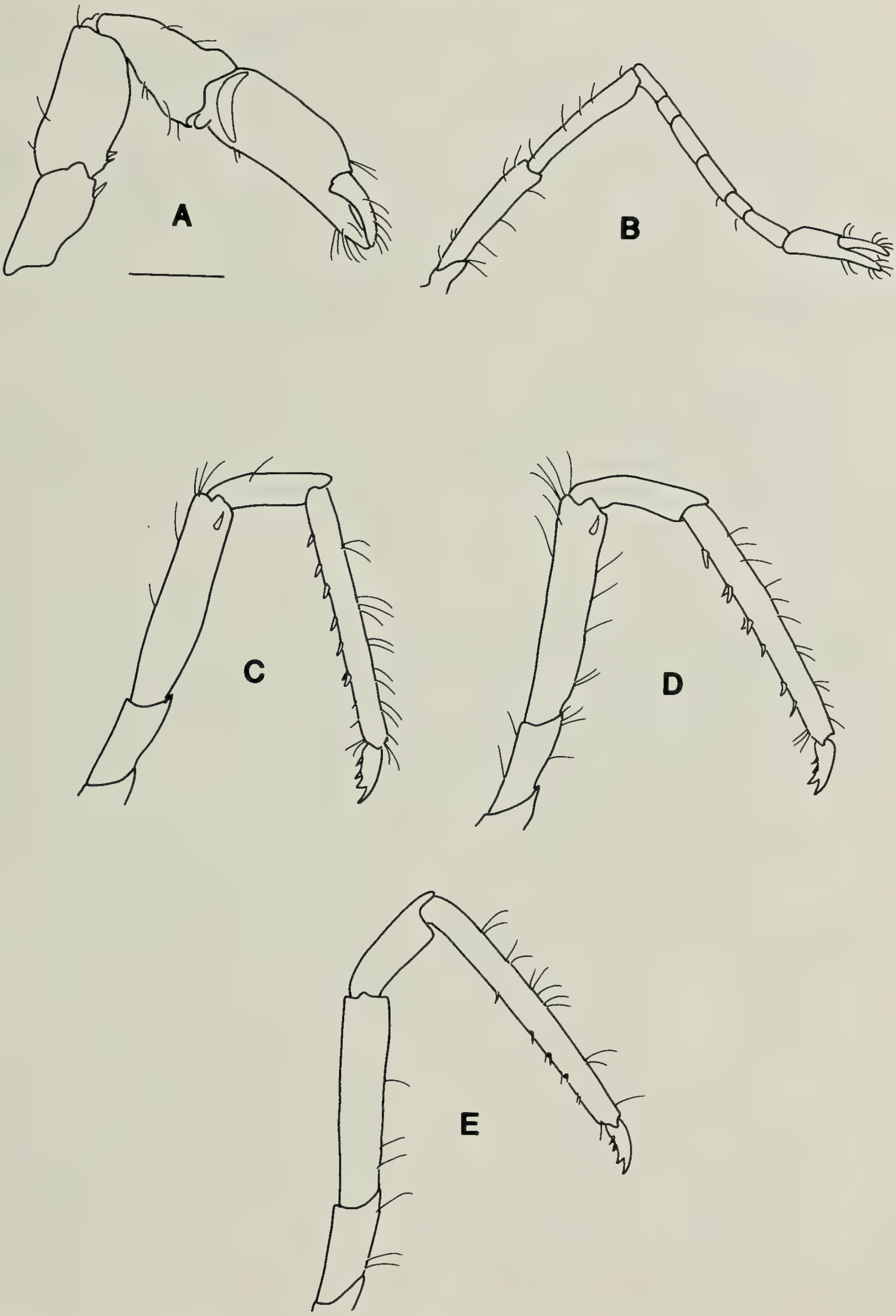

Fig. 4. *Thor cocoensis,* new species. Paratype female UCR-1760-02. A, left first pereopod, mesial view. B, right second pereopod, lateral view. C, right third pereopod, lateral view. D, right fourth pereopod, lateral view. E, right fifth pereopod, lateral view. Scale = 0.5 mm.

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The Indo-Pacific Pilumnidae XIV. On a new species of *Actumnus* (Crustacea: Decapoda: Brachyura) from Taiwan

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Abstract.—A new species of pilumnid crab, *Actumnus taiwanensis,* is described from southern Taiwan. The species is allied to *A. setifer* (De Haan, 1835) and *A. digitalis* (Rathbun, 1907), but can easily be distinguished by its flattened dorsal carapace surface, low frontal and anterolateral margins, characteristic form of the chela and diagnostic structure of the male first pleopod.

In a recent synopsis of the Taiwanese xanthoid fauna, Ho et al. (2000) listed 18 species of pilumnid crabs from this island. Ng (2000) subsequently described another species of *Pilumnus.* Of these, only one species of *Actumnus* was recorded, *A. squamosus* (De Haan, 1835). Over the years, however, the authors have been aware of an unusual species of *Actumnus* from southern Taiwan which superficially resembles *Actumnus setifer* (De Haan, 1835), a species with a wide Indo-West Pacific distribution. In recent months, through the help of various colleagues, we have finally managed to obtain a good series of specimens to enable us to describe this new taxon.

Specimens are deposited in the Taiwan Museum, Taipei (TMCD); Taiwan Endemic Species Research Institute, Nantou (TESRI); National Taiwan Ocean University, Keelung (NTOU); National Kaohsiung Institute of Marine Technology, Kaohsiung (NKMT); National Sun Yet-Sen University, Kaohsiung (NSYSU); National Museum of Natural Science, Taichung (NMNS); and Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC). Specimens of *Actumnus setifer* and *A. amirantensis* used for direct comparisons with the new species are deposited in the ZRC. The measurements are cited in the order cw (carapace width) × cl (carapace length). The abbreviations G1 and G2 are used for the male first and second pleopods respectively.

Actumnus taiwanensis, new species
Figs. 1–3

Material examined.—Holotype: male, 25.2 × 18.1 mm, TMCD (ex NTOU CX 9203-01-27), 20 m, Nanliao, Kaohsiung County, coll. 30 Jan 1992. Paratypes: 2 males, 24.3–21.8 × 17.5–15.9 mm, 2 females, 18.2–17.6 × 13.0–12.7 mm, ZRC 2000.2511–2514. 3 males, 1 female, NKMT, Mituo, Kaohsiung County, coll. J.-F. Huang, 2 May 1996. 2 males, 23.1–28.1 × 16.7–20.4 mm, TMCD, 30 m, Tsoying, Kaohsiung City, coll. H.-T. Shih, 1 Feb 1997. 2 males, 23.8–22.2 mm × 16.9–15.6 mm, NSYSU 980210B, 30 m, Tsoying, Kaohsiung City, coll. H.-T. Shih, 10 Feb 1998. 1 male, TESRI, 30 m, Tsoying, Kaohsiung City, coll. H.-T. Shih, 10 Dec 1996. 1 male, 1 female, TESRI, 10 m, Darlinpu, Kaohsiung City, coll. H.-T. Shih, 11 Dec 1996. 2 males, 27.9–26.8 × 19.7–18.5 mm, NMNS, 30 m, Tsoying, Kaohsiung City, coll. H.-T. Shih, 1 Feb 1997.

Description.—Carapace transversely ovoid, regions well demarcated, surface almost smooth, covered with very short pubescence. Frontal margin finely granulated, with 4 lobes just discernible; median lobes low, separated by broad, shallow cleft; lateral lobes separated from supraorbital margin by small cleft. Supraorbital margin granulated, with 1 deep median V-shaped cleft and shallower outer cleft. Anterolateral margin granulated to varying degrees, distinctly arcuate, distinctly demarcated from posterolateral margin, cut into 4 teeth (including external orbital tooth), separated by deep V- or U-shaped clefts; length of first to third teeth progressively shorter; first anterolateral tooth (external orbital tooth) low, subtruncate, anterior edge not produced; second tooth subtruncate; granules on third tooth largest; fourth tooth appearing very broad, with posterior part almost straight and subparallel to equivalent part of same tooth on other side of carapace. Posterolateral margin gently concave, distinctly converging towards posterior carapace margin.

Suborbital margin granulated, without pronounced tooth or spine present. Suborbital regions finely granulated. Basal antennal segment (true fused second and third antennal segments) subrectangular, just entering orbital hiatus. Orbits relatively large, transverse; eyes filling entire orbital space. Posterior margin of epistome with broad median lobe. Endostomial ridges discernible, but relatively weak, short. Third maxilliped completely covering buccal cavity when closed; ischium subrectangular, no distinct median longitudinal sulcus visible, smooth, inner margin weakly serrated; merus squarish, smooth, without distinct median depression; exopod stout, distal edge reaching anterior edge of merus, inner subdistal tooth prominent.

Surface of anterior thoracic sternites finely granulated, more so on lateral areas. Sternites 2 and 3 completely fused; sternites 3 and 4 separated by shallow but distinct groove which slopes to median part of abdominal cavity; male sternite 4 relatively narrow. Male abdominal cavity reaching to distal margin of sternite 4.

Chelipeds subequal in size or 1 slightly unequal in males. Anterior margin of fused basis-ischium gently granulated. Anterior margin of merus gently granulated, with 1 low subdistal tooth. Anterior margin of carpus granulated, with 2 distinct facets from dorsal view; inner facet narrower; inner distal angle with slightly larger granule but no distinct tooth or spine apparent. Entire outer surface of palm of chela distinctly granulated except for smooth, slightly flattened median part; outer surfaces covered with dense, very short pubescence not obscuring granules, pubescence on median part more prominent. Fingers shorter than palm; dactylus with 2 deep, pubescent longitudinal grooves and 3 flattened longitudinal carinae (median one broadest), proximal part of inner carina (nearest to carapace) distinctly granulated with rest of margin smooth, proximal part of median carina less weakly granulated.

Ambulatory legs not elongate, second leg longest. Margins of meri, carpi, propodi and dactyli lined with setae, particularly denser and longer on dorsal margins and ventral margins of propodus and dactylus; setae on dorsal (outer) margin of dactylus much denser than elsewhere, completely obscuring margin. Fourth dactylus shorter than those of other legs, dactylus of first and second leg substyliform, dactylus of second leg longest, distinctly styliform.

Male abdomen relatively narrow, surfaces relatively smooth; telson triangular, tip rounded; segment 6 squarish, lateral margins gently concave; segment 5 rectangular, lateral margins gently concave; segment 4 rectangular, lateral margins gently convex; segment 3 transversely subrectangular, strongly inflated, high, lateral margins strongly convex; segment 2 subtrapezoidal with rounded lateral margins; segment 1 trapezoidal with concave lateral margins.

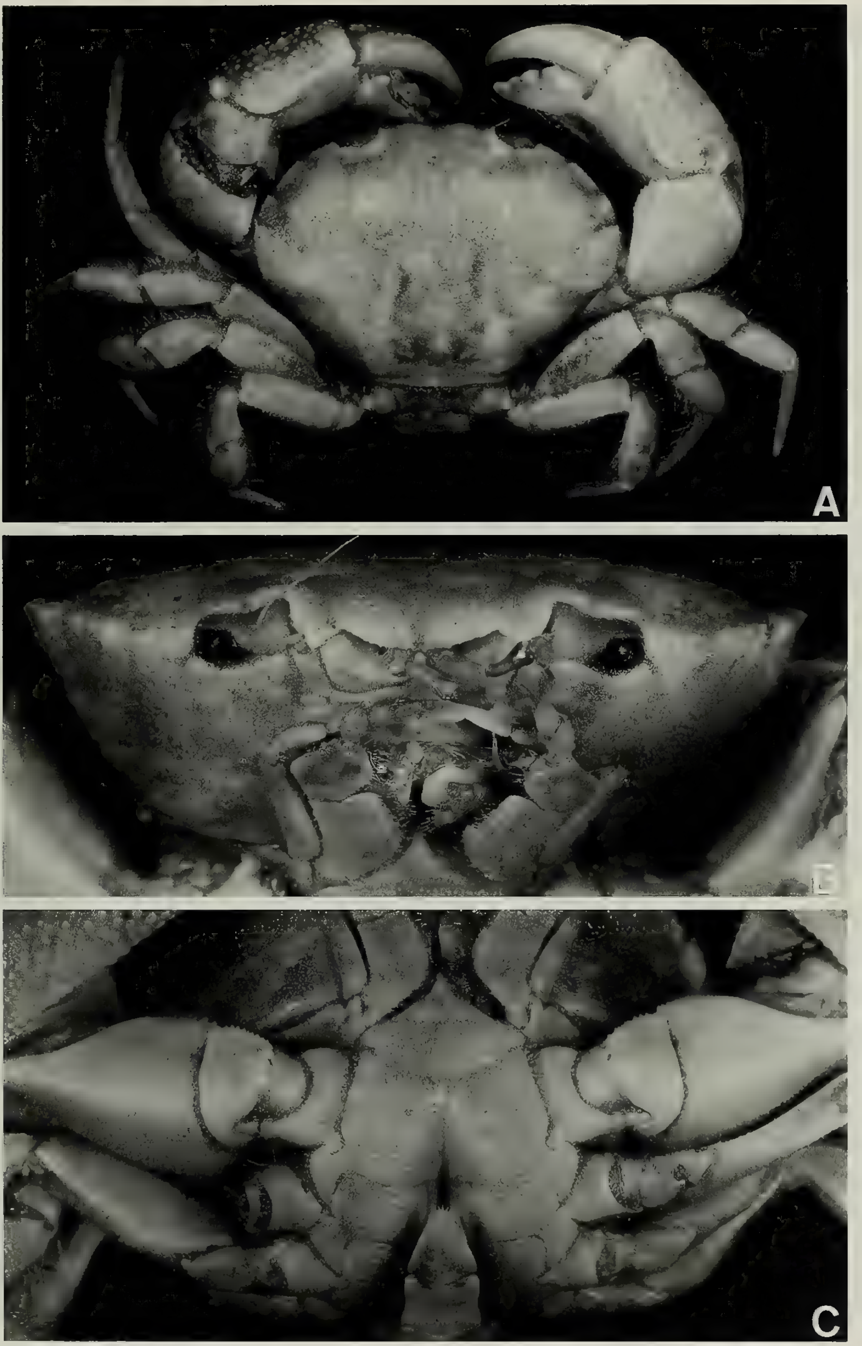

Fig. 1. *Actumnus taiwanensis,* new species. Paratype male, 24.3 × 17.5 mm, ZRC 2000.2511, A, dorsal view; B, frontal view; C, ventral view.

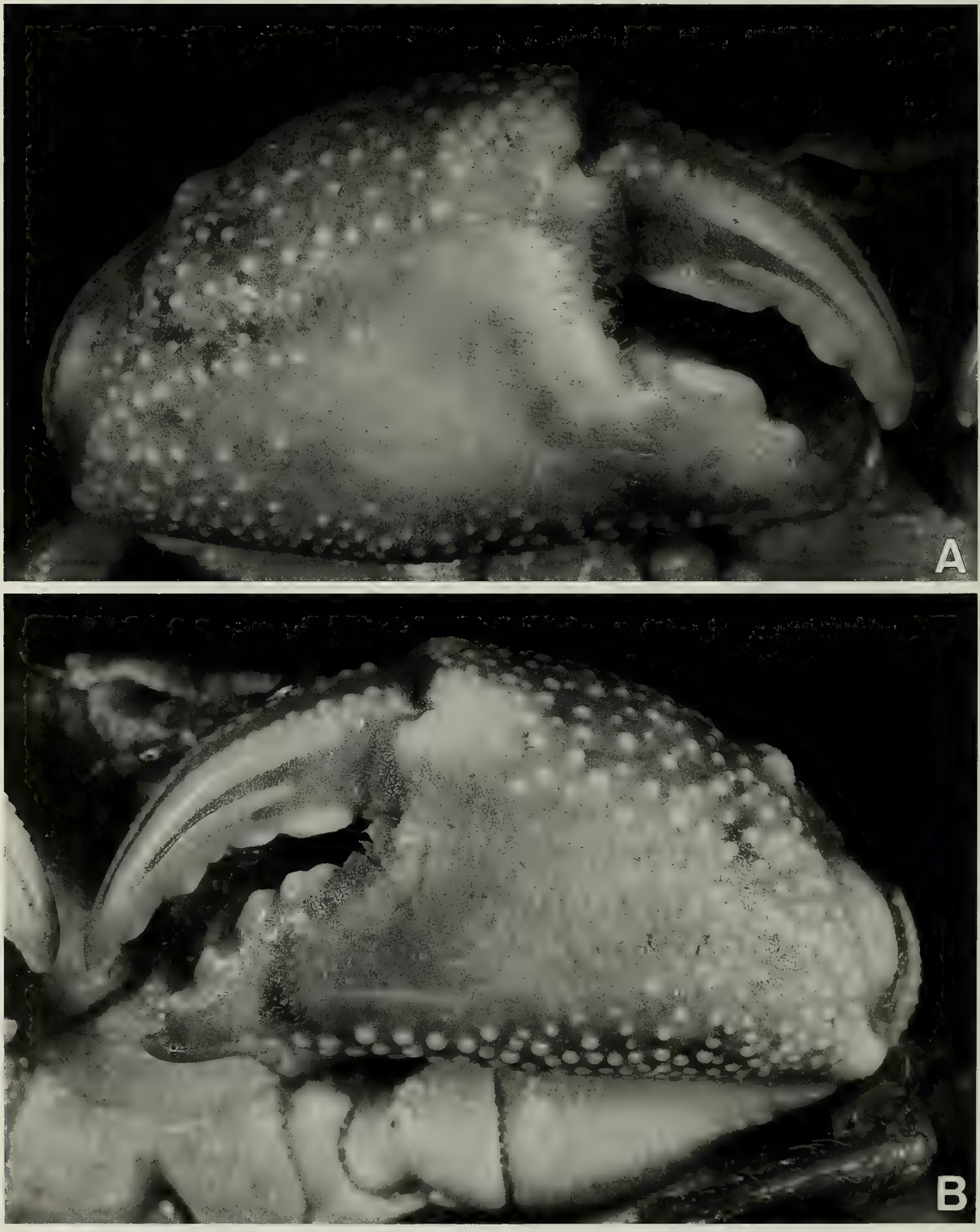

Fig. 2. *Actumnus taiwanensis,* new species. Paratype male, 24.3 × 17.5 mm, ZRC 2000.2511, A, right chela; B, left chela.

Female abdomen almost completely covering thoracic sternum; telson semicircular.

G1 very slender, strongly sinuous; distal part distinctly hooked, tip subtruncate; inner margin of distal part lined with numerous short, stiff setae. G2 very short, sigmoid; distal part spatuliform, tip rounded.

Color.—In life, uniform dull brown on

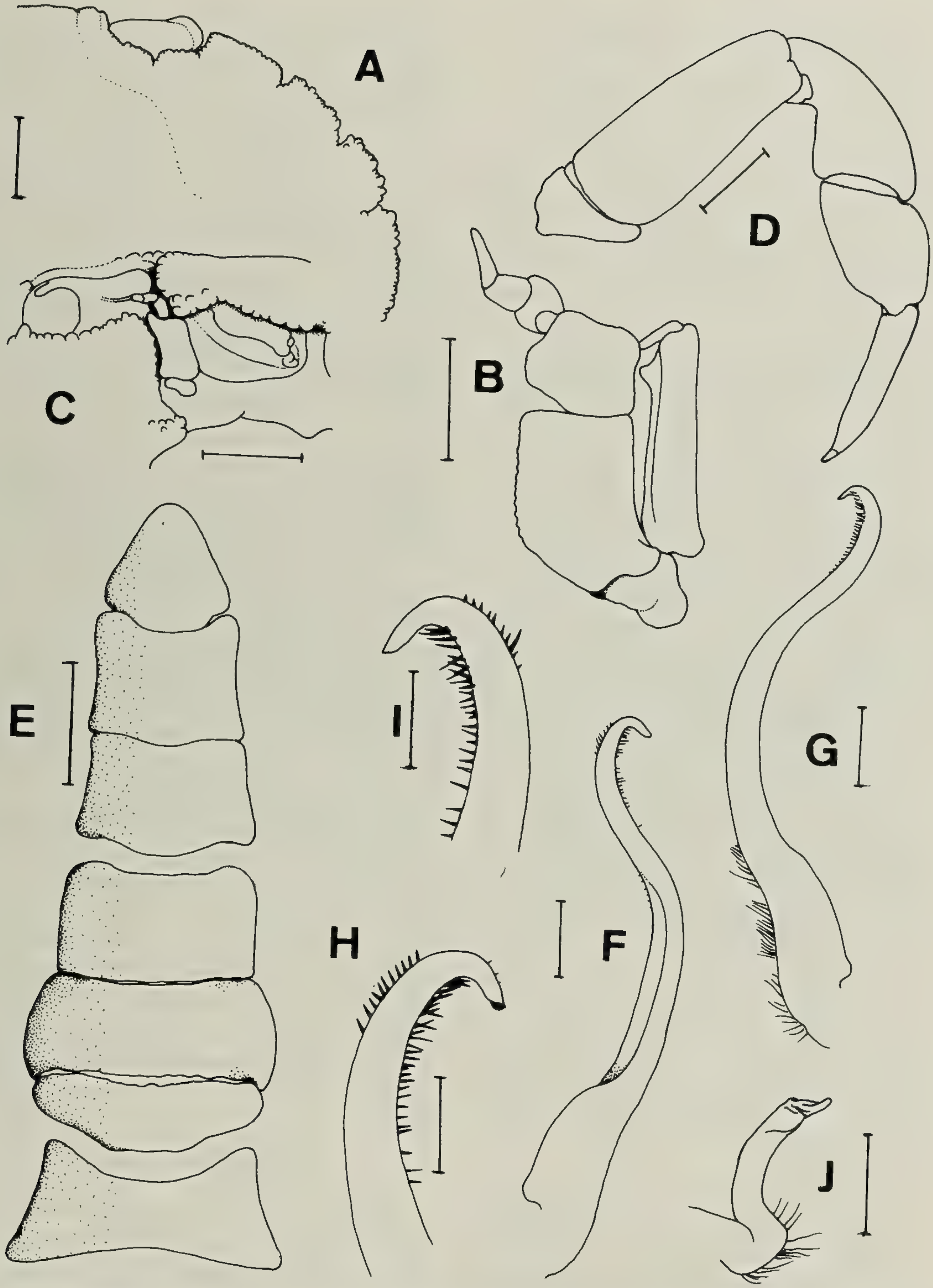

Fig. 3. *Actumnus taiwanensis,* new species. A, holotype male, 25.2 × 18.1 mm, TMCD; B–J, paratype male, 24.3 × 17.5 mm, ZRC 2000.2511. A, right side of carapace; B, left third maxilliped; C, frontal view showing antennae and antennules; D, right fourth ambulatory leg; E, abdomen; F, G, left G1; H, I, distal part of left G1; J, left G2. All structures (except gonopods) denuded of setae. Scales: A–E = 2.5 mm, F, G, J = 1.0 mm, H, I = 0.5 mm.

all dorsal surfaces; the ventral surface being dirty white.

Etymology.—The species is named after the island of Taiwan.

Remarks.—Actumnus taiwanensis is characterised by its low and poorly demarcated frontal margin, low anterolateral margins, relatively flat carapace and unusually sculptured chela. With regards to its frontal and anterolateral margins, it bears a close resemblance to the two known species in the genus *Neoactumnus* Sakai, 1965a, *N. convexus* Sakai, 1965a (type species of genus) and *N. unispinosa* Garth & Kim, 1983. *Neoactumnus* is characterized primarily by its entire frontal margin and a G1 which is not very sinuous and has a subtruncate tip (at least for *N. convexus*; as *N. unispinosa* is known only from a female). Although the frontal lobes of *A. taiwanensis* are poorly demarcated, they are nevertheless still clearly discernible, and as such, this species cannot be confidently referred to *Neoactumnus* as defined at present. In any case, *A. taiwanensis* also differs from both *N. convexus* and *N. unispinosa* in having the dorsal surface of the carapace much flatter (vs. distinctly convex, appearing swollen), the anterolateral teeth are separated by V-shaped clefts (vs. narrow fissures), proportionately longer ambulatory dactyli and a very sinuous G1 with the distal part hooked (vs. distinctly less sinuous with the distal part not hooked) (cf. Sakai 1965a:105, figs. 4a–d; 1965b:153, pl. 76 fig. 1, text fig. 18; 1976:498, pl. 177 fig. 4, text figs. 267a–c; Takeda 1982:189; Garth & Kim 1983:699, Fig. 8; Miyake 1983:133, pl. 45 fig. 3; Utsumi 1990:140).

With regards to its low anterolateral teeth, *A. taiwanensis* also bears a close resemblance to *A. setifer* and *A. digitalis. Actumnus taiwanensis* can be distinguished from *A. setifer* by its dorsal carapace surface bring almost flat (vs. strongly convex), weaker carapace areolation (vs. very distinct), more prominent frontal lobes separated by deep clefts (vs. lower lobes and shallow cleft), and the outer surface of the cheliped has the median part flattened and smooth (vs. uniformly convex and granulated) (cf. Takeda & Miyake 1969:115, Fig. 9d–f; Sakai 1976:496, pl. 177 fig. 2; Takeda, 1982:189; Miyake 1983:133, pl. 45 fig. 1). *Actumnus amirantensis* Rathbun, 1911, was regarded by Takeda & Miyake (1969) as a possible subspecies of *A. setifer,* but there are enough differences to regard *A. setifer* and *A. amirantensis* as separate species (P. K. L. Ng, personal observation). In any case, the differences enumerated between *A. taiwanensis* and *A. setifer* are also valid for *A. taiwanensis* and *A. amirantensis.*

Actumnus taiwanensis can be readily distinguished from *A. digitalis* by its dorsal carapace surface being almost flat (vs. strongly convex), anterolateral teeth being separated by V-shaped clefts (vs. narrow fissures), the much lower and less dense pubescence on the dorsal carapace surface, the outer surface of the cheliped having the median part flattened and smooth (vs. uniformly convex and granulated), and the distal part of the G1 is more strongly hooked (vs. bent gently) (cf. Rathbun 1907:38, pl. 1 fig. 6, pl. 9 fig. 4; Takeda & Miyake 1968:102, Figs. 3, 4).

Actumnus taiwanensis was obtained from relatively shallow waters with soft, muddy substrates. It was collected with another 39 species of crabs including the rare xanthid *Zalasius sakaii* (Balss) (H.-T. Shih, J.-F. Huang, pers. comm.). Among the sympatric species, half of them are swimming crabs (Portunidae).

Acknowledgments

The authors are most grateful to Dr. J.-F. Huang and Dr. H.-T. Shih for their help in getting more specimens of the new species. The first two authors were supported by a research grant on the Decapoda Crustacea of Taiwan from the National Science Council, Republic of China (NSC 85-2811-B019-002). The first author's research stay in Singapore was partially supported by a travel grant from the Raffles Museum of Biodiversity Research. The third author's work was supported by a research grant from the National University of Singapore.

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Cambarus (*Puncticambarus*) *hobbsorum,* a new crayfish (Decapoda: Cambaridae) from North Carolina

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Abstract.—*Cambarus* (*Puncticambarus*) *hobbsorum* is a new species of crayfish that occurs in parts of the Cape Fear and Yadkin-Pee Dee river basins of North Carolina. It differs from all other members of the subgenus in having a narrow areola; long, plumose setae on much of the opposable surface of the fixed finger of the chela of the cheliped in adults as well as juveniles; and a pronounced, disklike caudal knob on the gonopod of the form I male. These characters contradict some aspects of the diagnosis of the subgenus *Puncticambarus,* which is emended to accommodate *C. hobbsorum.*

The crayfish whose description follows is one of a number of undescribed species that for over a century have been indiscriminately subsumed under the name *Cambarus* (*Puncticambarus*) *acuminatus* Faxon, 1884. This melange inhabits most of the river basins in the Coastal Plain and Piedmont Plateau of the mid-Atlantic versant, ranging from the Patapsco River in Maryland to the Saluda River in South Carolina. Three decades ago Hobbs (1969:135) said, "It is almost certain that two, and possibly, three distinct species are presently assigned to *Cambarus acuminatus,*" and that this name very likely applied only to the "typical form" of the upper Saluda River basin. The confused state of this complex led Hobbs & Peters (1977) to refer to the North Carolina populations as *Cambarus* (*Puncticambarus*) sp. C, a designation later adopted by Cooper & Braswell (1995:88). Although in his final checklist of the American crayfishes Hobbs (1989:25) applied the name *C.* (*P.*) *acuminatus* to all of the Atlantic versant populations, he reiterated his earlier opinion, saying, "This highly variable species is also in need of attention."

I have undertaken an analysis of the "*C.* (*P.*) *acuminatus* complex," and the results to date show that Hobbs' opinion anent speciation in this group of crayfishes was not only characteristically astute, but may have been somewhat conservative. The still incomplete analysis has revealed four unique variants, two of which are so distinctive they can now be reported as new species without awaiting the final results of the study. The description of one of the two follows, and the description of the other is in progress.

The new species described below displays primary characters that contradict several aspects of the existing diagnoses of the subgenus *Puncticambarus* (Hobbs 1969:101, 1981:227). Nevertheless, since other characteristics of the species are more like those of a *Puncticambarus* than those of any other extant subgenus, I have at this time opted to take the conservative approach of emending *Puncticambarus* to accommodate the new species rather than introducing a new, monotypic subgenus.

Other members of the "*acuminatus* complex" are found in some of the same areas where the new species occurs. Thus, it is impossible to determine which, if any, published references to *C.* (*P.*) *acuminatus* might refer to the new species, and no synonymy can be presented.

Abbreviations used in the text are as follows: j, juvenile; NC, North Carolina State Highway; NCSM, North Carolina State Museum of Natural Sciences, Raleigh; PCL, postorbital carapace length; R, river; SR, State secondary road (formerly county road); TCL, total carapace length; US, United States highway; USGS, United States Geological Survey; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and UTM, Universal Transverse Mercator coordinates.

The diagnosis of the subgenus *Puncticambarus* requires the following modifications:

Puncticambarus Hobbs, 1969, emended

Areola 1.9 to 10.8 times as long as broad and comprising 29.4 to 40.0% of TCL and 39.2 to 49.2% of PCL, bearing many or few, shallow or deep, punctations. Opposable (mesial) margin of fixed finger of chela of adults sometimes bearing conspicuous tufts of plumose setae. Gonopod (first pleopod) of form I male sometimes with strong, disklike caudal knob at caudoproximal base of central projection.

Cambarus (*Puncticambarus*) *hobbsorum*, new species

Fig. 1, Table 1

Diagnosis.—Body and eyes pigmented, eye large ($\bar{X}$ adult diam 2.0 mm). Rostrum acuminate, often caret-shaped, lacking median carina; margins strongly to moderately converging to base of acumen, which is not delimited by marginal spines or tubercles; margins not strongly constricted at base of acumen, but sometimes more tapering from there to apical tubercle; rostrum longitudinally excavate, floor (dorsal surface) of cephalic half to three-fourths usually plane and with few punctations; acumen comprising 25.0 to 49.0% ($\bar{X}$ = 39.1%, n = 61) of rostrum length, latter constituting 17.3 to 25.0% ($\bar{X}$ = 20.5%, n = 65) of TCL. Areola 4.2 to 10.8 ($\bar{X}$ = 6.1, n = 70) times as long as broad, comprising 33.9 to 39.8% ($\bar{X}$ = 36.4%, n = 70) of TCL and 42.5 to 49.2% ($\bar{X}$ = 44.8%, n = 76) of PCL, with large punctations, usually 3 or 4 across narrowest part. Carapace dorsoventrally depressed; thoracic section dorsally punctate, dorsolaterally granulate, and laterally cobbled with large, rounded tubercles; cephalic section laterally covered with moderate to large tubercles; hepatic spines absent, but tubercles in region sometimes subspiniform; branchiostegal spine reduced to small tubercle or obsolete. Single cervical spine or large, spiniform tubercle present on each side of carapace, other smaller tubercles dorsal to it. Suborbital angle subacute or obtuse, with tubercle or spine. Cephalic margin of postorbital ridge with spine or tubercle. Antennal scale 2.3 to 3.1 ($\bar{X}$ = 2.7, n = 61) times as long as broad, widest distal to midlength; lateral margin thickened, terminating distally in long, acute spine; antennal peduncle with strong to moderate distolateral spine on basis, strong or weak distoventral tubercle on ischium. Pleura of abdomen usually with subtruncate ventral margins, subangular caudoventral corners, and subrectilinear caudal margins.

Palm of chela inflated, 1.5 to 1.9 ($\bar{X}$ = 1.7, n = 60) times wider than deep, width 1.3 to 1.7 ($\bar{X}$ = 1.5, n = 60) times length of mesial margin; mesial half of dorsal surface, and part of lateral half, often with small squamous tubercles; distolateral margin costate for short distance, with slight impression and aggregation of large punctations; mesial margin of palm with 2 rows of tubercles, and often others; mesial row of 6 to 10 (usually 7 to 9) tubercles, subtended dorsally by row of 3 to 11 (usually 5 to 8) somewhat smaller tubercles. Fixed finger of cheliped with strong to moderate longitudinal ridge on dorsal surface, weaker ridge on ventral surface; dorsolateral margin costate (continuous with palmar costa) and with moderate proximal impression; opposable surface of finger bearing tufts of long, plumose setae along proximal fourth to three-fourths of length, and row of 4 to 13 (usually 6 to 9) tubercles in addition to usual subconical tubercle ventral to denticles, third or fourth tubercle from base of finger larger than others. Dactyl of cheliped with weak to moderate longitudinal ridges on dorsal and ventral surfaces; mesial surface of finger with strong tubercles on proximal three-fourths, basal ones in 2 or 3 rows, encroaching dorsally; opposable surface bearing 7 to 13 tubercles, fourth (rarely fifth) tubercle from base offset ventrally; length of dactyl 1.7 to 2.3 ($\bar{X}$ = 1.9, n = 60) times length of mesial margin of palm.

Hook on ischium of third pereiopod of males, that of form I male (Fig. 1I) overreaching basioischial articulation by half or more of length, opposed by tubercle on basis. Gonopods (first pleopods) of form I male (based on holotypic male; Fig. 1B, C, G) symmetrical in caudal aspect, total length 22.7% of TCL; proximomesial apophyses large, lacking spiniform spur, bases slightly separated; gonopod in lateral aspect with prominent, disklike caudal knob at caudoproximal base of central projection, distal part of mesial surface of knob separated from shaft by deep cleft; central projection corneous, not tapered, curved slightly greater than 90° from axis of shaft and directed caudally; tip not reaching level of distal margin of mesial process or extending as far caudally as tip of latter; subapical notch strong, directed caudoproximally; mesial process inflated, directed caudoproximally and inclined caudolaterally, tapering to subacute distal terminus, which with 2 minuscule "spines"; in distal aspect, caudal end of central projection curving slightly caudomesially, mesial process directed caudolaterally, and caudal knob distinct.

Annulus ventralis (based on allotypic female; Fig. 1K) symmetrical, basically spindle-shaped in ventral outline, about twice as wide as long; caudal two-thirds heavy, walls thick, cephalic third depressed, membranous; cephalic margin with cephalomedian convexity, flanked each side by broad, shallow concavity; cephalomedian trough extremely narrow near cephalic margin, dissecting margin in midline, widening short distance caudal to margin and flanked each side by strong, relatively wide ridge; dextral ridge terminating caudally at base of transverse tongue, sinistral ridge joining upper arm of reverse C-shaped caudosinistral wall; tongue originating dextral to caudal midline, directed cephalosinistrally for short distance, then abruptly and obliquely turning caudosinistrally before plunging into deep fossa beneath sinistral wall. (Mirror image of this configuration occurs just as often as that described.)

Measurements (mm) of type specimens provided in Table 1.

Description of holotypic male, form I.—Body and eyes pigmented, eye 2.2 mm in diameter. Cephalothorax (Fig. 1A, D) subcylindrical; thoracic section of carapace dorsoventrally depressed (maximum width 1.6 times depth), dorsally punctate, dorsolaterally granulate, laterally cobbled with large, rounded tubercles, each with pair of short setae at cephalic margin; cephalic section of carapace covered laterally with large tubercles, gastric region with some scattered punctations. Areola 7.9 times as long as wide, constituting 38.4% of TCL (45.8% of PCL), with large punctations, 3 across narrowest part. Rostrum acarinate, acuminate, with elevated margins converging to base of acumen, then somewhat more strongly converging and concave to acute, corneous, cephalodorsally directed apex, tip of which extending to distal margin of penultimate podomere of antennular peduncle; rostrum without marginal spines or tubercles, margins flanked mesially by continuous row of setiferous punctations; acumen comprising 41.3% of rostrum length, latter constituting 19.0% of TCL; floor (dorsal surface) of rostrum moderately excavate longitudinally, subconcave, with punctations on caudal half only; subrostral ridge moderately developed, visible to base of acumen in dorsal aspect. Postorbital ridge strong, dorsolaterally grooved, cephalic margin with minuscule tubercle. Suborbital angle obtuse, with small tubercle; branchiostegal spine small, tuberculiform. Cervical spine area with 1 small spine and 1

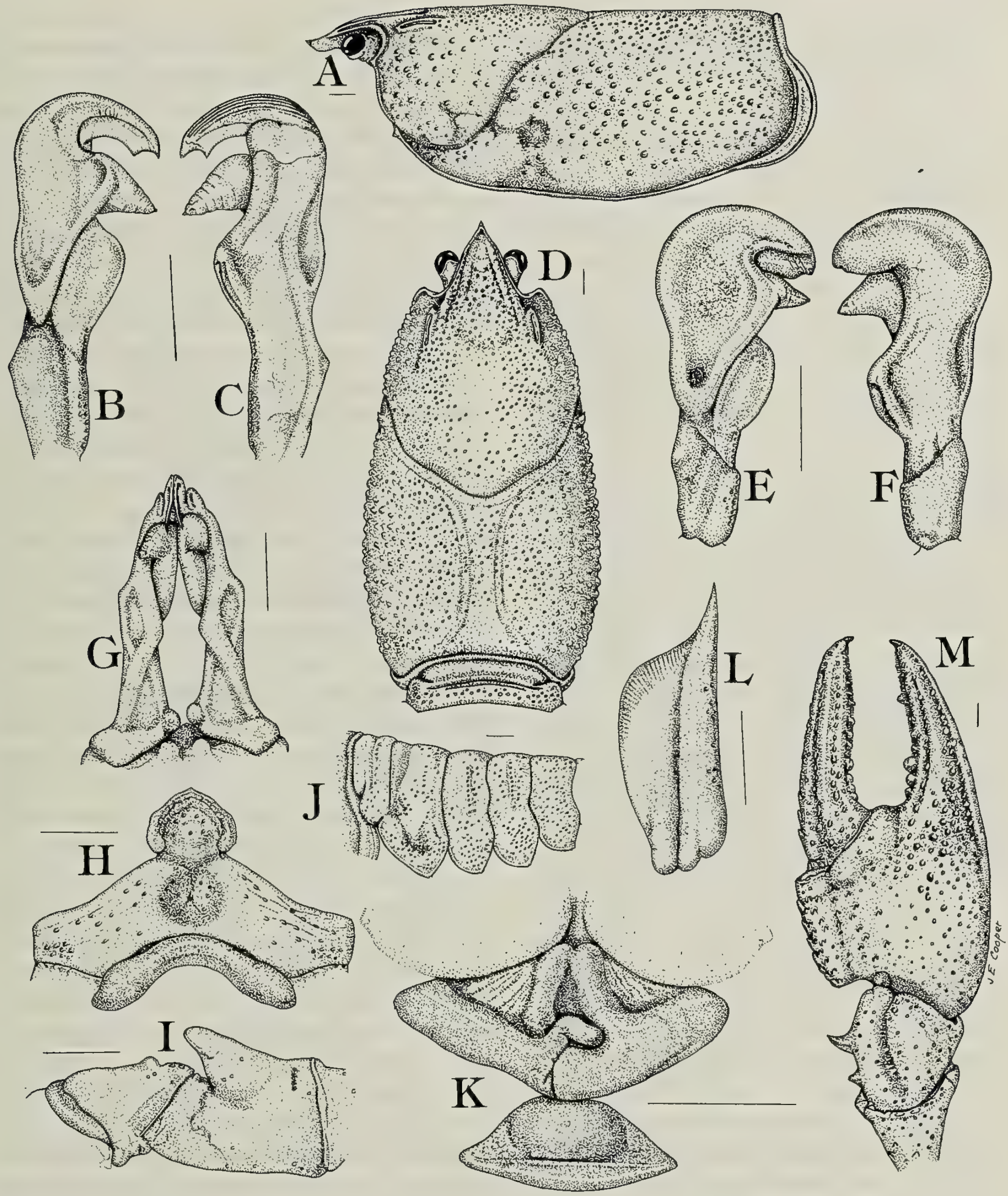

Fig. 1. *Cambarus* (*Puncticambarus*) *hobbsorum*, new species; all from holotypic male, form I (NCSM 5319), except E, F, from morphotypic male, form II (NCSM 5321), and K, from allotypic female (NCSM 5320): A, lateral aspect of carapace; B, E, mesial aspect of gonopod (first pleopod); C, F, lateral aspect of gonopod; D, dorsal aspect of carapace; G, caudal aspect of in situ gonopods; H, epistome; I, basis and ischium of third pereiopod, showing hook and opposing tubercle; J, lateral aspect of abdomen; K, annulus ventralis and postannular sclerite; L, antennal scale; M, dorsal aspect of distal podomeres of right cheliped. Setae not illustrated. Line = 2 mm.

Table 1.—Measurements (mm) of types of *Cambarus* (*Puncticambarus*) *hobbsorum,* new species.

	Holotypic male, form I	Allotypic female	Morphotypic male, form II
Carapace			
Total length	33.1	31.6	27.4
Postorbital length	27.7	25.4	22.5
Length cephalic section	20.4	20.1	17.3
Width	17.8	16.5	14.9
Depth	11.2	11.7	7.1
Length rostrum	6.3	7.1	5.4
Length acumen	2.6	3.2	2.2
Length areola	12.7	11.5	10.1
Width areola	1.6	2.2	1.3
Antennal scale			
Length	5.5	6.1	5.4
Width	2.1	2.2	2.0
Abdomen			
Length	32.6	31.0	27.2
Width	15.3	14.9	12.7
Cheliped			
Length lateral margin chela	31.6	24.2	21.6
Length mesial margin palm	9.8	7.3	6.8
Width palm	15.8	11.3	10.1
Depth palm	8.9	6.8	6.3
Length dactyl	19.5	14.8	12.7
Length carpus	11.4	9.4	8.1
Width carpus	9.0	7.5	6.7
Length dorsal margin merus	12.3	11.1	9.8
Depth merus	8.8	7.5	6.6
Gonopod length	7.5	N/A	6.5

tubercle each side of carapace; cervical groove uninterrupted, ventral margin of cephalic portion with row of small tubercles.

Antennal peduncle with short distolateral spine on basis (absent from right peduncle), and small, rounded tubercle on ventral surface of ischium; tip of adpressed antennal flagellum reaching just beyond cephalic margin of telson; antennular peduncle with small median spine situated just distal to midlength of ventral surface of basal podomere. Antennal scale (Fig. 1L) 2.6 times as long as wide, broadest distal to midlength; lateral margin thickened and terminating in long distal spine, tip of which reaching midlength of ultimate podomere of antennular peduncle; lamella approximately 1.6 times as wide as thickened lateral portion, distal margin moderately declivous to widest point, mesial margin somewhat rounded distally, subparallel to lateral margin for most of length.

Abdomen slightly shorter than carapace, latter wider than greatest width of abdomen; pleura of abdomen (Fig. 1J) with slightly rounded ventral margins, subangular caudoventral corners, and rectilinear caudal margins; terga quite punctate, except articular surfaces glabrous. Proximal podomere of uropod with very small caudolateral spine on lateral lobe, larger caudomedian spine on mesial lobe; mesial ramus of uropod with moderate caudolateral spine, and strong median ridge ending in small, subterminal caudomedian spine; lateral ramus with broad median ridge on cephalic section; transverse flexure on right ramus bearing row of 14 fixed spines (16 on left) and 1 large, articulated sublateral spine. Telson with 2 spines each caudolateral corner of cephalic section, mesialmost of which articulated; transverse flexure of telson moderately strong, caudal margin rounded.

Epistome (Fig. 1H) with subcordiform cephalic lobe bearing weak cephalomedian projection; lateral margins of lobe thickened; caudal half of floor (ventral surface) of lobe convex, floor moderately punctate; lobe constricted at base, transverse basal sulcus strong, with oblique arms leading into shallow central depression of body, depression with cephalomedian fovea; lamellae punctate, with truncate lateral corners devoid of tubercles; zygoma thick, well arched, cephalolateral margins flanked by usual pits.

Third maxilliped with tip of endopodite extending to distal margin of penultimate podomere of antennal peduncle; basal podomere of exopodite very hirsute, tip reaching base of distal fourth of merus of endopodite; longitudinal ridge of ventrolateral margin of ischium with row of punctations bearing long setae along inner edge; ventrolateral half of ischium moderately punctate, largely obscured by setae; distolateral corner slightly produced, acute; ventromesial half with rows of long, stiff bristles obscuring all but distalmost end of mesial margin; basis of endopodite with long setae. Right mandible with incisor ridge bearing 7 denticles.

Total chela length 95.5% of TCL; palm (Fig. 1M) 1.6 times wider than long, 1.8 times wider than deep; mesial margin of right palm bearing row of 8 strong tubercles, proximal pair fused at bases; mesial row subtended dorsally by row of 8 smaller tubercles, and others dorsal to them; dorsal surface of palm with many large punctations, some containing small squamous tubercles; distolateral portion of palm costate for about third of length, with mild impression and deep punctations; remaining lateral surface of palm rounded, with 1 or 2 rows of large punctations; ventral surface of palm with scattered punctations, distolateral portion with depression and large punctations; lateral eminence of articular ridge with weak subdistal tubercle, single tubercle proximal to ridge. Fingers of chela of cheliped gaping for most of length, width of gape at base equal to width of base of dactyl; opposable surface of fixed finger with clumps of long, plumose setae on proximal half. Fixed finger dorsolaterally costate, dorsal base of finger with large punctations and moderate impression; dorsal longitudinal ridge well defined, low, flanked each side by punctate groove; lateral surface of finger with staggered row of moderate punctations; ventral surface with very low ridge, flanked each side by row of punctations; opposable surface with subconical tubercle ventral to denticles at base of distal fourth of finger, and 9 tubercles (7 on left) along surface dorsal to denticles, third tubercle from base much larger than others; denticles small, in 2 rows to subconical tubercle, single row from there to third tubercle from base. Dactyl of chela 2.0 times as long as mesial margin of palm, comprising 61.7% of total chela length; dorsal surface of dactyl with weak longitudinal ridge, flanked laterally by punctate groove, mesially by row of spaced punctations; mesial surface of dactyl with strong tubercles on proximal half, basalmost tubercles in 2 rows, encroaching on dorsomesial surface; ventral surface with low, rounded ridge flanked each side by row of punctations; opposable surface with row of 12 tubercles (13 on left) dorsal to denticles, fourth from base largest and displaced ventrally; denticles small, in 2 rows on distal third of finger, single row to sixth tubercle from base.

Carpus of cheliped (Fig. 1M) 1.3 times as long as wide, 1.2 times length of mesial margin of palm; dorsal surface with deep, oblique sulcus, surface lateral and mesial to which punctate; mesial surface of carpus with large, curved distal spine and strong, subconical proximal tubercle; ventral surface with subconical distolateral tubercle, strong, acute distomedian tubercle, no proximomesial tubercle. Merus of cheliped 1.4 times longer than greatest depth, length 37.2% of TCL; dorsal surface with 2 small subdistal spines and 1 small tubercle; ventrolateral ridge with 2 acute tubercles and 1 rounded distal tubercle, ventromesial ridge with 5 (4 on left) acute tubercles and 1 large distal spine.

Hook on ischium of third pereiopod (Fig. 1I) simple, oblique, relatively acute, distally bent and overreaching basioischial articulation by about half of length; hook opposed by prominent tubercle on basis. Coxa of fourth pereiopod with strong, vertically disposed caudomesial boss. Coxae of third pereiopods, and sternites between third and fourth pereiopods, with long, dense setae obscuring distal portions of in situ gonopods.

Gonopod as described in "Diagnosis."

Description of allotypic female.—Except for secondary sexual characters, differing from holotypic male in following respects: Maximum width of carapace 1.4 times depth; areola 5.2 times as long as wide, constituting 36.4% of TCL (45.3% of PCL), with 4 punctations across narrowest part. Acumen comprising 45.1% of rostrum length, latter constituting 22.5% of TCL; apical tubercle directed dorsally, reaching distal margin of ultimate podomere of antennular peduncle; subrostral ridge narrow. Cephalic margin of postorbital ridge with strong spine; suborbital angle acute. Cervical spine area with 1 strong spine and several tubercles each side of carapace. Antennal peduncle with strong distolateral spine on basis, slightly weaker ventral spine on ischium; antennal scale 2.8 times as long as wide, mesial margin of lamella broadly rounded. Total chela length 76.6% of TCL; palm 1.5 times wider than long, 1.7 times wider than deep; dorsal punctations without basal tubercles; mesial margin with mesial row of 7 tubercles (8 on left), subtended dorsally by row of 5 smaller tubercles, and row of 3 proximal tubercles dorsal to this row; lateral eminence of ventral articular ridge with strong subdistal tubercle; 1 weak tubercle proximal to ridge. Fingers only slightly gaping in proximal two-thirds of length; dactyl comprising 61.2% of total chela length.

Carpus of cheliped 1.3 times length of mesial margin of palm, ventral surface with acute distolateral tubercle. Merus of cheliped 1.5 times longer than greatest depth, length 35.1% of TCL; dorsal surface with 2 very strong subdistal spines; ventrolateral ridge with 2 strong spines and 1 moderate distal spine; ventromesial ridge with 4 acute tubercles, 3 strong spines (2 on left), and 1 long distal spine.

Annulus ventralis as described in "Diagnosis." In addition, first pleopods strong, distally hirsute; postannular sclerite alate, ventral surface domed and pitted.

Description of morphotypic male, form II.—Differing from holotypic male in following respects: Maximum width of carapace 2.1 times depth; areola 7.8 times as long as wide, constituting 36.4% of TCL (44.9% of PCL), with 4 punctations across narrowest part. Acumen comprising 40.7% of rostrum length, latter constituting 19.7% of TCL. Cephalic margin of postorbital ridge with strong spine; suborbital angle subacute, with spine. Cervical spine area with 1 spine and several small tubercles each side of carapace. Antennal peduncle with strong distolateral spine on basis, acute ventral tubercle on ischium; antennal scale 2.7 times as long as wide, lamella about 1.4 times width of thickened lateral portion. Epistome with subcordiform cephalic lobe bearing short cephalomedian projection.

Total chela length 78.8% of TCL; palm 1.5 times wider than long, 1.6 times wider than deep; lateral eminence of ventral articular ridge with subacute distal tubercle; 2 moderate and several very small tubercles proximal to ridge. Fingers moderately gaping in proximal three-fourths of length; dactyl 1.9 times as long as mesial margin of palm, comprising 58.8% of total chela length.

Carpus of cheliped 1.2 times as long as wide; dorsal surface with 3 very weak dorsomesial tubercles; mesial surface with strong, curved proximal spine in addition to usual massive distal spine; ventral surface with strong distomedian spine and 1 very small tubercle proximomesial to it. Merus of cheliped 1.5 times longer than greatest depth, length 35.8% of TCL; dorsal surface with 2 strong subdistal spines and 1 small tubercle; ventrolateral ridge with 2 strong spines and 1 moderate distal spine; ventromesial ridge with 6 acute tubercles and 1 long distal spine.

Hook on ischium of third pereiopod small, opposed by weak tubercle on basis. Gonopod (Fig. 1E, F) length 23.7% of TCL; proximomesial apophyses weak, bases separated; central projection curved at 90° to shaft, tapered, apex complete, rounded; mesial process inflated at base, tapered, caudally acute, directed caudolaterally; strong juvenile suture present.

Color notes.—Ground color variable, even within same population, but usually olivaceous, greenish, or bluish green. Lateral surfaces of carapace covered with orangeish, pale tan, or white tubercles, creating densely spotted appearance; dorsomedian half of thoracic section of carapace with broad brown or rust-colored area; cephalolateral rim of carapace, including branchiostegal spine, with narrow orange or tan band. Lateral margin of antennal scale dark; dorsal surface of lamella light and flecked with small, dark spots, ventral surface pale; antennal flagellae green, or brown with greenish tinge. Dorsal surfaces of chelae and fingers olivaceous, orangeish, dark blue-green, or aquamarine; articular ridge tan or orange; lateral surface of entire propodus striking orange, bleeding into orangeish tan on ventral surface of chela and fixed finger, which usually bluish or yellowish tan; mesial area of ventral surface of chela often dark; tips of both fingers orange, tan, or yellowish, color not subtended by black band. Tubercles on mesial margin of palm either ground-color, deep amber, or light tan; those on opposable surfaces of fingers pale tan, white with orange base, or ivory-tan; those on ventral carpus and merus orangeish. Most podomeres of other pereiopods aquamarine.

Dorsal and dorsolateral abdomen dark blue-green, each tergite with narrow dark or iodine band along caudal margin; cephalicmost tergite with relatively discrete pale lateral blotch each side, or entire lateral corner pale; ventrolateral pleura with tan blotch or diagonal bar. Dorsal surfaces of telson and uropods dark blue-green proximally, tan or orange distally, spines orange. All ventral surfaces caudal to mandibles pale tan, abdomen often with narrow, pale blue banding; all structures cephalic to light mandible very dark. Annulus dark olive, postannular sclerite deep blue; central projection of male gonopod sometimes red or orange.

Disposition of types.—The holotypic male, form I, allotypic female, and morphotypic male, form II, are in the NCSM crustacean collection (catalogue numbers NCSM 5319, 5320, 5321, respectively), as are the following paratypes and paratopotypes: 2 ♂ I, 1 ♂ II (510), 3 ♂ II, 3 ♀, 2 j ♀ (2079), 1 ♂ I, 1 ♂ II (3322), 2 ♂ II, 3 ♀ (4378), 1 ♂ I, 2 ♂ II, 3 ♀ (4550), and 1 ♂ I, 4 ♂ II (4571). Paratopotypes consisting of 3 ♂ I, 4 ♂ II, 1 j ♂, 3 ♀, 2 j ♀ are deposited at USNM (291470).

Type locality.—North Carolina, Union Co., Bearskin Creek (tributary Richardson Creek, Rocky River subdrainage, Yadkin-Pee Dee River basin) near NC 200 bridge, about 2.4 air km NE of center of Monroe (Monroe 7.5′ USGS quadrangle, UTM zone 17, coordinates 3872500/543500).

Range and specimens examined.—Currently known with certainty only from the Cape Fear and Yadkin-Pee Dee river basins in North Carolina, but undoubtedly has a wider distribution. A total of 291 voucher specimens, all at NCSM (except USNM paratopotypes), has been collected at 22 localities in the Cape Fear River basin and 36 localities in the Yadkin-Pee Dee River basin by 51 collectors. A list of localities, dates, sexes, collectors, and catalogue numbers will be included with reprints, available from ⟨John.Cooper@ncmail.net⟩

Variations.—In addition to those addressed in the "Diagnosis," the following variations have been noted. The rostrum varies from caret-shaped (with slight if any increase in convergence of the margins from the base of the acumen to the apex), to moderately constricted and slightly rounded at the base of a long, narrow acumen. In some specimens, the margins of the rostrum terminate abruptly at the base of the acumen, where they are notably rounded or even slightly produced. The single cervical spine varies from long and acute to a relatively short, spiniform tubercle, and the usually weak branchiostegal spine is strong and well developed in some populations. The cephalic margin of the postorbital ridge may bear a strong, acute spine or a very small tubercle. The width of the lamella of the antennal scale varies from 1.2 to 2.1 ($\bar{X} = 1.6$, $n = 54$) times the width of the thickened lateral margin, and its distal margin is gently to moderately declivous, rarely strongly so or subtransverse. There are usually 2 spines in each caudolateral corner of the cephalic section of the telson, but several specimens have a single spine in one or the other corner, and 9 of 72 specimens have 3 spines in either corner (a single animal has 3 spines in each corner). The disklike caudal knob is weaker than usual in a few form I males. Of 38 females, the deepest part of the fossa of the annulus is sinistral in 17, dextral in 21. The total length of the chela averages around 98% of TCL for form I males, about 76% of TCL for form II males and adult females.

Size.—The largest specimen is a female with a TCL of 48.2 mm (PCL 39.5 mm). Form I males (n = 12) ranged from 27.0 to 42.5 mm TCL (22.2 to 35.3 mm PCL), with means of 32.7 mm TCL (26.9 mm PCL).

Life history notes.—Form I males have been found from late March through early June, and from late September through early November. A female, measuring 26.8 mm TCL (21.9 mm PCL) and bearing 17 third-instar young, was collected on 27 June 1997.

Crayfish associates.—Within the Yadkin-Pee Dee River basin, *C. hobbsorum* has been found with *Procambarus* (*Ortmannicus*) *acutus* (Girard, 1852) and *Cambarus* (*Depressicambarus*) *reduncus* Hobbs, 1956. Within the Cape Fear River basin, the new species has been collected with *P.* (*O.*) *acutus* and *Cambarus* (*Depressicambarus*) *latimanus* (Le Conte, 1856). At several localities in both river basins, a number of specimens of another member of the "*acuminatus* complex" have been found in fairly close proximity to *C. hobbsorum* sites, but the two have not yet been found syntopically.

Remarks.—It would be premature at this time to attempt to assess the relationships of *C. hobbsorum.* The species is easily distinguished from all other members of the subgenus *Puncticambarus,* including other known but undescribed species, by the combination of a narrow areola; long, plumose setae on the opposable surface of the fixed finger of the chela of adults as well as juveniles; a disklike caudal knob on the gonopod of the form I male; and abdominal pleura that are usually subtriangular in outline.

When the analysis of the "*acuminatus* complex" has been completed, the range of *C.* (*P.*) *hobbsorum* will almost certainly be found to include other river basins in central North Carolina, and probably South Carolina.

Etymology.—Patronymic, honoring the contributions made to our knowledge of the biology of crayfishes and other decapod crustaceans by the late Horton H. Hobbs, Jr., and Horton H. Hobbs, III, father and son.

Suggested vernacular name: Rocky River crayfish.

Acknowledgments

As usual, my thanks go to those collectors who provided specimens of this and other crayfishes. Although the list of names is too long for inclusion here, the value of their contributions cannot be overstated. Particular thanks must go to the biologists at NCSM, at the Division of Water Quality, and at the Wildlife Resources Commission, all Divisions of the North Carolina Department of Environment and Natural Resources. I am also grateful for the thoughtful reviews of the manuscript by two anonymous referees and Rafael Lemaitre. And, of course, my sincerest thanks are extended to Alvin L. Braswell and Don Howard for their many kindnesses. Nancy Childs, NCSM, provided technical assistance in the final preparation of the figure.

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A new species of the genus *Neopetrolisthes* Miyake, 1937 (Crustacea: Decapoda: Porcellanidae) from the Ryukyu Islands, southwestern Japan

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Abstract.—A new porcellanid crab, *Neopetrolisthes spinatus,* is described and illustrated based on the specimens collected from Okinawa Island of the Ryukyus, southwestern Japan. This species is well characterized and distinguished from the other species of *Neopetrolisthes* Miyake by having an uneven dorsal surface of the carapace and supraocular spines. *Neopetrolisthes spinatus* occurs as a male/female pair on a sea anemone, *Heteractis malu* (Haddon & Shackleton). Although most of the morphological characters considered to distinguish *Neopetrolisthes* from *Petrolisthes* Stimpson are found in some or many species of the latter genus, *Neopetrolisthes* differs from *Petrolisthes* by having the gastric region of the carapace strongly elevated.

The genus *Neopetrolisthes* Miyake, 1937 contains two or three Indo-West Pacific species and they are usually associated symbiotically with large sea anemones of the genus *Stichodactyla* Brandt (this genus has been treated as *Stoichactis* Haddon) (see Miyake 1942, Haig 1979, Debelius 1984). These porcellanid crabs are well known as one of the common crustaceans in subtropical and tropical shallow waters because of their beautiful spots of red, brown or blue color on the carapace and pereiopods.

Haig (1965, 1979) considered *N. ohshimai* Miyake, 1937 as a junior synonym of *Porcellana maculata* H. Milne Edwards, 1837 (=*N. maculatus*), and pointed out that the Indian and Pacific Ocean populations of *N. maculatus* have different spot patterns. In the former population, the carapace and pereiopods are covered with small, rounded, evenly distributed spots; whereas in the latter population, the color pattern takes the form of large, uneven blotches. However, Debelius (1984) expressed the opinion that the spot pattern was a specific character, and that the Indian Ocean population was applicable to *N. maculatus* and the Pacific Ocean population to *N. ohshimai.* As shown in the color illustrations provided by Kamezaki et al. (1988), we also found that both spotted crabs co-existed in the Ryukyu Islands, but could not distinguish them using morphological structures. To confirm the correct taxonomic status of the anemone crabs having different spot patterns, detailed morphological observations combined with ecological or molecular/genetic data of specimens from various Indo-Pacific localities are needed. Until such observations are made, we prefer to treat them under the name *N. maculatus,* and consider that this species has various spot sizes of red, reddish purple, or brown color on the carapace and pereiopods.

The remaining known species of *Neopetrolisthes, N. alobatus* (Laurie, 1926), has been recorded only from the Cargados Carajos Islands (the type locality) and Mozambique, located in the eastern African coast (Laurie 1926, Kensley 1970, as *Pe-*

trolisthes alobatus). *Neopetrolisthes alobatus* is easily distinguished from *N. maculatus* by numerous strong, transverse striae and large blue spots on the dorsal surface of the carapace, and lack of distinct teeth on the dorsoflexor margin of the carpus of the chelipeds (Haig 1966, Kensley 1970 as *Petrolisthes alobatus,* Debelius 1984).

The second author recently collected unusual porcellanid crabs associated symbiotically with the sea anemone *Heteractis malu* (Haddon & Shackleton) (fide Gosliner et al. 1996), from Okinawa Island of the Ryukyus. Examination of these crabs revealed that they belong to the genus *Neopetrolisthes,* but are distinguished from all known species of this genus by having an uneven dorsal surface of the carapace and supraocular spines. Herein, we describe and illustrate them as a new species.

Measurements of carapace length (CL), chelipeds, and ambulatory legs follow those of Osawa (1998b). The type specimens are deposited in the National Science Museum, Tokyo, Japan (NSMT).

Neopetrolisthes spinatus, new species
Figs. 1–4

Neopetrolisthes maculatus.—Masuda, 1999:58, unnumbered figure. [Not *Neopetrolisthes maculatus* (H. Milne Edwards, 1837)]

Type material.—Holotype: male (CL 8.6 mm), Zanpa Promontory, Okinawa Island, associated with *Heteractis malu,* 5.0 m, 30 Oct 1998, coll. Y. Fujita, NSMT-Cr 13062. Paratypes: 1 female (CL 10.6 mm), data as in holotype, occurred with holotype as male/female pair on same host, NSMT-Cr 13063; 1 male (CL 6.0 mm), 1 female (CL 9.5 mm); Zanpa Promontory, Okinawa Island, associated with *Heteractis malu,* occurred as male/female pair on same host, 19.7 m, 12 Jun 1999, coll. Y. Fujita, NSMT-Cr 13064.

Description.—Carapace (Fig. 1A–C) 1.1 (paratype female, NSMT-Cr 13063)-1.3 (holotype male) times as long as broad, usually broadest at anterior to median branchial regions (median region in holotype). Dorsal surface moderately convex in general appearance, covered with short transverse rugae; those of median branchial regions being longer and stronger than other regions, those of hepatic regions weaker and fewer in number. Rostrum (Fig. 1D) broad, slightly bent ventrally; frontal margin sinuously triangular; median lobe strongly produced forward, with narrowly rounded apex; lateral lobes with oblique anterior margin. Orbits moderately concave; supraorbital margins strongly oblique, with distinct spine on slightly elevated ridge; outer orbital angles strongly produced but unarmed. Protogastric ridge well developed, divided into 2 lobes by median groove extending to tip of rostrum; lobes directed anteriorly, with strong spine-like appearance in lateral view. Gastric region strongly elevated. Cervical grooves deep. Acute epibranchial spines present. Branchial margins with longitudinal edges bearing strong elevation on anterior to median region; anterior margins moderately to strongly convex; median margins subparallel. Branchial regions with broad, well elevated part situated slightly behind of marginal elevation; anterior branchial regions slightly depressed, with small, flattish, rounded squamae.

Pterygostomian flaps (Fig. 1C) entire, unarmed, moderately narrowing posteriorly, with longitudinal, long rugae.

Third thoracic sternite (Fig. 1E, F) strongly depressed, incompletely divided from fourth sternite by large, median interruption, trilobate anteriorly; median lobe distinctly exceeding laterals, with moderately (male) or very broadly (female) rounded apex; lateral lobes narrow. Fourth sternite with series of short rugae along concave anterior margin; rugae of male stronger than those of female; setae on anterior sides of rugae of female longer and much more in number than those of male.

Telson (Fig. 1G) as illustrated, consisting of 7 plates with short distal plates.

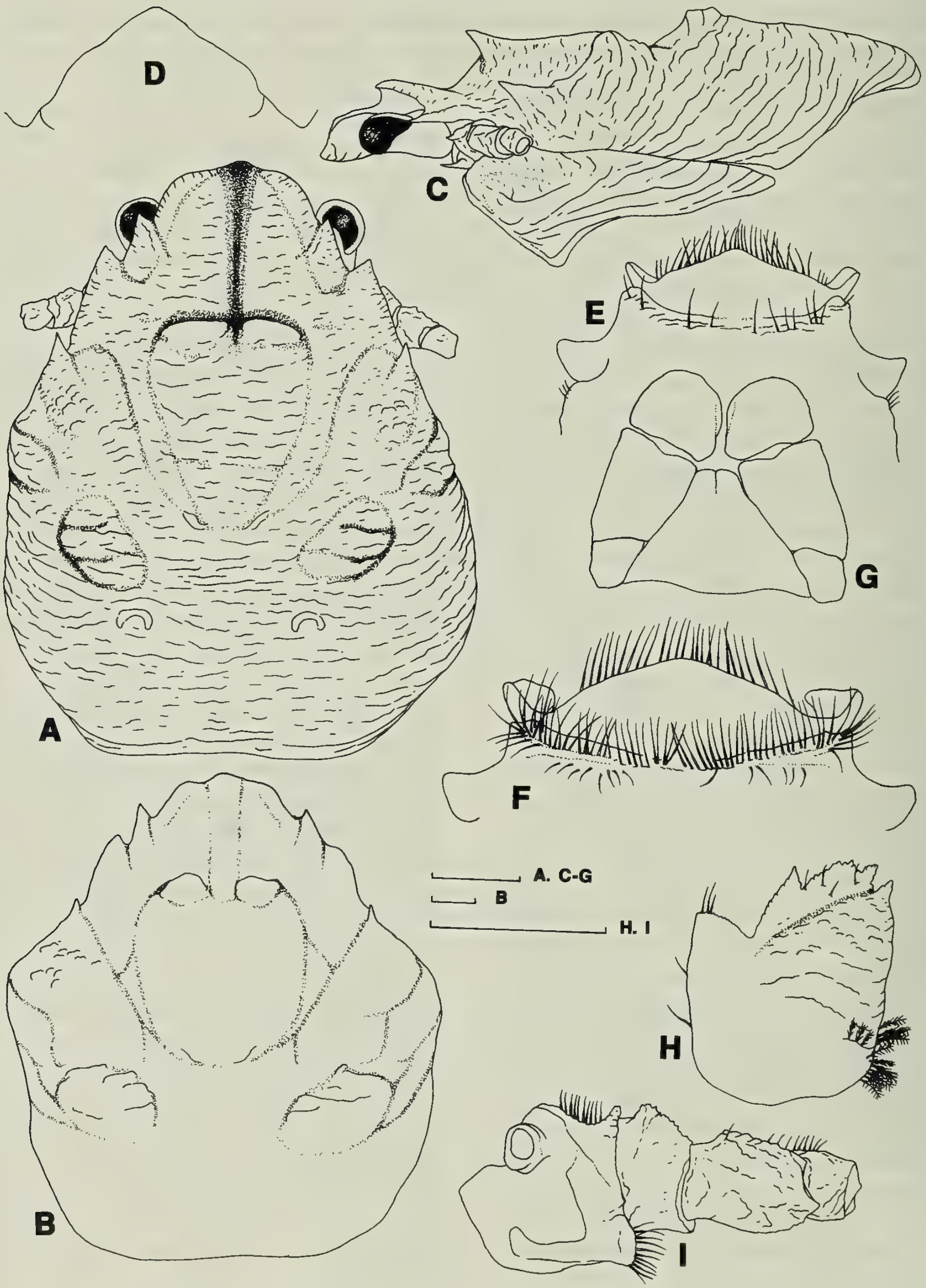

Fig. 1. *Neopetrolisthes spinatus,* new species. A, C–E, G–I, holotype, male (NSMT-Cr 13062, CL 8.6 mm); B, F, paratype, female (NSMT-Cr 13063, CL 10.6 mm). A, B, carapace, dorsal; C, carapace and pterygostomian flap, lateral; D, rostrum, dorsofrontal; E, F, anterior thoracic sternites, ventral; G, telson, extensor; H, left basal segment of antennular peduncle, ventral; I, left antennal peduncle, ventral. Scales equal 1.0 mm.

Ocular peduncles moderately large, with few short striae on dorsal surface; dorsal extension onto cornea broadly subtriangular with rounded apex, margin without setae.

Basal segment of antennular peduncles (Fig. 1H) transversely rugose on anterior lateral region of ventral surface, with short plumose setae on proximal lateral margin; anterior margin tuberculate, with acutely pointed tooth at mesial and lateral corners; margin between teeth with broad and narrow projections.

Antennal peduncles (Fig. 1I) with first segment not strongly produced forward in lateral view, provided with bluntly pointed, narrow projection at anterodistal end. Second segment provided with low, subtriangular anterior crest; dorsal and ventral surfaces slightly rugose. Third segment rather weakly elongated; anterior margin weakly produced in submedian region, tuberculate; dorsal and ventral surfaces rugose. Fourth segment small, dorsal and ventral surfaces slightly rugose.

Third maxillipeds (Fig. 2A) with coxa bearing narrow, roundly pointed distoflexor projection; distomedian projection incompletely articulated, with shallow suture. Basis articulated from ischium, subtriangular with rounded edges. Ischium broad, ovate, transversely rugose on ventral surface, with longitudinal ridge along extensor margin; distoextensor projection tapering. Merus rugose on ventral surface, with laminate, ovate lobe on ventroflexor margin. Carpus moderately rugose on ventral surface, with subtriangular projection near median region of flexor margin and with longitudinal row of short rugae along extensor margin on ventral surface. Propodus relatively slender, rugose and tuberculate along extensor margin. Dactyl small, subtriangular; ventral surface smooth. Exopod laminate, slender, with short setae marginally; proximal region inflated; distal region narrow, with flagellum.

Chelipeds (Fig. 2B–F) subequal. Ischium slightly crenulated but unarmed on ventroflexor margin, dorsal and ventral surfaces slightly rugose. Merus with dorsal surface transversely rugose, provided with distinct, transverse ridge submedially; dorsoflexor margin with small, ovate lobe crenulated but unarmed marginally; dorsodistal and dorsolateral margins without spines; ventral surface rugose, distoflexor margin unarmed. Carpus 2.1–2.2 times as long as broad; dorsal surface moderately convex along longitudinal median line, with numerous transverse rugae, those on proximal region tending to be much larger than other parts, those on part along flexor margin smaller, rounded; very or moderately shallow, longitudinal sulcus present along dorsoextensor margin; dorsoflexor margin transverse, slightly crenulated, without teeth and lobes; dorsoextensor margin unarmed entirely, slightly elevated, distal end not produced; distal margin with broad, rounded lobe on flexor part and small or moderately large, rounded projection near extensor end; ventral surface transversely rugose, flexor and extensor margins crenulated. Chela rather narrow, flattened (in holotype, larger chela slightly inflated), elongate, 2.0–2.3 times as long as carpus, 2.8–3.2 times as long as high, lying on extensor side; dorsal surface covered with short, transverse and oblique rugae, those on fingers replaced by small rounded granules; extensor margin thin, unarmed, slightly crenulated by marginal rugae, very weakly concave on distal third; ventral surface with numerous short, transverse and oblique rugae, those on fingers being smaller; fingers crossed distally; dactyl opening at slightly oblique angle. Palm with dorsal surface provided with weakly or moderately developed, median longitudinal ridge extending from proximal end of palm to base of dactyl; dorsoflexor margin with longitudinal rugose ridge. Fixed finger with rounded ridge along cutting margin; dorsoflexor proximal part with broad, weakly developed, subrectangular or rounded projection extending onto dactyl; distal claw slightly or moderately curved; cutting edge minutely tuberculate. Dactyl 0.3–0.4 times as long as chela, subequal in length

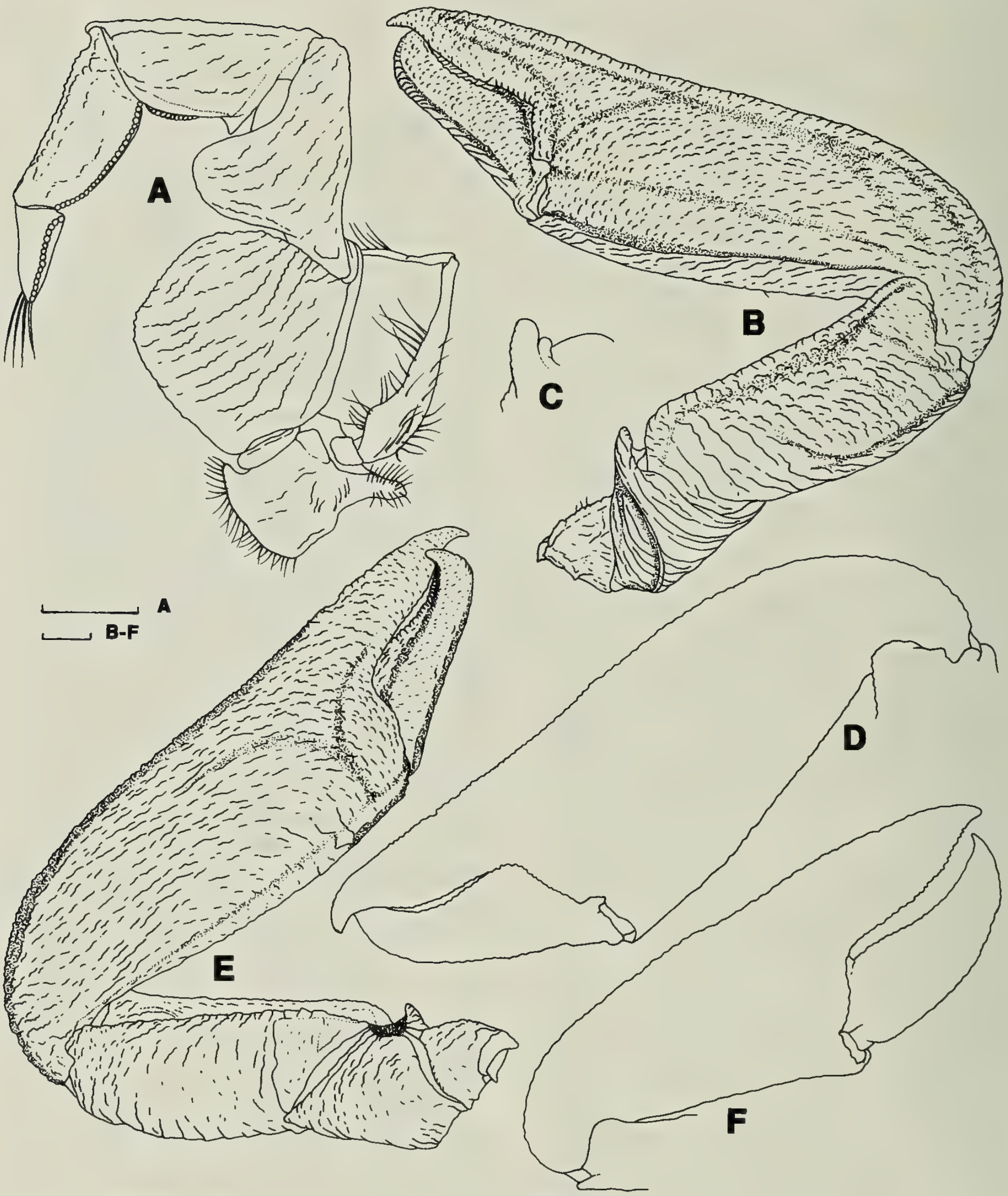

Fig. 2. *Neopetrolisthes spinatus,* new species. A–E, holotype, male (NSMT-Cr 13062, CL 8.6 mm); F, paratype, female (NSMT-Cr 13063, CL 10.6 mm). A, left third maxilliped, ventral; B, right cheliped, dorsal; C, same, merus, distoflexor corner, dorsoflexor; D, same, chela, dorsoextensor; E, same, ventral; F, left chela, dorsoextensor. Scales equal 1.0 mm.

to fixed finger, with strongly curved distal claw; dorsal surface provided with rugose longitudinal ridge along flexor margin; cutting margin minutely tuberculate. Rugae on dorsal surface of merus to dactyl with few minute setae arising from distal sides.

Ambulatory legs (Fig. 3A–D) rather short, with few short setae except for several tufts of setae on dactyls. Merus elongatedly subrectangular to ovate in lateral view, with length decreasing from first to third legs; extensor margin unarmed, slightly swollen; lateral surface with numerous short, transverse rugae, indistinct and reduced in number on flexor region; distoflexor margin unarmed; mesial surface without decalcified region (narrow, weakly calcified band present along proximal margin), distoflexor margin unarmed. Carpus with short longitudinal rugae on lateral surface, series of rugae along extensor margin present on first and second legs but absent on third leg; distoextensor margin unarmed. Propodus approximately as long as carpus and 2.7 (third leg)–3.2 (first leg) times as long as high; lateral surface with very short, transverse rugae; flexor margin provided with pair of movable spines at distal end, lateral spine larger than mesial. Dactyl terminating in strongly curved claw; flexor margin with 2 movable spines, distal spine larger than proximal.

Males with pair of developed pleopods on second abdominal somite (Fig. 3E); protopod with few setae on proximal region; endopod not tapering distally (with broadly rounded apex), with numerous setae except for proximal region, those on outer margin longer and stiff; exopod small, ovate, naked. Pleopods on third to fifth abdominal somites each reduced to small, rounded, inconspicuous rudiment with small pore. Females with pairs of developed pleopods on third to fifth abdominal somites, those on fourth and fifth somites large.

Color (Fig. 4).—The carapace, abdomen, and chelipeds are usually covered with very small red spots on pale or deep, reddish brown background, except for the elevated regions of white color or having few number of spots. In the holotype, the frontal and lateral regions of the carapace have white background. Meri of ambulatory legs have very small red spots on deep reddish brown background proximally, remaining parts of merus and following segments usually white.

Habitat.—Although *Neopetrolisthes maculatus* and probably *N. alobatus* have been known to live only on *Stichodactyla* species, *N. spinatus* was collected from a different sea anemone, *Heteractis malu.* The existence of *N. spinatus* on the host was also confirmed in a photograph provided by Masuda (1999, as *N. maculatus*). This species occurred as a male/female pair (the male is smaller than the female) on the sea anemone in shallow water ranging from 5.0 to 19.7 m.

Distribution.—The type locality is Okinawa Island, Ryukyu Islands, southwestern Japan. As mentioned above, Masuda (1999) showed a photograph of this species from Bali Island, Indonesia.

Etymology.—The specific name is derived from the Latin, *spinatus* (with spines), referring to the possession of supraocular spines.

Remarks.—Miyake (1937) described *Neopetrolisthes ohshimai* for a male/female pair of unusual crabs living symbiotically with a large sea anemone. *Neopetrolisthes* is closely allied to *Petrolisthes* Stimpson, 1858, but is considered to differ from the latter in several morphological characters. The features of *Neopetrolisthes* that distinguish it from *Petrolisthes* include: the carapace is elongate and the dorsal surface is strongly convex; the rostrum is laminated and lacks a median longitudinal groove on the dorsal surface (the dorsal surface is gradually oblique towards the median longitudinal line); the eyes are small; the chelipeds are short and the palms are much flattened and broad; and the ambulatory legs are subcylindrical and have few setae and spines.

Johnson (1960) concluded that *Neopetrolisthes* was not distinct enough to warrant generic status and placed it in synonymy with *Petrolisthes* arguing that the distinguishing characters provided by Miyake (1937) do not reflect a proper generic boundary. It is true that most of the generic characters of *Neopetrolisthes* are also found in some or many species of *Petrolisthes.* In

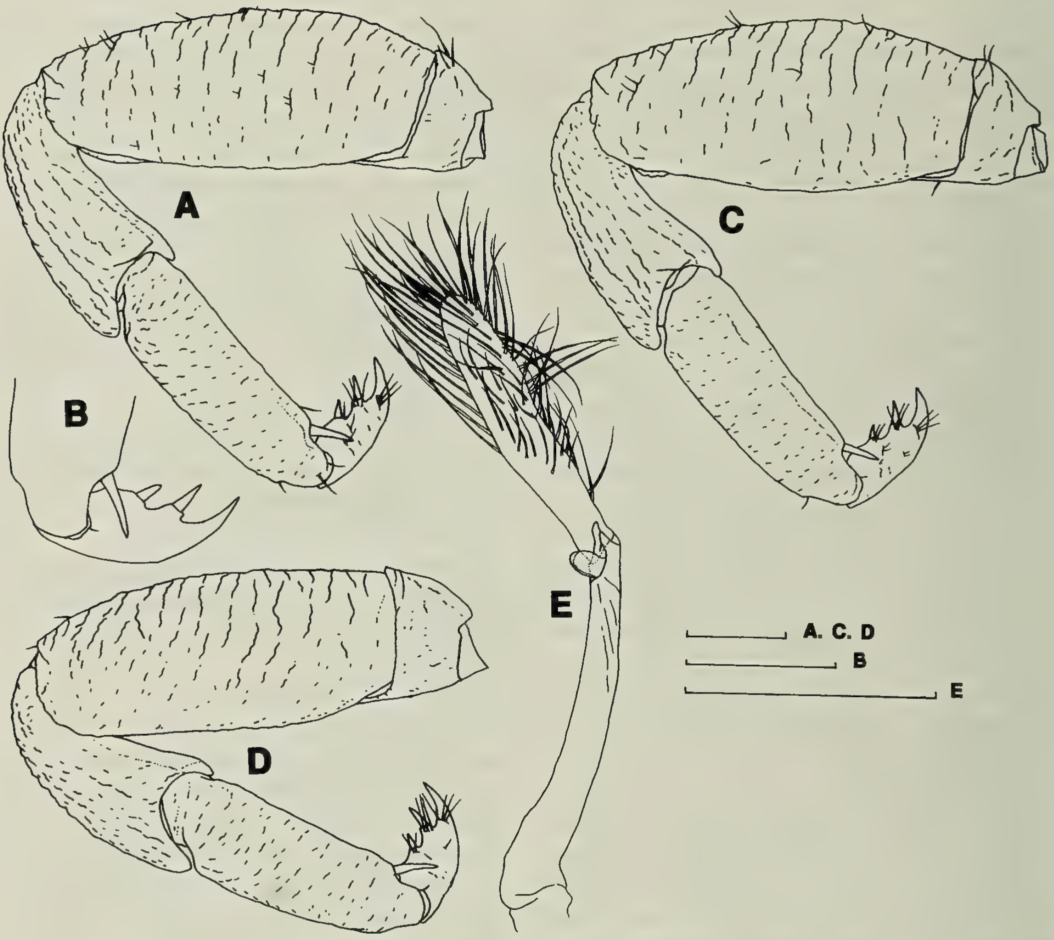

Fig. 3. *Neopetrolisthes spinatus,* new species. Holotype, male (NSMT-Cr 13062, CL 8.6 mm). All appendages dissected from left side. A, first ambulatory leg, lateral; B, same, dactyl and distal region of propodus, lateral; C, second ambulatory leg, lateral; D, third ambulatory leg, lateral; E, pleopod on second abdominal somite, internal. Scales equal 1.0 mm.

particular, it seems difficult to distinguish each of the two genera by the size and structure of the eyes, chelipeds, and ambulatory legs. The elongate carapace can be observed in *Petrolisthes virgatus* Paulson, 1875 (see Lewinsohn 1969: fig. 32a; Nakasone & Miyake 1972: fig. 1A). *Neopetrolisthes spinatus* and *N. alobatus* (see Laurie 1926: 145, pl. 9, fig. 6, as *Petrolisthes alobatus*) have a median longitudinal groove on the dorsal surface of the rostrum as in *Petrolisthes* species. The possession of only a distal pair of spines on the flexor margin of the ambulatory propodus is also seen in *Petrolisthes haplodactylus* Haig, 1988 (see Haig 1988: fig. 4D). The third thoracic sternite incompletely divided from the fourth sternite is observed in *Neopetrolisthes spinatus* and *N. maculatus* (personal observation); this seems to be an unusual character in porcellanid crabs. However, several Indo-West Pacific species of *Petrolisthes* such as *P. asiaticus* (Leach, 1820), *P. fimbriatus* Borradaile, 1898, *P. haswelli* Miers, 1884, *P. lamarckii* (Leach, 1820), *P. moluccensis* (de Man, 1888), *P. pubescens* Stimpson, 1858, *P. scabriculus* (Dana, 1852), *P. tomentosus* (Dana, 1852),

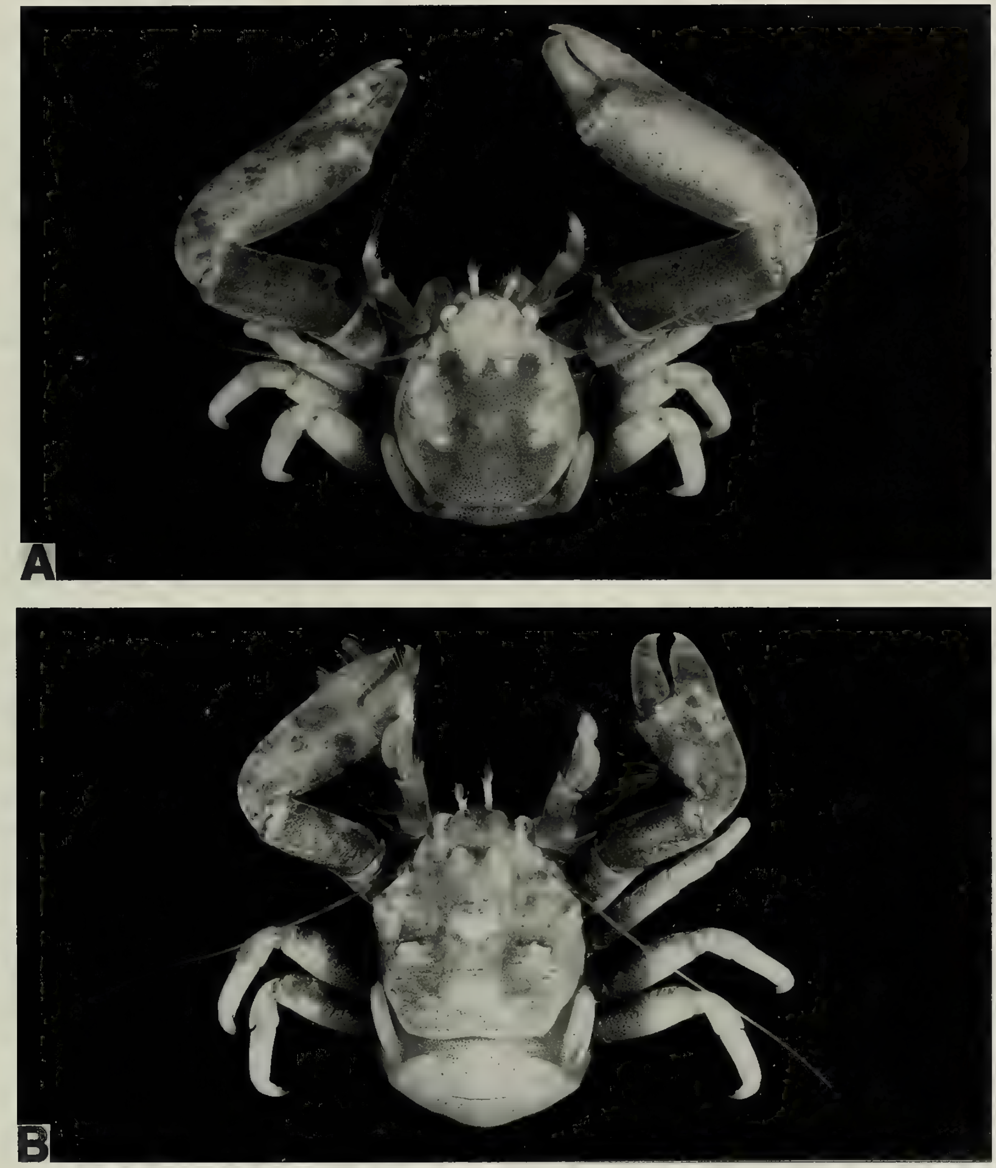

Fig. 4. *Neopetrolisthes spinatus*, new species. Entire animal, dorsal. A, holotype, male (NSMT-Cr 13062, CL 8.6 mm); B, paratype, female (NSMT-Cr 13063, CL 10.6 mm).

P. varicolor Osawa, 1998a, and *P. virgatus*, also have this structure with a small or large, median interruption (personal observation). We believe that the strongly elevated gastric region of the carapace is a character that clearly distinguishes *Neopetrolisthes* from *Petrolisthes*. *Petrolisthes* species have a flattish or weakly convex body.

As pointed out by Osawa (1995), *Petrolisthes* is considered a heterogeneous genus, which is evident even in the zoeal characters. The generic status of *Neopetrolisthes* is supported by the larval morphology. Zoeae of this genus closely resemble those of the Indo-West Pacific species of *Petrolisthes* Group 4 (see Osawa 1995, 1997), but are distinguishable from the latter by the setation on the third endopod segment of the second maxilliped through the two zoeal stages. The species of *Petrolisthes* Group 4 have a median seta on the ventral margin, but *Neopetrolisthes maculatus* and *N. spinatus* lack it (Sankarankutty & Bwathondi 1974, as *Petrolisthes ohshimai*; personal observation). More accurate relationships of *Neopetrolisthes* and *Petrolisthes* would be clarified considering larval and adult characters.

Neopetrolisthes spinatus resembles the "small, evenly distributed spots" morph of *N. maculatus* in color and spot patterns, but is rather allied to *N. alobatus* in morphology. *Neopetrolisthes spinatus* and *N. alobatus* have the carpus of the chelipeds without distinct teeth or projections on the dorsoflexor margin and distoextensor end (see Laurie 1926: pl. 9, fig. 8; Kensley 1970: fig. 7b). However, *Neopetrolisthes spinatus* is clearly distinguished from the other two species of the genus by having an uneven dorsal surface of the carapace, i.e., well developed, elevated parts on the protogastric region, the anterior to the median branchial margins and the inner median branchial regions, and having supraocular spines. The anteriorly directed protogastric lobes are not known in any porcellanid crabs and are unique to *N. spinatus*. *Neopetrolisthes alobatus* merely has a pair of short, transverse elevations on the protogastric region and two slightly elevated parts on each the branchial regions, that of the anterior to median margin is surmounted by one or two tubercles (see Laurie 1926).

Acknowledgments

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A new fossil geryonid crab (Crustacea: Decapoda: Brachyura) from the late Pliocene to early Pleistocene of Japan

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Abstract.—A new fossil geryonid crab, *Chaceon matsushimai* is described from the uppermost Pliocene to lower Pleistocene Ofuna and Koshiba formations, Kazusa Group in Kamakura and Yokohama cities, central Japan. The new species resembles members of the extant *Chaceon granulatus* species group, but is distinguished by having very faint frontal, second, and fourth anterolateral spines and a proportionately narrower male abdomen. This is the first fossil record of the genus *Chaceon* from Japan.

Recent revisions of deep sea geryonid crabs (Manning & Holthuis 1987, 1989) previously placed in the genus *Geryon* Krøyer, 1837, have shown that species which possess five anterolateral spines on the carapace and four distinct spines on the frontal margin should be referred to the genus *Chaceon* (Manning & Holthuis, 1989). Species of *Geryon* [type species: *Geryon trispinosus* (Herbst, 1803)] have only three anterolateral spines, and less pronounced frontal spines. Based on these carapace features, the new species of fossil described herein is referable to *Chaceon,* which has eight living species in the Pacific Ocean, two of which are found in Japanese waters (Ng & Manning 1998).

Koizumi & Matsushima (1992) first reported fossils of *Geryon* species in association with molluscs and fishes indicative of lower sublittoral to upper bathyal waters from the lower Pleistocene Ofuna Formation, Kazusa Group in Kamakura City (referred to here as the Ofuna specimens). Poorly preserved cyclodorippid crab *Tymolus* species were also obtained from the locality. As noted by these authors, two specimens deposited in the Kanagawa Prefectural Museum of Natural History, which had been collected by Mr. Syozo Aizawa from the overlying Koshiba Formation, are assignable to the same species (here referred to as the Koshiba specimens).

In addition, a fossil specimen in the collection by late Professor Rikizo Imaizumi preserved in the Institute of Geology and Paleontology, Tohoku University, is also identical to the present new species (here referred to as the IGPS specimen). Although this specimen lacks a label and information about the locality, stratigraphic horizon and name of collector, a piece of card belonging to the specimen and probably written by Imaizumi reads "Kamakura". The matrix of this specimen is indistinguishable from those of the Ofuna specimens.

The Ofuna specimens occurred in massive, light gray-colored siltstone exposed in the land-development field for residential construction in Iwase, Kamakura City, Kanagawa Prefecture, central Japan (35°20′58″N, 139°32′51″E). The crab-bearing horizon is stratigraphically situated between the Ny Tuff Bed (Nakaya Tuff bed: same as O26 (Of2) in Mitsunashi & Kikuchi, 1982) and the Is Tuff bed. The former is a remarkable key bed widely traceable in the Yokohama-Kamakura area.

The Koshiba specimens had been obtained from the massive, light gray-colored pumiceous sandy siltstone of the lower part of the Koshiba Formation exposed in the land-development field in the Seibu-danchi, Nishishiba, Kanazawa-ku, Yokohama City (35°21′N, 139°38′E). They are mostly impressions and/or molds due to compression and weathering.

Mitsunashi & Kikuchi (1982) correlated several remarkable tuff beds in the Ofuna Formation with those in the lower Pleistocene Otadai and Kiwada formations of the Boso Peninsula. Eto et al. (1987) considered the age of the Ofuna Formation to be early Pleistocene based on the planktonic foraminifera (N22 Zone of Blow 1969) and calcareous nannoplankton ("CN12" Zone of Okada and Bukry 1980). However, the calcareous nannoplankton assemblage of the formation identified by them indicates that the age extends into the latest Pliocene (CN13a Zone of Okada & Bukry 1980: Y. Tanaka pers. comm.). Considering these facts, the geologic age of the fossils from the Ofuna and Koshiba formations is most likely to be latest Pliocene to earliest Pleistocene (ca. 1.9–1.7 Ma).

The specimens are deposited in the Kanagawa Museum of Natural History (KPM-NN) and Institute of Geology and Paleontology, Faculty of Science, Tohoku University (IGPS coll. cat. no.). The abbreviations cl and cw indicate carapace length and carapace width.

Family Geryonidae Colosi, 1923

Genus *Chaceon* Manning & Holthuis, 1989

Chaceon matsushimai, new species
Figs. 1–4

Geryon sp.: Koizumi & Matsushima, 1992, p. 127, figs. 8–1–3.

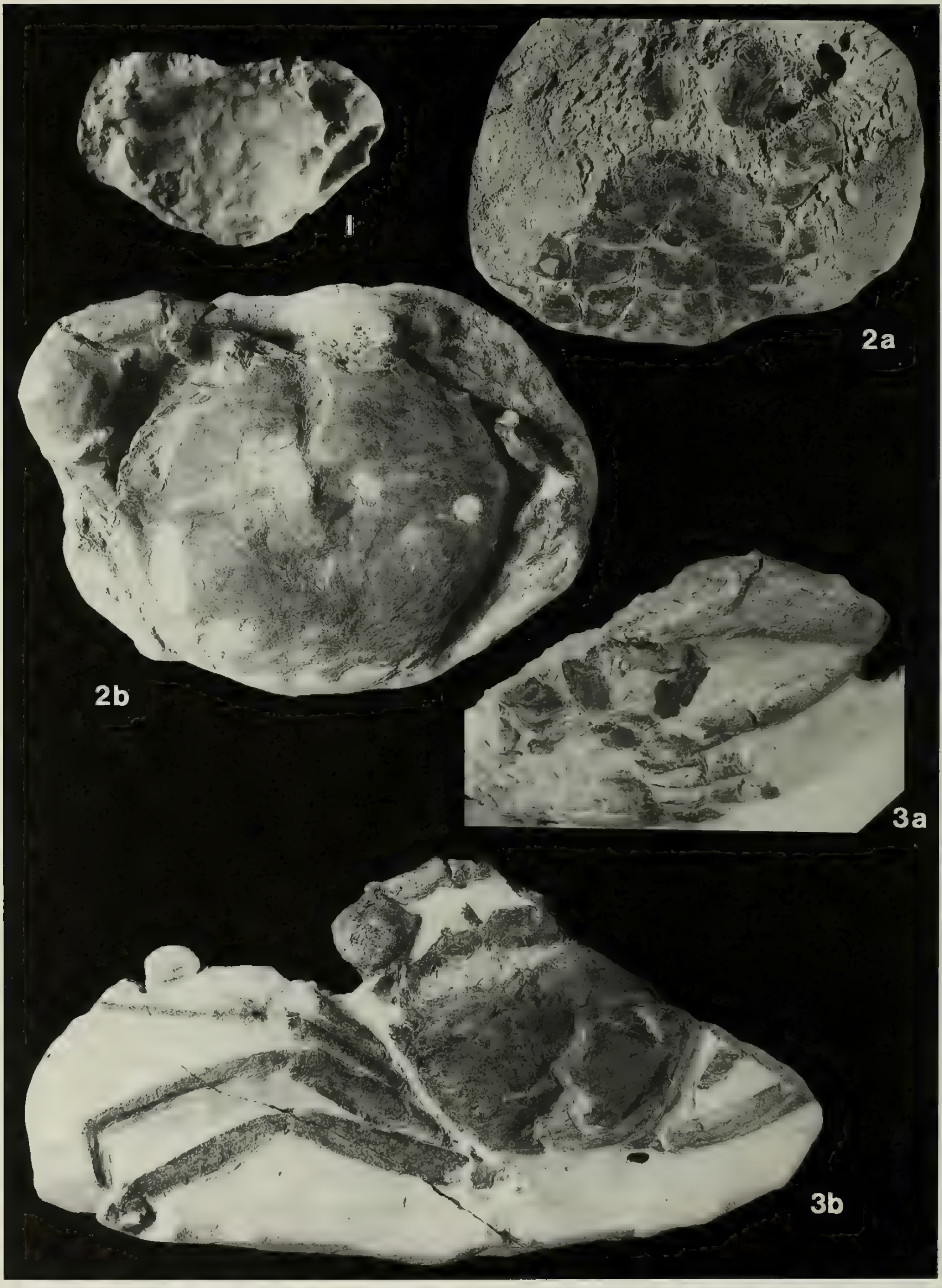
Material examined.—KPM-NN-5941 (holotype; cw 66.0+ mm, ca. 70 mm, cl 55.9 mm), 5942 (cw 15.5+ mm, cl 15.8 mm), 5943 (paratype 2; cw 32.5 mm, cl 24.4 mm), 198A (cw 31.4 mm, cl 28.3 mm), 198B (cw 49+ mm, cl 44+ mm), IGPS coll. cat. no. 103703 (paratype 1; cw 59.0 mm, cl 51.5 mm).

Diagnosis.—Small *Chaceon* with 4 faint projections on frontal margin, and 3 distinct spines and 2 very faint spines or lobes on anterolateral margin. Male abdomen relatively narrow.

Description.—Carapace hexagonal in outline, broader than long. Frontal margin about 0.25 of maximum width with 2 very low medial and 2 lateral lobes. Orbit large; relatively shallow; margin rounded. Anterolateral margin convex with first, third, and fifth spines distinct and second and fourth present as very low spines or lobes. First spine (outer orbital) directed obliquely anteriorly. Second minute spine observed in smaller specimen (paratype 2: Figs. 1, 4a), being indistinct lobe in largest specimen (paratype 1: Figs. 2, 4c). Third spine pointed with broad base. Fourth spine very low with blunt tip. Fifth spine triangular, largest, directed laterally. Distance from first to third spines slightly shorter than that from third to fifth. Dorsal surface moderately convex; rugose, granulated in posterior half of large specimen (Figs. 2, 3). Branchial region sparsely granulated. Sparse granules on protogastric, mesogastric, and cardiac regions. Regions divided by shallow depressions. Weakly developed transverse ridge extends from branchiocardiac groove to fifth anterolateral spine. In smallest specimen (KPM-NN-5942), however, dorsal regions well divided by deep grooves; proto-, meso- and metagastric, cardiac and branchial regions convex; an arched convex, well demarcated ridge extends from branchiocardiac groove to fifth anterolateral spines. Frontal and anterolateral spines of carapace proportionally larger than in other larger specimens.

Male abdomen relatively narrow; fourth segment slightly shorter than fifth; lateral margins of fifth segment almost parallel; telson triangular.

Chelipeds nearly equal in size. Upper surface of merus with small subdistal spine; carpus with strong inner distal spine. Palm



Figs. 1–3. *Chaceon matsushimai,* new species. 1, Paratype 2, KPM-NN-5943, carapace, ×1.0; 2, Paratype 1, IGPS coll. cat. no. 103703, ×1.0, 2a, thoracic sternites and abdominal somites, 2b, carapace and cheliped; 3, Holotype, KPM-NN-5941, 3a, left cheliped, ventral view, ×0.7, 3b, left cheliped, pereiopods and carapace, ×1.0.

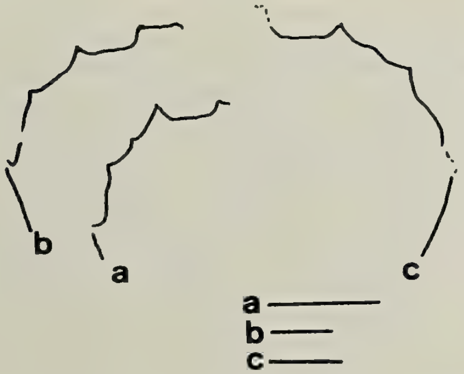


Fig. 4. *Chaceon matsushimai,* new species. Front-orbital and anterolateral margins. a, paratype 2; b, holotype; c, paratype 1. Scales: 1 cm.

sparsely granulated on outer and upper surfaces. Both fingers with strongly serrated occlusal margins; longitudinal furrow and row of pits present on outer surface.

Ambulatory legs long; dactyli dorsoventrally compressed, slightly curved downward.

Etymology.—In honor of Dr. Yoshiaki Matsushima of the Kanagawa Prefectural Museum of Natural History who has made great contributions to the geology and paleontology of the Kanto region as well as to Quaternary molluscan paleontology and paleoecology.

Remarks.—The present new species most closely resembles members of the living *Chaceon granulatus* species group, viz. *C. granulatus* (Sakai, 1978), *C. manningi* Ng et al., 1994, *C. karubar* Manning, 1993, and *C. micronesicus* Ng & Manning, 1998, in having granulose branchial region, very low second and fourth anterolateral spines, and dorsoventrally flattened dactyli of ambulatory legs. In addition to the small adult size, however, *Chaceon matsushimai* is easily distinguished from these living species by having very faintly projected frontal spines, relatively weaker second and fourth anterolateral spines, a broader and shallower orbit and a less granulated carapace. Moreover, the male abdomen, especially the fourth and fifth segments, are proportionately narrower than those of above mentioned living species (see Ng & Manning 1998). The present new species also resembles *Chaceon bicolor* Manning & Holthuis, 1989, from the North and South Pacific Ocean in having lobiform second and fourth anterolateral spines, but is distinguished from that extant species by having dorsoventrally flattened dactyli of ambulatory legs and exhibiting less developed frontal spines.

The general outline of the carapace of the new species resembles those of the genus *Geryon* Krøyer, 1837, in appearance, i.e., frontal spines are very low and the anterolateral margin has very faint second and fourth spines which are sometimes undiscernible, instead of five distinct spines. Although the second spine of the left anterolateral margin is entirely undiscernible in the holotype specimen (Figs. 3, 4b), minute spines or convexities are observed in paratypes 1 and 2 (Figs. 4a, c).

The length/width ratio of the merus of the fifth ambulatory leg of the holotype specimen is 4.3. Due to compression after burial, unfortunately, this value is by no means reliable.

The only known other fossil species of the genus is *Chaceon peruvianus* (d'Orbigny, 1842) from the middle Eocene of Argentina, which was recently transferred from the extinct genus *Archaeogeryon* Colosi, 1923 (Schweitzer & Feldmann 2000).

The fossil species of the genus *Geryon* had hitherto been restricted to the Miocene to Pliocene of Europe-Tethys region (see Dawson & Webber 1991). Other records of fossil Geryonidae are the extinct genera *Archaeogeryon* Colosi, 1923, *Coeloma* A. Milne-Edwards, 1865 and *Archaeoplax* Stimpson, 1863 (Glaessner 1969). *Archaeogeryon* was known from the Miocene of South America (Glaessner 1969, Morris, 1980; the geologic age may have to be reassigned, see Schweitzer & Feldmann 2000). *Archaeoplax* has been reported from the Miocene of North America (Rathbun 1935). Although *Coeloma* has been reported from the Eocene to Oligocene rocks of Europe and North America, the placement within the Geryonidae is still uncertain because it differs considerably from the living species of Geryonidae in morphology of the dorsal carapace (Schweitzer & Feldmann 2000).

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A new species of freshwater crab (Brachyura: Potamoidea: Potamonautidae) from the Ruwenzori region of western Uganda, East Africa

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Abstract.—We report here on a collection of freshwater crabs of the family Potamonautidae Bott, 1970 from Uganda, East Africa, as part of a study on the relationships between freshwater crabs and river blindness (onchocerciasis). The collection comprised more than a hundred specimens belonging to two species of *Potamonautes* MacLeay, 1838, *P. aloysiisabaudiae* Nobili, 1905, and *P. rukwanzi,* new species. The new species described here was collected from an isolated crater lake in the Ruwenzori Mountain region of western Uganda. The species is distinguished by a combination of characters of the carapace, abdomen, sternum, chelipeds, and the first gonopod. Intraspecific comparisons between adults, subadults and juveniles, and between males and females, are also presented. The addition of *P. rukwanzi,* brings to twelve the number of species of freshwater crabs reported from Uganda.

The freshwater crabs reported on here were obtained during a long-term study of onchocerciasis (river blindness) in Uganda carried out by scientists from the Bernhard Nocht Institute for Topical Medicine, Hamburg, Germany. The survey aimed to identify associations between freshwater crabs and the aquatic larval stages of the biting blackflies of the genus *Simulium* Latreille, 1802 that serve as vectors for the parasite *Onchocerca volvulus* Leuckart, 1893. The immature stages of *Simulium* need to develop in fast-flowing rivers and streams, and must attach themselves to supports (e.g., floating vegetation or rocks). An interesting exception are those few species (including those that function as vectors of onchocerciasis in East and Central Africa) that develop in an obligate phoretic association with river crabs in order to complete their development into adult flies (McMahon 1951, Barnley & Prentice 1958, Williams et al. 1964, Warner 1977, Katz et al. 1982).

Control measures for the vectors of onchocerciasis depend (in part) on the understanding of the relationships between *Simulium* larvae and freshwater crabs (McMahon et al. 1958, Rodger 1977, Williams 1991). This close ecological association between the blackfly vectors of onchocerciasis and freshwater crabs in this part of Africa means that researchers need to be able to distinguish between different species of freshwater crabs and to understand the composition of the crab fauna of this region. However, identification of African freshwater crabs has long been problematic (Williams 1991, Cumberlidge 1999) and misidentification of species is common in many studies. Furthermore, the freshwater crab fauna of East and Central Africa is poorly known and it is likely that there are still a large number of species still to be discovered. This situation further contributes to the confusion that surrounds studies involving the freshwater crabs of this region of Uganda.

The freshwater crabs used were collected in the Ruwenzori Mountain region of western Uganda. Fast-flowing mountain streams, major rivers and a series of small crater lakes associated with the Western Rift Valley characterize the region. The vegetation includes moist tropical forest on the mountain slopes and dry savanna in the lowland areas.

The specimens of the new species from Rukwanzi Crater Lake have a number of important characters that do not conform to the descriptions of any known species (Bott 1955, Cumberlidge 1999). This new species is described from an adult male, and the taxonomically important characters of the gonopods, abdomen, mouthparts, carapace, sternum, and chelipeds are illustrated. This is the 55th species of *Potamonautes* MacLeay, 1838 to be described (Bott 1955, Williams 1991, Cumberlidge 1999).

Materials and Methods

In 1993 a total of 86 crab specimens were collected from Rukwanzi Crater Lake in the Ruwenzori Mountains of western Uganda (0°28′41″N, 30°16′44″E) by one of the authors (RG). Air and water temperature data were collected and the ecological conditions of each locality in the lake were noted. Each freshly collected crab was immediately examined in the field for attached blackfly larvae or pupae, and this information was used by the onchocerciasis research team. Specimens were preserved in formalin in the field and sent to Northern Michigan University (NMU) for identification. Upon arrival at NMU, the specimens where transferred to 70% alcohol and added to the collection. Next, the gender and stage of development of each freshwater crab specimen was noted (whether juvenile, subadult, or adult) and features of the carapace, cheliped, pereiopods, sternum, abdomen, and gonopods of the largest adult male and female specimens were examined and drawn to scale. The terminology used to describe the anatomical features is that proposed by Cumberlidge (1999).

Four dimensions of the carapace were recorded from all available specimens: length, width, height, and front width. Measurements of carapace width (cw), carapace length (cl), carapace height (ch), and front width (fw) were made with digital vernier callipers (Mitutoyo Digimatic Model CD-6″P), and are given correct to at least 0.1 mm. Carapace proportions were calculated according to fw or cl. The ratios of carapace width, carapace length and carapace height to front width (cw/fw, cl/fw and ch/fw) and front width relative to carapace length (fw/cl) were examined using linear regression analysis, and were each found to provide a useful index for making intraspecific and interspecific comparisons. Two-tailed t-tests were used to test for differences between the mean values of carapace proportions between males and females, and between adults and non-adults.

Crabs carrying eggs or hatchlings were assumed to be sexually mature. Sexual maturity in females was otherwise determined by the extent of the development of the female abdomen (which is broad enough to cover the entire sternum and to touch the bases of the coxae of the walking legs in adults) and of the female pleopods (which are noticeably broader and more hair-fringed than those of juvenile and sub-adult females) (Cumberlidge 1999). This permitted the separation of adult females from juveniles and subadults, and allowed an estimate of the molt of puberty for the species. Because male and female freshwater crabs of the same species grow at similar rates and reach a comparable range of body sizes as adults, this measurement also allows an estimate of the stage of development of male crabs of the same species.

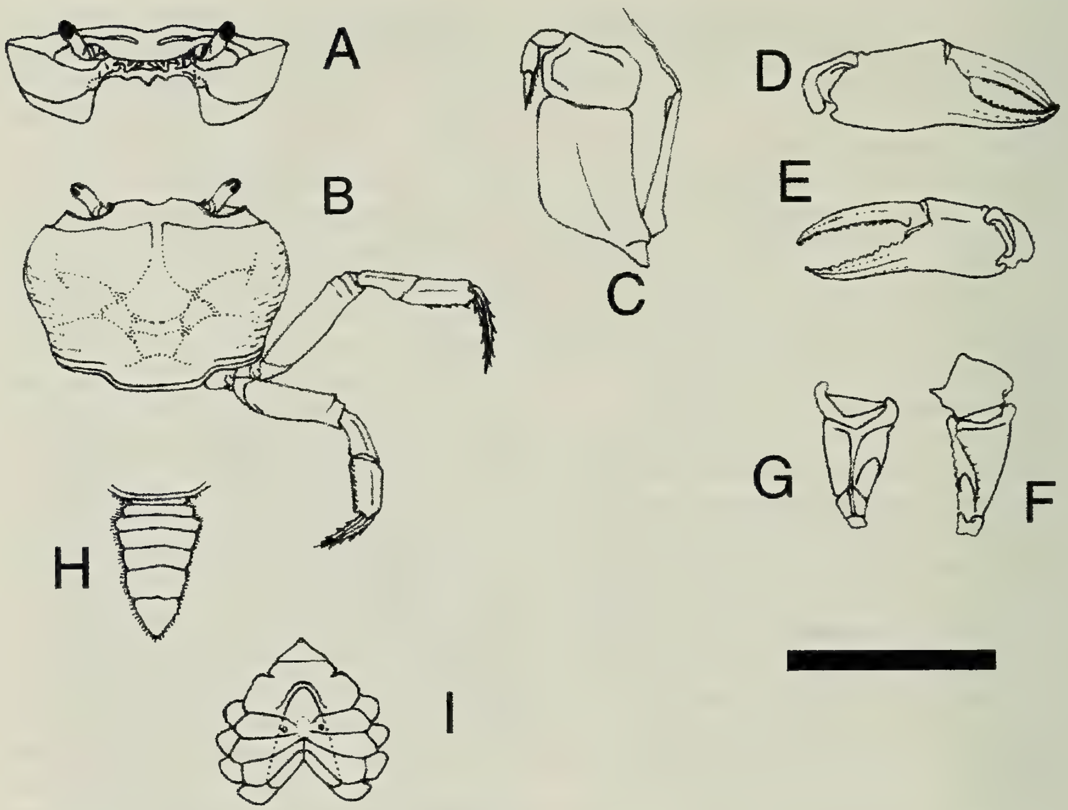

Fig. 1. *Potamonautes rukwanzi,* new species, adult male holotype from Rukwanzi Crater Lake, Uganda (cw 23 mm), NMU. A, cephalothorax, frontal aspect; B, whole animal, dorsal aspect; C, left third maxilliped; D, male right cheliped; E, male left cheliped; F, merus of cheliped, superior view; G, merus of cheliped, ventral view; H, male abdomen; I, male sternum. Scale bar equals 20 mm (a, b, d–i), and 7 mm (c).

Systematic Account

Potamonautes rukwanzi, new species

Figs. 1, 2

Type material and type locality.—Holotype NMU 16.07.1993, adult male, cw 23.0 mm, paratype adult female, Rukwanzi Crater Lake, Uganda (0°28′41″N, 30°16′44″E) 16 Jul 1993. Paratypes: same locality as holotype, 1 female, NMU; 1 female, 4 males, Zoologisches Museum Hamburg, Germany.

Material examined.—Including holotype and paratypes: 46 males cw 28.10–30.80 mm, 41 females cw 28.02–31.67 mm, same locality as types.

Diagnosis.—Vertical suture on carapace sidewall present. Carapace flat (ch/fw = 0.95), dorsal surface texture of carapace smooth, conspicuously sculpted by deep cervical, cardiac, semi-circular, urogastric, transverse branchial grooves. Exorbital tooth small, low, blunt. Epibranchial tooth low, small, not distinguishable from rest of anterolateral margin. Anterolateral margin posterior to epibranchial tooth smooth, distinctly raised, posterior end curving inward slightly in branchial region, not continuous with posterolateral margin.

Description of holotype.—Carapace outline transversely oval, 1.36 times as wide as long, widest on anterior third (cw/fw = 3.15), flattened (ch/fw = 0.95); dorsal surface texture smooth, conspicuously sculpted by deep cervical, cardiac, semi-circular, urogastric, transverse branchial grooves. Front slightly bilobed, relatively wide,

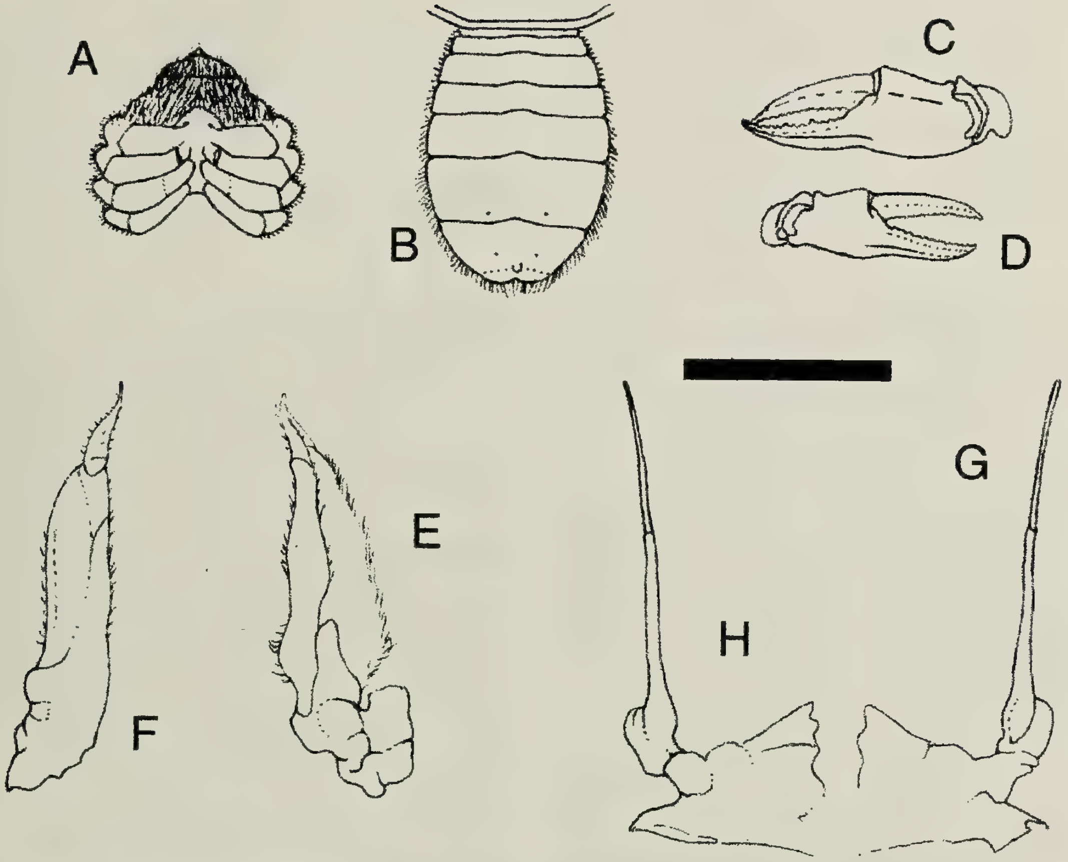

Fig. 2. *Potamonautes rukwanzi,* new species, features of a selected female and reproductive characters of adult male holotype from Rukwanzi Crater Lake, Uganda (cw 23 mm), NMU. A, female sternum; B, female abdomen; C, female left cheliped; D, female right cheliped; E, male right gonopod 1, ventral view; F, male right gonopod 1, dorsal view; G, male right gonopod 2, ventral view; H, male right gonopod 2, dorsal view. Scale bar equals 20 mm (a–d), and 5 mm (e–h).

about one-third cw (fw/cw = 0.31), front moderately deflexed, not meeting inferior margins of antennulular fossae. Postfrontal crest spanning entire carapace, consisting of fused epigastric, postorbital crests, meeting anterolateral margins at epibranchial teeth. Anterolateral margin between exorbital angle and epibranchial tooth lacking intermediate tooth; anterolateral margin posterior to epibranchial tooth smooth, distinctly raised, posterior end curving inward slightly in branchial region, not continuous with posterolateral margin. Exorbital tooth small, low, blunt, epibranchial tooth extremely reduced, not distinguishable from granules on rest of anterolateral margin. Carapace sidewalls completely smooth, each sidewall divided into 2 parts by longitudinal (epimeral) suture, beginning medially at lower margin of orbit, curving backward across sidewall; vertical suture absent.

Mandibular palp 2-segmented; terminal segment single, undivided, with hair but no hardened process at junction between segments. Epistomial tooth triangular, pointed downward, lined by granules. Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings at superior lateral corners; long flagellum on exopod of third maxilliped; ischium of third maxilliped smooth, vertical groove

Table 1.—The ratio of carapace width (cw), carapace length (cl), and carapace height (ch) to front width (fw) in male and female *Potamonautes rukwanzi,* new species from Uganda (n.s. = not significant).

Sex	cw/fw Mean ± *SD*	cl/fw Mean ± *SD*	ch/fw Mean ± *SD*
Male	3.17 ± 0.10 (n = 46)	2.36 ± 0.06 (n = 46)	0.95 ± 0.05 (n = 46)
Female	3.14 ± 0.13 (n = 41)	2.37 ± 0.09 (n = 41)	0.94 ± 0.05 (n = 41)
	($p > 0.05$, n.s.)	($p > 0.05$, n.s.)	($p > 0.05$, n.s.)

present. First thoracic sternal sulcus, between sternite one (s1) and sternite two (s2), short; second sulcus (s2/s3) deep, running horizontally across sternum; third sternal sulcus (s3/s4) consisting of 2 short notches at edges of sternum, but continuing as shallow, barely visible, v-shaped groove; anterior margin of sterno-abdominal cavity raised, in advanced position on sternite four (s4), almost meeting s3/s4. All episternal sulci (i.e., s4/e4, s5/e5, s6/e6 and s7/e7) distinct. Fifth sternite (s5) with pair of sternal knobs. Fourth to sixth sternites (s4/s5, s5/s6, s6/s7) within sterno-abdominal cavity discontinuous (i.e., separated medially), seventh sternite (s7/s8) continuous; short median line running perpendicular to s6/s7 and s7/s8. Adult male abdomen segment three (a3) to abdomen segment seven (a7) tapering inward to form long triangle, a3 widest, telson (a7) narrowest. Telson sides straight, triangular, not bell-shaped; abdomen segment six (a6) long, almost as long as width of distal margin of a6. Sternal suture s4/s5 meeting margin of telson close to (but not at) junction between a7/a6; s5/s6 meeting margin of a6 in middle of segment, s6/s7 meeting a5 just short of a5/a6 junction.

Terminal article of gonopod 1 (go1) short (ratio of length of terminal article to subterminal segment 0.30), longitudinal groove on terminal article narrow along entire length, clearly visible on ventral, superior sides, but not visible on dorsal side; lateral, medial folds of ventral side of terminal article equal in height, width; terminal article slim, cone-shaped, almost straight, directed slightly outward; tapering to upcurved tip with clear apical opening. Junction between terminal article and subterminal segment of go1 marked by deep sulcus ventrally and dorsally; go1 with broad dorsal membrane. Gonopod 2 (go2) longer than go1; terminal article of go2 with long flagellum, slightly shorter than subterminal segment (ratio of length of terminal article to subterminal segment 0.70).

Dactylus of right cheliped arched, curving downward, relatively slim (0.33 height of palm); upper margin of dactylus smooth; finger of propodus slim (0.33 height of palm), lower margin of propodus of cheliped slightly indented. Fingers of propodus, dactylus each with row of small, even-sized teeth, closed fingers leaving wide oval interspace. Inner margin of inferior face of merus of pereiopod one (P1) lined by row of small uneven teeth, outer margin lined

Table 2.—The ratio of carapace width (cw), carapace length (cl), and carapace height (ch) to front width (fw) in adult and non-adult (combined juveniles and sub-adults) of *Potamonautes rukwanzi,* new species from Uganda (n.s. = not significant, s. = significant).

Age class	cw/fw Mean ± *SD*	cl/fw Mean ± *SD*	ch/fw Mean ± *SD*
Adult	3.17 ± 0.10 (n = 78)	2.38 ± 0.06 (n = 78)	0.95 ± 0.05 (n = 78)
Non-adult	3.00 ± 0.15 (n = 8)	2.28 ± 0.12 (n = 8)	0.88 ± 0.00 (n = 8)
	($p < 0.05$, s.)	($p > 0.05$, n.s.)	($p > 0.05$, n.s.)

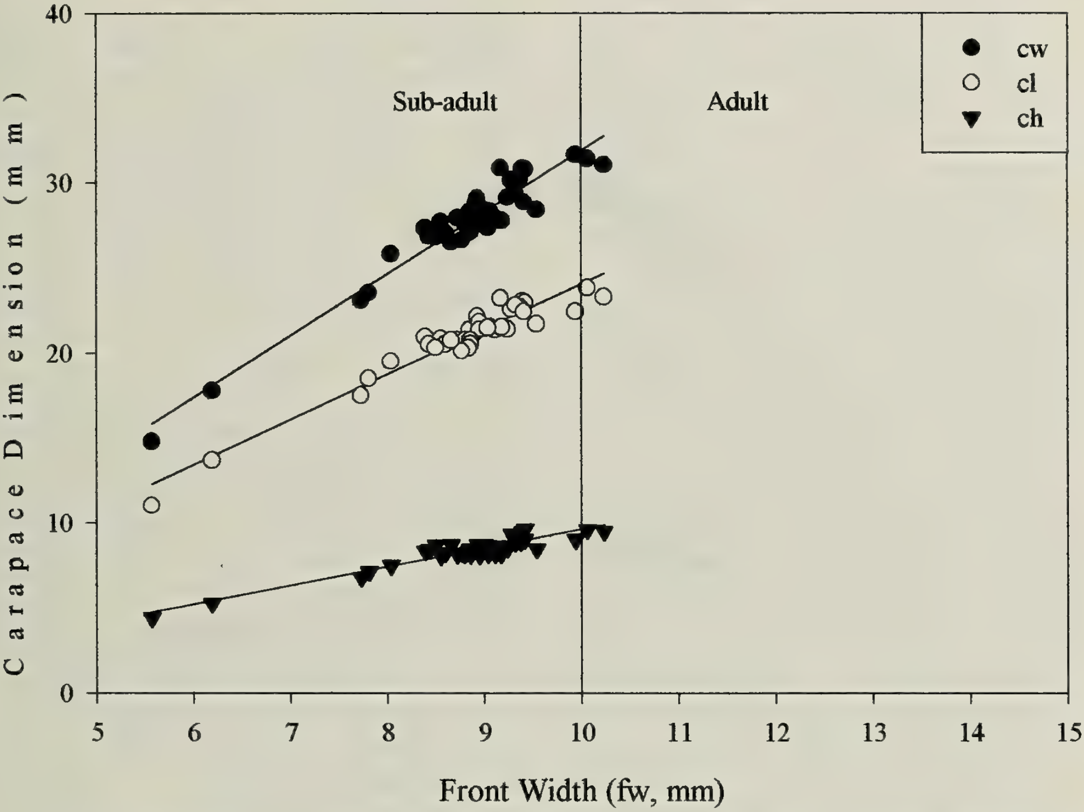

Fig. 3. Comparison of the dimensions of the carapace relative to body size for 40 female specimens of *Potamonautes rukwanzi,* new species. R-values (all at df = 39) indicate very highly significant ($P < 0.001$) correlation between size classes. cw = 3.63 + 4.44, R = 0.97; cl = 2.70–2.827, R = 0.97; ch = 1.10–1.35, R = 0.94. cw = carapace width at the widest point; cl = carapace length, measured along the median line; ch = cephalothorax height, the maximum depth of the cephalothorax; fw = front width, the width of the front measured along the anterior margin; r = correlation coefficient.

by small even teeth; tooth on distal merus small but detectable; superior surface of merus smooth. Inner margin of carpus of P1 with two teeth, second much smaller than first; first carpal tooth broad, triangular, pointed, second carpal tooth low, blunt, with several granules on raised margin behind it. Merus, carpus, propodus, dactylus of pereiopods 2 to 5 (P2 to P5) all shortened: P3 longest, P5 shortest, inner margin of propodus of P5 with broad, raised ridge along length, dactyli of P2-5 tapering to point, each bearing 4 rows of downward-pointing sharp bristles; dactylus of P5 shortest.

Size.—Dimensions of largest available adult male measured in millimeters are: cw 31.12, cl 22.9, ch 9.42, fw 9.60. Mean carapace proportions (n = 86) are: cw/fw = 3.15, cl/fw = 2.39, cw/cl = 1.36, ch/fw = 0.95, fw/cl = 0.42 and fw/cw = 0.31.

Pubertal molt.—A female with hatchlings (cw 22.9 mm) and three other ovigerous females (cws 29.7, 31.0, 36.3 mm) indicate an adult size range of cw from approximately 22 to 37 mm. The largest immature female with a slim abdomen that did not overlap the coxae of walking leg measured cw 17.80 mm. The pubertal molt, from sub-adult to sexually mature adult, was estimated to occur between cw 22 to 25 mm.

Etymology.—The species is named for the Rukwanzi Crater Lake, the only known

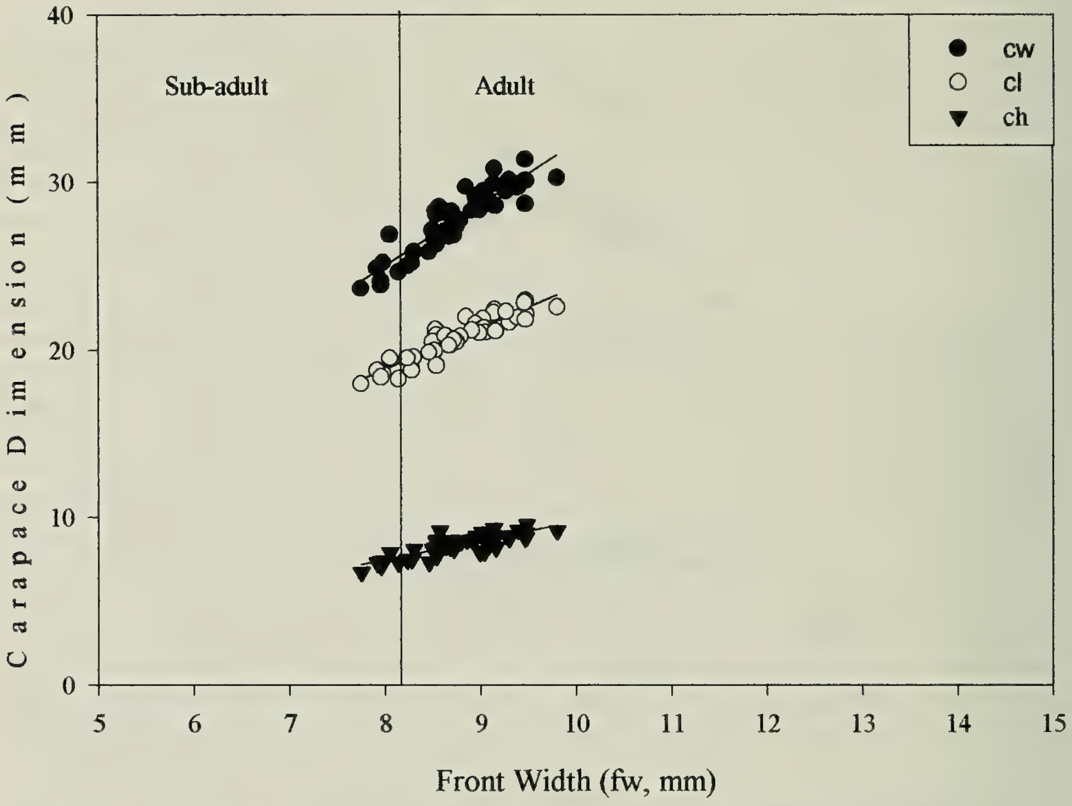

Fig. 4. Comparison of the dimensions of the carapace relative to body size for 46 male specimens of *Potamonautes rukwanzi,* new species. R-values (all at df = 45) indicate very highly significant ($P < 0.001$) correlation between size classes. cw = 3.65 + 4.20, r = 0.91; cl = 2.45–0.76, r = 0.92; ch = 1.14–1.62, r = 0.83. cw = carapace width at the widest point; cl = carapace length, measured along the median line; ch = cephalothorax height, the maximum depth of the cephalothorax; fw = front width, the width of the front measured along the anterior margin; r = correlation coefficient.

locality where it occurs. The specific name *rukwanzi* is a noun in apposition.

Remarks.—The new species is assigned to the family Potamonautidae Bott, 1970 because it conforms with the diagnosis provided by Bott (1955) and Cumberlidge (1999). These characters include a two-segmented mandibular palp, antennules folding horizontally, anterior respiratory openings that are simple holes, and a male abdomen with seven visible segments, where abdominal segment 1 is clearly visible. The new species is assigned here to *Potamonautes* because it has a number of characters that conform to the revised diagnosis of the genus provided by Cumberlidge (1999). These characters include a postfrontal crest that completely crosses the carapace to meet the anterolateral margins at the epibranchial teeth; an anterolateral margin lacking an intermediate tooth between the exorbital angle and the epibranchial tooth; a two-segmented mandibular palp with terminal segment single, undivided, and with hair at junction between segments; a third maxilliped with exopod having a long flagellum; a first gonopod with terminal article short, about one-third as long as the subterminal segment of gonopod 1; and a second gonopod with the terminal article a long flagellum about 0.75 times as long as the subterminal segment of gonopod 2.

Ecology.—Rukwanzi Crater Lake (altitude 1340 m) has a diameter of approximately 300m. When crabs were caught and abiotic features of Rukwanzi Crater Lake were measured, the lake was warm (mean water surface temperature 25.1°C), highly saline (mean conductivity 393 μS/cm) and highly alkaline (pH 9.5).

Distribution.—Uganda. Known only from Rukwanzi Crater Lake, which is a steep-walled crater lake that was probably formed during the Pleistocene (Beadle 1981).

Comparisons.—Other freshwater crabs found in lakes associated with the East African rift valley include species belonging to two families, the Potamonautidae and the Platythelphusidae Colosi, 1920 (Bott 1955, Cumberlidge 1999). *Potamonautes rukwanzi* is clearly distinguished from any of the six species in the Platythelphusidae by clear differences in the characters of the carapace, mandible, third maxilliped, sternum, gonopods 1 and 2, pereiopods and chelipeds (Cumberlidge 1999). Preliminary cladistic studies (Cumberlidge 1999) indicate that these six species form a monophyletic group that is distinct from the clade that includes members of *Potamonautes* (Potamonautidae).

Potamonautes rukwanzi is most likely to be confused with other small species of freshwater crabs occurring in East Africa because all have a weak postfrontal crest, a distinct vertical sulcus on the ischium of the third maxilliped, and a reduced or absent epibranchial tooth (Cumberlidge 1999). However, all of these taxa can be distinguished from *P. rukwanzi* by examination of the carapace sidewall: they all possess a distinct vertical sulcus in the subhepatic region that divides the sidewalls into three parts, while this vertical sulcus is completely absent in *P. rukwanzi* so that the carapace sidewalls are divided into only two parts.

Morphometric Analysis

In general, the carapace proportions of *P. rukwanzi* are typical of those found in species of lake-living or river-living freshwater crabs in Africa (Cumberlidge 1999). For example, the mean cw/fw ratio in *P. rukwanzi* = 3.15 ± 0.11 (n = 86) falls within the range of species with a carapace of medium width (cw/fw = 3.1–3.5) defined by Cumberlidge (1999). In West Africa, where there are few lakes, a moderately widened carapace is commonly associated with stream-living species (Cumberlidge 1993a, 1993b, 1993c; Cumberlidge 1994a, 1994b). Moreover, the mean ch/fw ratio in *P. rukwanzi* = 0.95 ± 0.05 (n = 86), falls within the range of species with a flat carapace (ch/fw = 0.8–1.0) also identified by Cumberlidge (1999). A flattened carapace is commonly associated with completely aquatic species in West Africa (Cumberlidge 1999). Finally, the mean fw/cl ratio in *P. rukwanzi* = 0.42 ± 0.07 (n = 86) falls within the range of species with a relatively wide front (fw/cl = 0.4–0.5) identified by Cumberlidge (1999). A wide frontal margin is associated with aquatic freshwater crabs and is found in all species of West African *Potamonautes* (fw/cl = 0.46–0.5) (Cumberlidge 1999).

The relative proportions of the carapace of juvenile and subadult males of *P. rukwanzi* differ from adult male crabs in that the carapace of juveniles is significantly more narrow than that of adults (cw/fw = 0.059fw + 2.65, df = 85, R = 0.3, $P < 0.05$). In contrast, the carapace length (cw/fw) and carapace thickness (ch/fw) do not show any real increases as crabs grow. These relationships are described by cl/fw = 0.01fw + 2.26, df = 85, R = 0.104 (indicating no significant correlation, $P > 0.05$) and by ch/fw = 0.02fw + 0.75, df = 85, R = 0.25 (indicating no significant correlation, $P > 0.05$) between size groups. In summary, the carapace of adult male *P. rukwanzi* is relatively wider than that of juvenile crabs, but the carapace length and carapace height are similar in all age groups.

The relative proportions of the carapace of juvenile and subadult female *P. rukwanzi* were not found to differ from adult female crabs. The relative carapace width (cw/fw), relative carapace length (cl/fw) and relative carapace height (ch/fw) of juveniles were all found to be different from those of adults. These relationships are described by $cw/fw = 0.08fw + 2.38$, $df = 85$, $R = 0.58$ (indicating a significant correlation, $P < 0.001$) between size groups; $cl/fw = 0.06fw + 1.861$, $df = 85$, $R = 0.55$ (indicating a significant correlation, $P > 0.001$) between size groups; $ch/fw = 0.03fw + 0.7$, $df = 85$, $R = 0.50$ (indicating a significant correlation, $P > 0.001$) between size groups. In summary, the carapace of adult female *P. rukwanzi* is significantly wider, longer and higher than that of juvenile females. The finding that the carapace height of female *P. rukwanzi* increases significantly as a crab grows agrees with the assertion by Warner (1977) that the carapace of adult female freshwater crabs become "thicker" (i.e., higher) than those of non-adult females. The positively allometric increase in branchial chamber volume may reflect the increased oxygen demands placed on females by the developing ova.

Comparisons of the mean carapace proportions of male and female crabs, and between adult and non-adult crabs (juveniles and sub-adults grouped together) are shown in Tables 1 and 2. No significant difference ($P > 0.05$) was found between adult male and female *P. rukwanzi* for any of the three carapace proportions (cw/fw, cl/fw, and ch/fw) so morphometric data for adult crabs of both sexes was pooled.

A significant difference ($P < 0.05$) was found between the carapace width (cl/fw) of adult and non-adult crabs indicating positive allometric growth, but no significant difference ($P > 0.05$) was found between the carapace length (cl/fw) or carapace height (ch/fw) of adults and non-adults, indicating isometric growth. This means that valid comparisons of carapace proportions such as length (cl/fw) and height (ch/fw) can be made between crabs of any size and age, but comparisons of carapace width (cw/fw) should be restricted to adult specimens only. Characters for which isometric (relatively equal) growth was found to occur can be used for identification of the species and for interspecific comparisons, because these proportions do not differ between adult, sub-adult and juvenile crabs. For male *P. rukwanzi,* the characters for which isometric growth occurs include cl/fw and ch/fw. Because the growth rate of these characters does not vary between age classes, these two proportions may prove to be useful descriptive morphometric characters for making interspecific comparisons.

The abiotic conditions of Rukwanzi Lake such as water temperature and conductivity were typical of the values recorded from other lakes that make up the chain of late Pleistocene volcanic crater lakes in the Western Rift Valley (Beadle 1981). Further studies of the ecology and distribution of *P. rukwanzi* are warranted because this species may be endemic to this lake, making a determination of its conservation status important. No specimens of *P. rukwanzi* were found to harbour *Simulium* larvae and pupae. This is not surprising because the blackfly vector of onchocerciasis depends on well shaded streams in forest environments and is not adapted to the conditions in an open and stagnate crater lake (Williams 1991).

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Redescription of *Dynameniscus carinatus* (Richardson, 1900) (Crustacea: Isopoda: Sphaeromatidae)

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Abstract.—*Dynameniscus carinatus,* originally described one hundred years ago from a single female from deep water off Georgia, U.S.A., is redescribed, based on an additional male and two females, all from the Caribbean. The genus is redefined, and its affinities briefly discussed. Its subfamilial placement remains uncertain, however, given a number of unusual features in the mouthparts, pleopods, and uropods.

Harriet Richardson described *Cilicaea carinata* in 1900, from a single specimen collected in 1885 from deep water off Georgia, U.S.A. In 1905, Richardson placed the species in the new genus *Dynameniscus,* but unfortunately, this genus was not included in Hansen's (1905) monographic review of the family, and has since been largely overlooked. Richardson (1906) gave a further account of the genus which thereafter remained unmentioned until Harrison (1984) referred to an ovigerous female of *Dynameniscus* sp., from which he extracted brood-pouch information. This specimen, the source of the deep water (804–1033 m) Caribbean record later mentioned in Harrison & Ellis (1991:938), was never described, but is included in this study. In 1999, a female specimen was found in a small collection of material from Texas A&M University Oceanographic Department, and two months later a male was found in a small collection of material from the University of the West Indies, from the vicinity of Jamaica. This new material significantly extends the known range of the species, and presents an opportunity to redescribe the species and to redefine the genus.

Family Sphaeromatidae

Dynameniscus Richardson, 1905

Dynameniscus Richardson, 1905:x, xi; 1906:16.—Harrison, 1984:379.—Harrison & Ellis, 1991:921, 938.

Diagnosis.—Male: Body fairly strongly vaulted, able to enroll (conglobate). Dorsal integument finely granulate and with larger tubercles, lacking setae. Anterior rostral process present, consisting of rounded boss-like process separating antennular bases (Fig. 1D). Anterior cephalon margin simple, not produced, not incised. Eyes simple, dorsolateral, ommatidia not visible. Pereonite 1 lateral margin somewhat produced anteriorly below eye, lacking 'keys'. Sternite 1 lacking mesial extensions. Coxae ventrally narrowed, with groove articulation; coxae 2–6 triangular, not overlapping, laterally contiguous when animal enrolled; coxae 4–5 not overlapping; coxa 6 acute but not produced ventrally, shorter than coxa 5; coxa 7 short, rounded, not ventrally produced. Marsupium lacking anterior and posterior pocket, formed by 4 pairs of medially overlapping oostegites. Pereonites 2–7, posterior margin not raised, all segments ornamented; pereonite 7 almost as wide as 6,

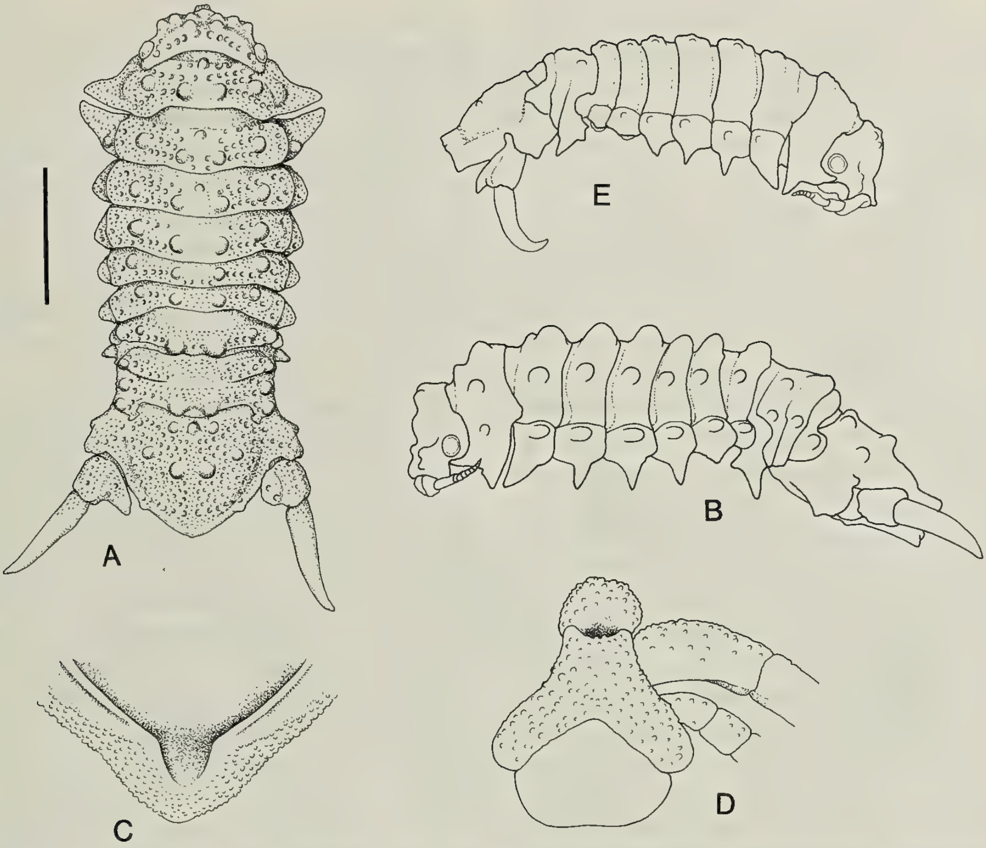

Fig. 1. *Dynameniscus carinatus* (Richardson, 1900). A, female, USNM 298346, off Aruba, in dorsal view, scale = 3 mm; B, same specimen, lateral view outline; C, same specimen, pleotelsonic apex in ventral view; D, same specimen, rostrum, epistome and left antennular and antennal bases in anterior view; E, holotype female, USNM 23907, lateral view outline, same scale as A.

similarly ornamented to preceding segments. Pereonite 6 not produced as in pereonites 5 and 7. Pleon consisting of 4 pleonites plus pleotelson, anterior 3 incomplete dorsally, sutures separate, reaching to lateral margin. Pleon sternite 1 wide. Pleonite 4 with complete posterior margin. Pleotelson similar in male and female, as wide as anterior pleon, somewhat domed, lacking dorsal processes, lateral margin entire, forming ridge; apex rounded in dorsal view, with strong median notch or incomplete groove in marginal flange in ventral view (Fig. 1C).

Antennular and antennal peduncles robust, calcified, not in contact mesially. Antennular peduncle (Fig. 2A) article 1 not anteriorly produced, lacking anterior lobe; peduncle article 2 twice longer than wide, lacking anterodistal or posterior lobe; peduncle article 3 about twice longer than wide; articles 2 and 3 colinear, not compressed; flagellum shorter than peduncle, but longer than peduncle article 3. Antennal peduncle articles colinear (Fig. 2B), articles 4 and 5 somewhat enlarged. Epistome anteriorly sessile, without median constriction, barely visible in dorsal view, anterior part not extended, anterior margin truncate to faintly concave. Mandible (Fig. 2C, D) incisor narrow, bicuspid; strongly sclerotised lacinia mobilis on left side having 3 or 4 cusps; spine row 'normal'; molar distally truncate, surface granular; palp of 3 articles

(Fig. 2E). Maxillule (Fig. 2G), lateral lobe spines smooth and serrate; mesial lobe with 3 robust setae. Maxilla (Fig. 2H) with distal setae pectinate or circumplumose. Maxillipedal palp articles 2–4 lobed (Fig. 2F), not elongate; article 2 somewhat expanded, article 5 4 times longer than basal width, distal margin of endite truncate to rounded, bearing several setulose setae, lacking clubbed setae, dorsomedial corner lacking long curving setae. Pereopods all ambulatory, robust, covered with pile of very short setules; accessory unguis simple, slender; ischium with sinuate seta. Pereopod 1 (Fig. 3A) barely subchelate, merus somewhat expended anteriorly. Pereopod 2 (Fig. 3B) similar to 3. Penes (Fig. 4F) basally separate, relatively slender-elongate, distally rounded. Pleopod 1 (Fig. 4A) lamellar, not operculate; exopod and endopod of similar size; exopod mesial margin of triangular endopod not indurate, endopod longer than wide, lacking lateral heel; exopod oblique, distal margin narrowly rounded, lacking serrations. Pleopod 2 (Fig. 4B) appendix masculina slender, elongate, slightly longer than ramus, articulating basally on endopod, latter longer than wide. Pleopod 3 (Fig. 4C), endopod longer than exopod; exopod lacking transverse suture; endopod lacking ridges. Pleopods 4 and 5, both rami lamellar, lacking folds and plumose marginal setae. Pleopod 4 (Fig. 4D) endopod lacking ridges and proximomedial lobe; exopod lacking transverse suture and ridges, lateral margin not thickened. Pleopod 5 (Fig. 4E, G) endopod lacking ridges; exopod with incomplete transverse suture in distal third, with three thin-walled scale patches on lateral margin. Uropodal rami similar in male and female, endopod reduced, fused with protopod; exopod elongate, articulated, terete.

Female: Similar to male, not strongly sexually dimorphic. Mouthparts not metamorphosed.

Remarks.—The generic status of *Dynameniscus* has long remained unassessed, given that *D. carinatus* was briefly described from a single female specimen (Richardson 1905, 1906). Because of this uncertainty, Harrison & Ellis (1991) excluded *Dynameniscus* from their key to the sphaeromatid genera. With a male and two females now available, details of at least some of the features considered to be of generic value can be provided, and a detailed generic diagnosis provided. Even with these additional characters, however, the affinities of the species still remain unclear.

The generic key (Harrison & Ellis 1991), while not a phylogenetic key, is nonetheless the only recent global identification guide to the sphaeromatid genera. This key takes *Dynameniscus* to a dead-end at the *Neonaesa-Geocerceis* couplet, neither of these genera sharing any characters in common that would suggest a close affinity. Marine genera with similar uropod morphology include the *Cilicaea-Cilicaeopsis-Paracilicaea* group (see Harrison & Holdich 1984), *Discerceis* Richardson, 1905, *Neonaesa* Harrison & Holdich, 1982, *Naesicopea* Stebbing, 1893, *Paracerceis* (see Harrison & Holdich 1982), *Pistorius* (see Harrison & Holdich 1982), *Cymodetta* (see Holdich & Harrison 1983), *Campecopea* Leach, 1814, and *Bathycopea* Tattersall, 1905 (see Bruce 1991, now placed in the Ancinidae, see Bruce 1993). Most of these genera belong to the subfamily Sphaeromatinae or Dynameninae, having the endopods or both rami of pleopods 4 and 5 with thickened fleshy ridges and folds; most of these genera also have metamorphosed mouthparts, and substantially different morphology to pleopods 1 and 2.

While *Dynameniscus* unambiguously belongs to the Sphaeromatidae, we refrain here from making any definitive statements on its phylogenetic position within the family, preferring to give a detailed generic diagnosis and description which includes most characters used in generic discrimination in this family. The lack of pleopodal folds or thickenings is a common reversal in the Sphaeromatidae (see Bruce, 1993,

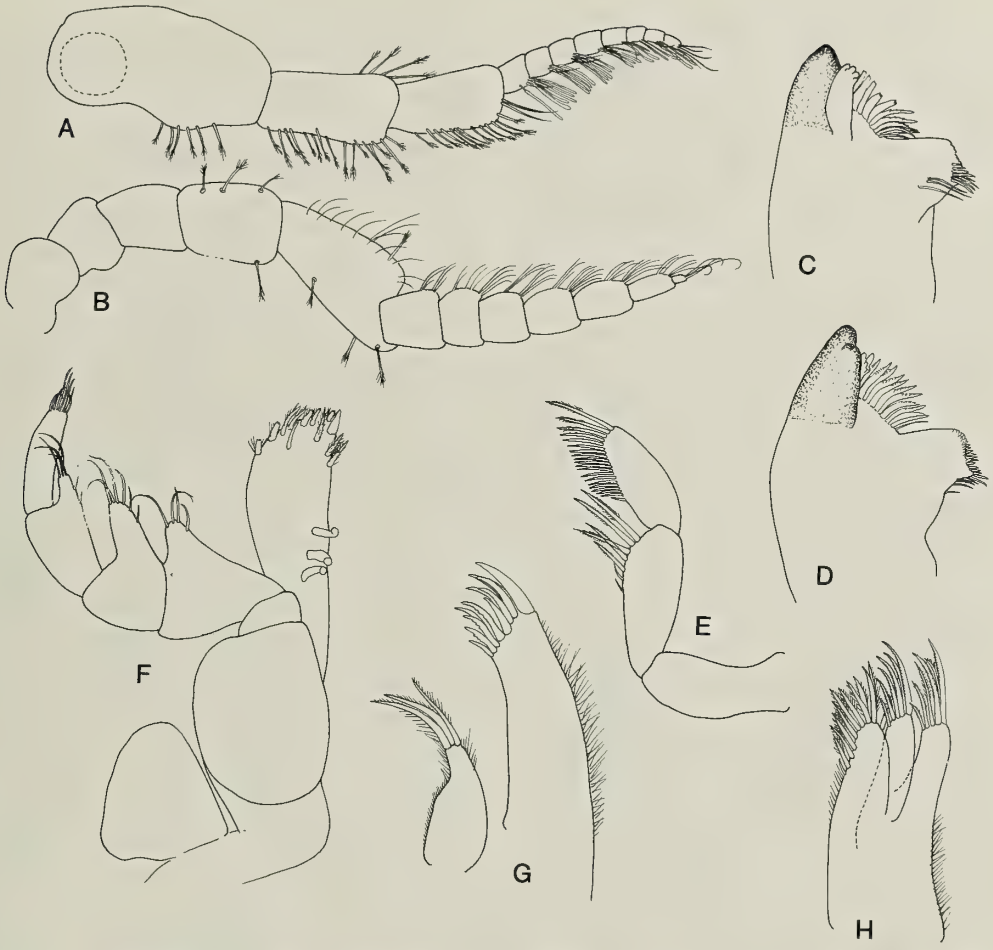

Fig. 2. *Dynameniscus carinatus* (Richardson, 1900), female, USNM 298346, off Aruba. A, antennule; B, antenna; C, left mandible; D, right mandible; E, mandibular palp; F, maxilliped; G, maxilla 1; H, maxilla 2.

1994, 1995, 1997), and we can deduce little from that character state. Until a phylogenetic character assessment exists for the family, we regard *Dynameniscus* as incertae sedis.

Dynameniscus carinatus (Richardson, 1900)
Figs. 1–4

Cilicaea carinata Richardson, 1900:224; 1901:535, fig. 17–19; 1905:309 [key], 319, fig. 350, 352.

Dynameniscus carinata: Richardson, 1905: x, xi [designation of new genus in Introduction].

Dynameniscus carinatus: Richardson, 1906:16, fig. 20.—Schultz, 1969:118, fig. 164.—Harrison, 1984:379.—Harrison & Ellis, 1991:921, 938, fig. 7a.

Material examined.—Holotype, USNM 23907, ♀ tl 10.1 mm, R/V *Albatross* sta 2415, 30°44′N, 79°26′W, off Georgia, U.S.A., 805 m, coral and coarse sand, shells and foraminiferans, 1 Apr 1885. USNM 298346, (ex TAMU 2—5584), ♀ 12.5 mm, sta 70A10-41, 12°53′N, 69°58′W, off Aruba, Netherlands Antilles, 550–610 m, coll. W. Pequegnat, 19 Jul 1970.—USNM 298347, University of the West Indies EST.861, 1 ♂ 12.8 mm, sta EST 5/72,

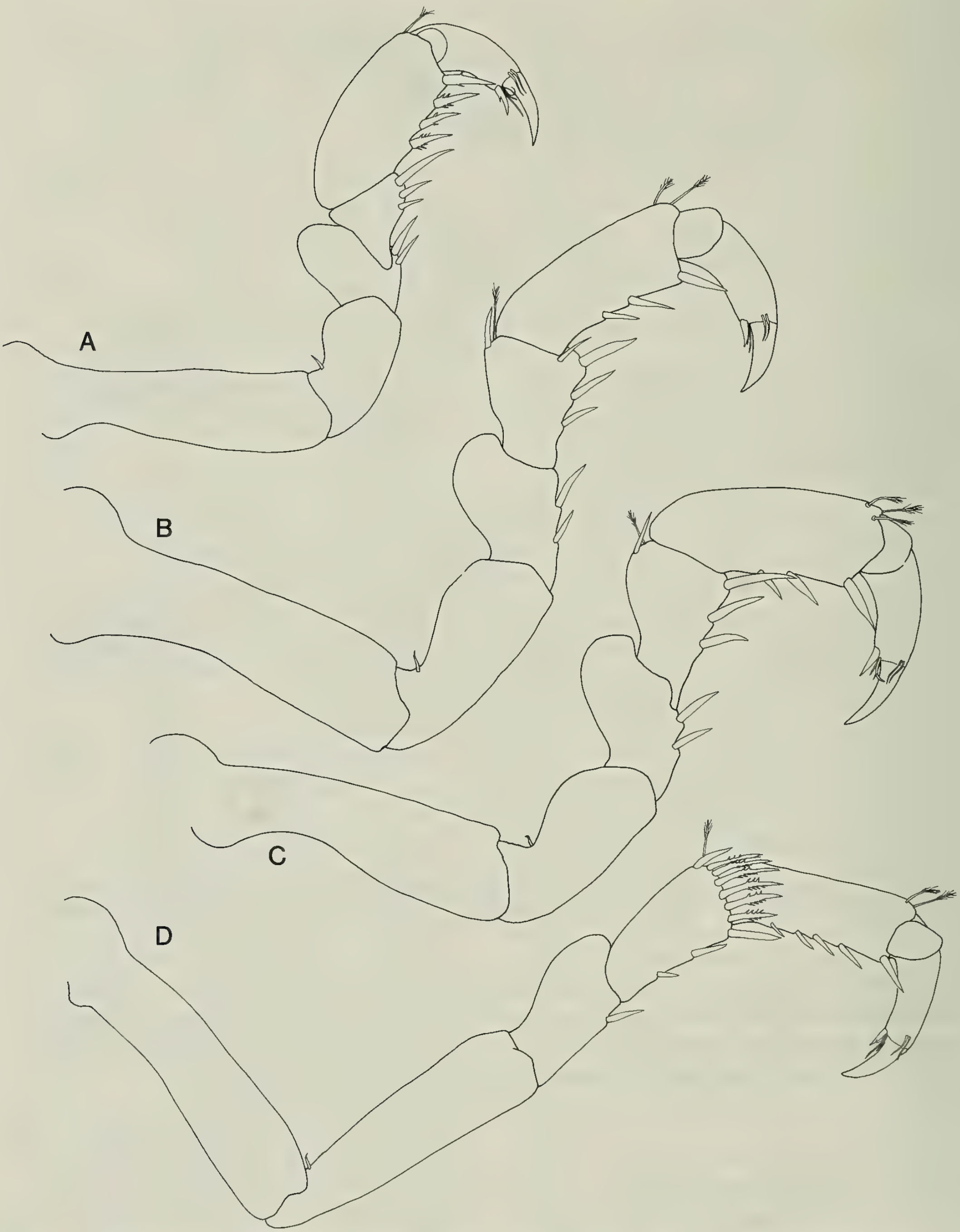

Fig. 3. *Dynameniscus carinatus* (Richardson, 1900), female, USNM 298346, off Aruba. A, pereopod 1; B, pereopod 2; C, pereopod 4; D, pereopod 7.

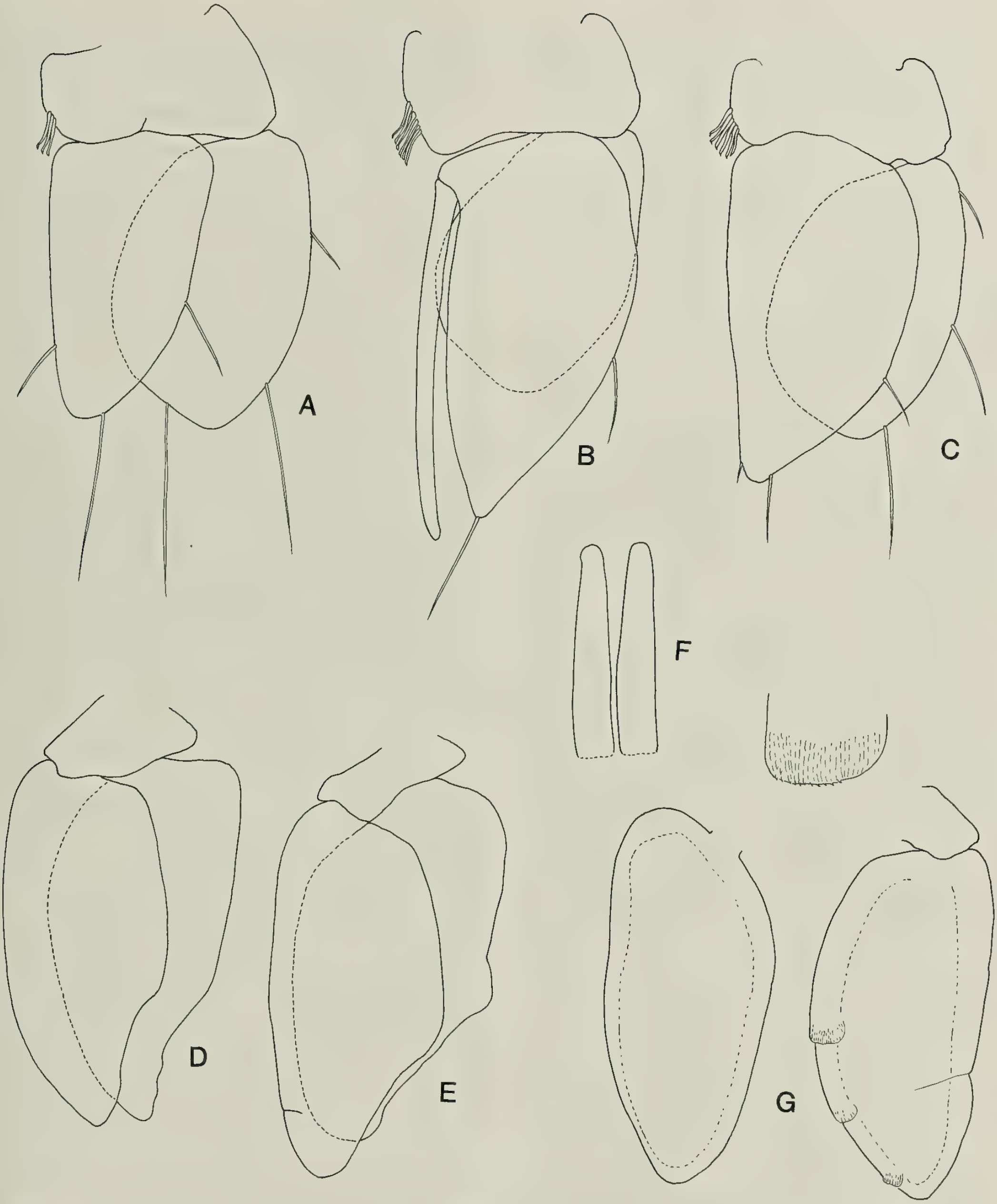

Fig. 4. *Dynameniscus carinata* (Richardson, 1900), male, USNM 298347, off Jamaica. A, pleopod 1; B, pleopod 2; C, pleopod 3; D, pleopod 4; E, pleopod 5; F, penes, same scale as pleopods; G, pleopod 5 of ovigerous female, ZMUC, with scale patch enlarged.

17°53′N, 78°38.5′W, off Jamaica, 1260 m, 17 Feb 1972.—ZMUC, 1 ovigerous ♀ 11.5 mm, R/V *Pillsbury* sta P-1187, 18°17′N, 75°05′W, between Jamaica and Haiti, 1034 m, 2 Jun 1970.

Description.—Male: Integument indurate, brittle, rugose, with numerous large and small rounded tubercles. Cephalon with 8 large rounded tubercles. Eyes poorly pigmented (in preservative), ommatidia not visible. Pereonites each with 4 large rounded tubercles plus smaller anterior median tubercle on first 3 pereonites. Pereonites 1 and 2 each with large triangular ventrally-directed coxal plate; pereonites 3–5 each with strong ventrally directed spike-like process on coxal plate; pereonite 6 coxal plate ventrally with low triangular process, pereonite 7 ventrally rounded, shorter than preceding coxa. Anterior pleonite with lateral ventrally-directed triangular process bearing smaller tubercle on anterior margin. Pleotelson dorsally convex, with 7 larger rounded tubercles, posterior margin broadly rounded. Epistome separating antennal and antennular bases, anteriorly with 2 low rounded tubercles, hollowed between, touching well marked, rounded rostral process dorsally; posterior lobes divergent, distally rounded.

Antennular basal peduncle article almost twice length of article 2; latter subequal to article 3; flagellum of 8 aesthetasc-bearing articles. Antennal peduncle with 3 basal articles short, subequal, article 4 one-fourth longer than 3, article 5 longer than 4; flagellum of 7 setose articles. Mandible with strongly corneous incisor, about 12 dentate setae in setal row plus lacinia or robust lacinioid seta; molar truncate, bearing numerous simple short setae. Maxilla 1, inner ramus with 3 stout fringed setae distally; outer ramus with about 11 distal spine-like setae, some dentate. Maxilla 2, inner ramus bearing about 9 stout fringed setae on mesial and distal margins; lobes of outer ramus each with 6 fringed distal setae. Maxillipedal palp of 5 articles, article 1 short, article 2 largest, articles 2–4 bearing setose lobe mesiodistally; article 5 slender, almost 4 times longer than wide, with distal cluster of setae; endite with 3 mesial coupling hooks, several circum-plumose setae on distal margin.

Pereopods generally covered with very short dense pile of fine setules (not shown in figures). Pereopod 1 ambulatory, merus bearing 2 robust setae posterodistally; carpus triangular, with very short free anterior margin, bearing 3 robust setae on posterior margin; propodus twice longer than wide, with 4 robust dentate setae on posterior margin; dactylus with unguis more than half length of rest of article, with strong accessory setae at its base. Pereopods 2–4 similar, with merus bearing 2 robust setae on posterior margin; carpus with anterior margin only slightly shorter than posterior, latter with 3 robust setae, single setae anterodistally; propodus about 2.5 times longer than wide, with 3 robust setae on posterior margin; dactylus with strong accessory setae at base of unguis. Pereopods 5–7, ischium becoming more elongate than in anterior pereopods, about 3.5 times longer than distal width; merus with single robust seta on posterior margin; carpus with 3 robust spines on posterior margin, group of about 7 dentate robust setae on distal margin; propodus with 5 setae on posterior margin; dactylus with unguis half length of rest of article, with accessory seta at its base.

Penes separate, elongate-tapering, about 5 times as long as basal width, distally rounded. Pleopod 1, endopod elongate-triangular, exopod broadly ovate, both rami bearing marginal plumose setae. Pleopod 2, appendix masculina articulating basally on endopod, stylet slender, just reaching beyond apex of ramus, distally rounded; endopod distally triangular, reaching well beyond ovate exopod, both rami bearing plumose marginal setae; pleopod 3, endopod distally triangular, reaching well beyond exopod; latter ovate, both rami with marginal plumose setae. Pleopods 4 and 5, rami lamellar, of similar size, lacking folds and marginal plumose setae. Pleopod 5 exopod with incomplete suture in distal third, with three scale patches on lateral margin. Scale patches thin-walled, scales poorly defined, more like surface striations, and with few distal points. Uropod consisting of fused protopod and endopod, latter a short immobile triangular lobe; exopod articulating, terete, gently tapering, very slightly curved, about 4.5 times longer than basal width.

Ovigerous female: External morphology very similar to male, but cephalic, pereonal and pleonal dorsal rounded tubercles slightly smaller. Number, size, and distribution of finer granulations very similar. Apart from the secondary sexual structures, the only difference between the male and female that could be discerned was a small variation in the number of robust setae on the posterior margins of the pereopod articles, i.e., five, rather than four setae on the propodus of pereopod 1, and two, rather than three setae on the carpus of some pereopods.

Remarks.—There are some differences between the holotype from Georgia, and the Caribbean specimens, the most noticeable being the shape of the uropodal exopod. In the holotype, these are distinctly curved, the tips being laterally directed. In the Caribbean specimens, the uropodal exopod has a barely noticeable curve. In the recent specimens, integumental tubercles are much stronger and more prominent, while the dorsal integument generally is more rugose, than in the type. With the limited material available, and in comparison to variation shown by other sphaeromatid species, this variation can, at present, be only considered as regional or possibly related to the relative maturity of the specimens.

Richardson (1906) described (and figured) pleopod 4 as having "transverse folds, fleshy". Close examination of all specimens here reveal that is not the case and that the rami of pleopods 4 and 5 are lamellar.

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Telacanthomysis, a new genus, for *Acanthomysis columbiae,* and redescription of *Columbiaemysis ignota* (Crustacea: Mysidacea: Mysidae)

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Abstract.—Two mysids found in the northeastern Pacific are revised. *Acanthomysis columbiae* (Tattersall, 1933) is transferred to the new genus, *Telacanthomysis,* based on the characters of the slender antennal scale, the postorbital spines on the anterior margin of the rostrum, the pleopods with developed pseudobranchial lobe, the endopod of the uropod without spines in the statocyst region, and the armature of the telson. *Columbiaemysis ignota* Holmquist, 1982, is redescribed in detail. *Acanthomysis brunnea* Murano & Chess, 1987, described from Californian waters is judged to be a junior synonym of *C. ignota.*

Holmquist (1979, 1980, 1981a, 1981b) carried out a systematic study on *Acanthomysis* s. l. distributed in the coastal waters of the western North America, and removed nine species to new genera. Holmquist left *Acanthomysis columbiae* (Tattersall, 1933) in *Acanthomysis* s. l., because it did not agree with her diagnosis of *Acanthomysis* s. s. and Holmquist had no adult specimens of the species to study. Kathman et al. (1986) used "*Acanthomysis*" forma *supraoculospinifera columbiae* for this.

Holmquist (1982) established *Columbiaemysis ignota* based on the two female and seven juvenile specimens collected from British Columbia. The male was reported first by Kathman et al. (1986), but the description was brief.

This paper deals with the establishment of the genus *Telacanthomysis* for *Acanthomysis columbiae* and the redescription of *Columbiaemysis ignota.*

The body length was measured along the dorsal median line from the tip of the rostrum to the posterior end of the telson excluding spines. Some of the present specimens examined are deposited in the National Science Museum, Tokyo (NSMT), Japan.

Subfamily Mysinae

Tribe Mysini

Telacanthomysis, new genus

Diagnosis.—Carapace produced into short rostral plate with rounded anterior margin bearing pair of postorbital spines; anterolateral corner of carapace acutely pointed. Eyes large. Antennal scale remarkably narrow with rounded apex, setose on all margins, apical suture present. Antennal sympod with spiniform process at inner and outer distal angles. Labrum with acute, spiniform, anterior process. Endopod of third to eighth thoracic limbs with carpopropodus divided into 6–9 subsegments. Penis armed with many setae on posterior margin and several inwardly curved setae on apical margin. Marsupium composed of 2 pairs of ordinary oostegites. First to third and fifth pleopods of male and all pleopods of female reduced to unsegmented lobe, gradually increasing in length posteriorly. Fourth pleopod of male biramous; endopod reduced to unsegmented lobe; exopod developed, long, slender, 2-segmented, proximal segment long, distal segment armed with 2 long terminal setae. Pseudobranchial lobes of all pleopods well developed. Endopod of uropod without spines in statocyst region. Telson linguiform, armed with spines throughout margins; distal margin armed densely with many spines slightly shorter than those of lateral margins.

Type species.—*Neomysis columbiae* Tattersall, 1933.

Etymology.—The generic name is derived from the Greek "*tele*", which refers to "far" and *Acanthomysis.* This species occurs in different habits compares to *Acanthomysis.* The name is feminine in gender.

Remarks.—*Telacanthomysis* differs not only from *Acanthomysis* s. s. but also from *Acanthomysis* s. l. in the following characters: the anterolateral corner of the carapace is acute, the anterior margin of the carapace bears a pair of the postorbital spines, the antennal scale is long and remarkably narrow, the antennal sympod is armed with a spiniform process at each distal angle, all pleopods have a well developed pseudobranchial lobe, the exopod of the fourth pleopod of male is extremely long (extending posteriorly beyond the apex of the telson) and slender, the endopod of the uropod is not armed with spines, and the telson is linguiform and armed with many short apical spines on the apical margin.

Telacanthomysis is allied to *Xenacanthomysis* Holmquist, 1980, in the acutely pointed anterolateral corner of the carapace, the number of the subsegments of the carpopropodus of the endopod of the third to eighth thoracic limbs, and the shape and armature of the telson. However, *Telacanthomysis* is easily distinguishable from *Xenacanthomysis* as follows: in the former genus the antennular peduncle of male is normal without peculiar process, whereas in the latter genus it is provided with a curious knob-like process on the dorsal surface of the second and third segments; in the former genus the exopod of the fourth pleopod of male is very long, slender and divided into two segments, while in the latter genus it is remarkably robust and clear segmentation does not exist; and in the former genus the pseudobranchial lobes of all pleopods are well developed, while in the latter genus these are less developed.

Telacanthomysis is also similar to *Alienacanthomysis* Holmquist, 1981b, in the character of the rostrum and telson, but it differs from *Alienacanthomysis* with respect to the postorbital spines on the anterior margin of rostrum, the more robust antennular peduncles, the spiniform anterior process on the labrum, and the well-developed pseudobranchial lobe of the pleopods.

Telacanthomysis columbiae (Tattersall, 1933), new combination
Figs. 1, 2

Neomysis columbiae Tattersall, 1933:12–14, figs. 5, 6 (type locality: Port Alexander, western Canada).

Acanthomysis columbiae: Ii, 1936:589 (list).—Banner, 1948:88, 89 (diagnosis).—Tattersall, 1951:204–207, figs. 80–82.—Gordan, 1957:337 (list).—Mauchline & Murano, 1977:44 (list).—Müller, 1993:191 (list).

"*Acanthomysis*" *columbiae:* Holmquist, 1981b:407, fig. 11.—1982:491.—Daly & Holmquist, 1986: 1208 (list).

"*Acanthomysis*" f. *supraoculospinifera columbiae:* Kathman et al., 1986:82, fig. (p. 83).

Material examined.—6 males (16.4–18.8 mm) and 1 female (20.2 mm); California, 20 m, 2 Aug 1991, provided by J. R. Chess (1 male and 1 female: NSMT-Cr 12980). 1 male (16.0 mm) and 1 female (19.6 mm); from stomach of a bird, Cassin's auklet

(*Ptychoramphus* sp.), Stinson Beach, California, 6 Aug 1997, borrowed from M. Galbraith.

Description.—Body robust; integument smooth. Thoracic somites without sternal process.

Carapace produced into short rostral plate extending to base of antennular peduncles; anterior margin rounded, armed with pair of prominent, acutely pointed postorbital spines (Fig. 1A–C); anterolateral corner acutely pointed (Fig. 1C); posterior margin smooth, emarginate, leaving last two thoracic somites exposed dorsally.

Eye well-developed, 1.2–1.4 times as long as broad; cornea large, globular, more than half as wide as carapace, wider than eyestalk, occupying more than half of entire eye in dorsal view; eyestalk armed with setae on basal part, without papilliform process on dorsal surface (Fig. 1A, B).

Antennular peduncle of male more robust than that of female, first segment slightly shorter than distal two segments combined, third segment with appendix masculina, which is almost same in length with segment supporting it (Fig. 1A); in female first segment as long as distal two segments combined (Fig. 1B). Inner antennular flagellum narrower than outer in male, wider in female (Fig. 1A, B).

Antennal scale extremely narrow with rounded apex, almost straight, extending to apex of appendix masculina of antennular peduncle in male (Fig. 1A, D), in female extending beyond distal end of antennular peduncle for $\frac{1}{5}$ of its length (Fig. 1B), 12.8–13.6 times as long as broad, all margins setose, apical suture marked off at distal $\frac{1}{14}$ (Fig. 1D). Antennal peduncle of male more robust than that of female, extending to distal $\frac{2}{5}$ of scale, third segment as long as second (Fig. 1D); in female extending to proximal $\frac{3}{7}$ of scale, third segment $\frac{2}{3}$ length of second. Antennal sympod with spiniform process at inner and outer distal angles (Fig. 1D).

Labrum with short, spiniform process on anterior margin. Mandibular palp with second segment slightly expanded mesially, 3–3.8 times as long as broad, third segment slender, about 6 times as long as broad, about $\frac{2}{3}$ of second in length. Outer lobe of maxillule armed with 12 stout spines on distal margin and 3 setae on surface, hump-like process present in middle of outer margin. Maxilla with exopod extending near anterior margin of first segment of endopod and armed with plumose setae on outer and apical margins; endopod with second segment 1.5 times as long as broad, with setae on distal margin but not with spines.

Endopod of first thoracic limb short and robust, preischium, ischium and merus with inner margin swollen. Endopod of second thoracic limb short, rather slender. Endopod of third to eighth thoracic limbs slender. Endopod of third to eighth thoracic limbs with small triangular process in inner distal part of basis. Ischium with numerous setae on inner margin of endopod of third to sixth thoracic limbs of both sexes (Fig. 1E), with 11–18 short and long setae on distal half in seventh endopod, and with several setae on distalmost part in eighth endopod (Fig. 1F). Carpopropodus of endopod of third to eighth thoracic limbs divided into 6–9 subsegments, setae at outer distal angle of proximal 2–4 subsegments and often, those on distal half of outer margin of first subsegment, provided with serration on distal half of anterior margin (Fig. 1E, F). Dactylus of endopod of third to seventh thoracic limbs with short and stout terminal claw (Fig. 1E), that of eighth thoracic limb with short, inwardly curved claw (Fig. 1F). Exopods of thoracic limbs with flagellum 8-segmented in first and eighth limbs and 9-segmented in second to seventh limbs; outer distal corner of basal plate rounded, smooth (Fig. 1F).

Penis about 3 times as long as broad in lateral view, armed with 17–19 setae on posterior margin and 6 inwardly curved setae on apical margin, anterior margin smooth (Fig. 1F).

Female with rudimentary oostegite on sixth thoracic limb and ordinary oostegites

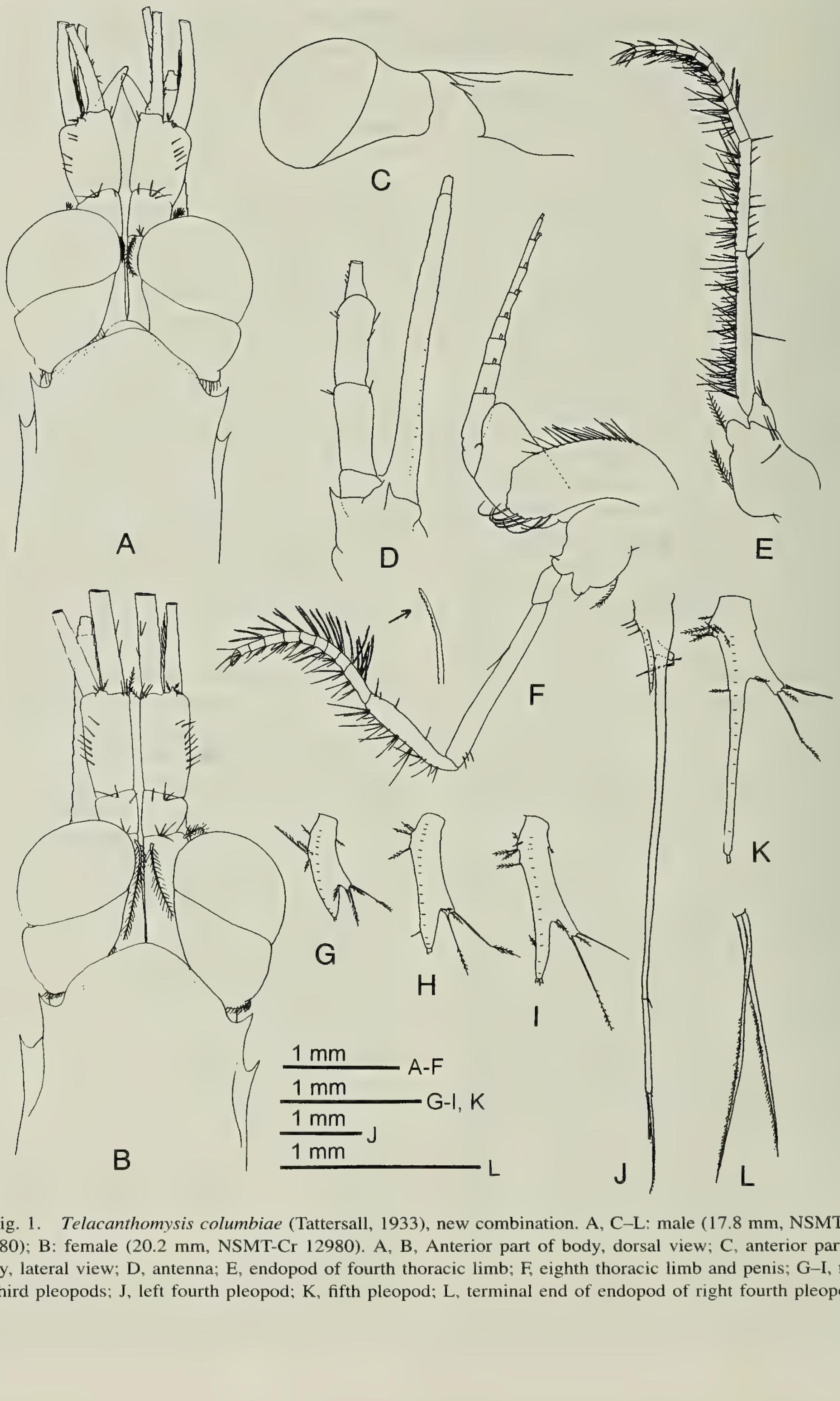

Fig. 1. *Telacanthomysis columbiae* (Tattersall, 1933), new combination. A, C–L: male (17.8 mm, NSMT-Cr 12980); B: female (20.2 mm, NSMT-Cr 12980). A, B, Anterior part of body, dorsal view; C, anterior part of body, lateral view; D, antenna; E, endopod of fourth thoracic limb; F, eighth thoracic limb and penis; G–I, first to third pleopods; J, left fourth pleopod; K, fifth pleopod; L, terminal end of endopod of right fourth pleopod.

on seventh and eighth thoracic limbs; oostegite of seventh limb with bailing lobe.

First to third abdominal somites with 2 or 3 dorsal grooves (Fig. 2A), fourth to sixth somites without grooves, folds or spine rows, sixth somite with posterolateral corners acutely pointed (Fig. 2B); first to fifth somites subequal in length, sixth somite 1.4 times as long as fifth.

All pleopods in both sexes, except fourth of male, reduced to unsegmented lobe, gradually increasing in length posteriorly, fifth pair slender, 1.6 times as long as third; pseudobranchial lobe well developed, situated in distal half of outer margin in first to third pleopods, at middle in fourth female pleopod, and in proximal half in fifth pleopod (Figs. 1G–I, K, 2C–G). Fourth pleopod of male biramous; endopod rudimentary, unsegmented; exopod developed, long, slender, extending posteriorly beyond apex of telson, 2-segmented, proximal segment more than 6 times as long as endopod, armed with 1 tiny seta at outer distal corner, distal segment ¼ length of proximal segment, armed with tiny seta at each distal corner and 2 long, barbed setae on terminal end, latter setae subequal in length, 1.1 times longer than distal segment (Fig. 1J, L).

Endopod of uropod extending slightly beyond apex of telson, without spines on inner margin; exopod slender, about 1.6 times longer than endopod (Fig. 2H).

Telson elongate, linguiform, 1.3 times as long as last abdominal somite, 2.1 times as long as widest part at base, narrowing towards basal ¼ at which slight constriction is present, gradually broadened towards middle, again narrowing gradually towards broadly rounded apex which is ⅓ as broad as at base (Fig. 2H). Lateral margin of telson armed along whole length with about 50 small, variously sized spines which are arranged more densely in distal half, not arranged in groups (Fig. 2H, I). Apical margin armed densely with 25–30 various sized spines slightly shorter than lateral ones (Fig. 2J).

Remarks.—Holmquist (1981b) discussed the morphological differences in the antennal scale and telson among specimens examined by her with differences shown in Tattersall's illustrations (Tattersall 1933: Figs. 5–6, 1951: Figs. 80–81).

The antennal scale was shown by Tattersall (1933) to be unarmed on the basal portion of the inner and outer margins. Holmquist (1981b) also observed the same features in juvenile specimens from British Columbia. In the present specimens, however, the antennal scale is armed with strong plumose setae along whole length of the inner and outer margins such as the specimens examined by Tattersall (1951).

Holmquist (1981b) described the apex of the telson as follows: the apex of the adult specimens from British Columbia was relatively square and armed with a dense row of small, equal-sized spines (Tattersall 1933); in the immature or semi-adult specimens from California, the apex was more rounded and armed with a dense row of unequal spines, which were slightly longer than the closest lateral spines (Tattersall 1951). In the juvenile specimens from British Columbia (Holmquist 1981b), the apex was more narrowly rounded, and armed with some large spines, which were larger than the lateral spines, and a pair of median small spines at the middle. She suggested that the differences above were associated with the stage of growth and/or population. The present adult specimens from California agree well with the original description in the shape and armature of the telson. The differences are judged to be a morphological change with growth.

Columbiaemysis Holmquist, 1982

Columbiaemysis Holmquist, 1982:496.—Kathman et al., 1986:123.

Diagnosis.—Carapace anteriorly produced into triangular rostral plate; anterolateral corner acutely or bluntly pointed. Antennal scale lanceolate with rounded apex, all margins setose, apical suture pre-

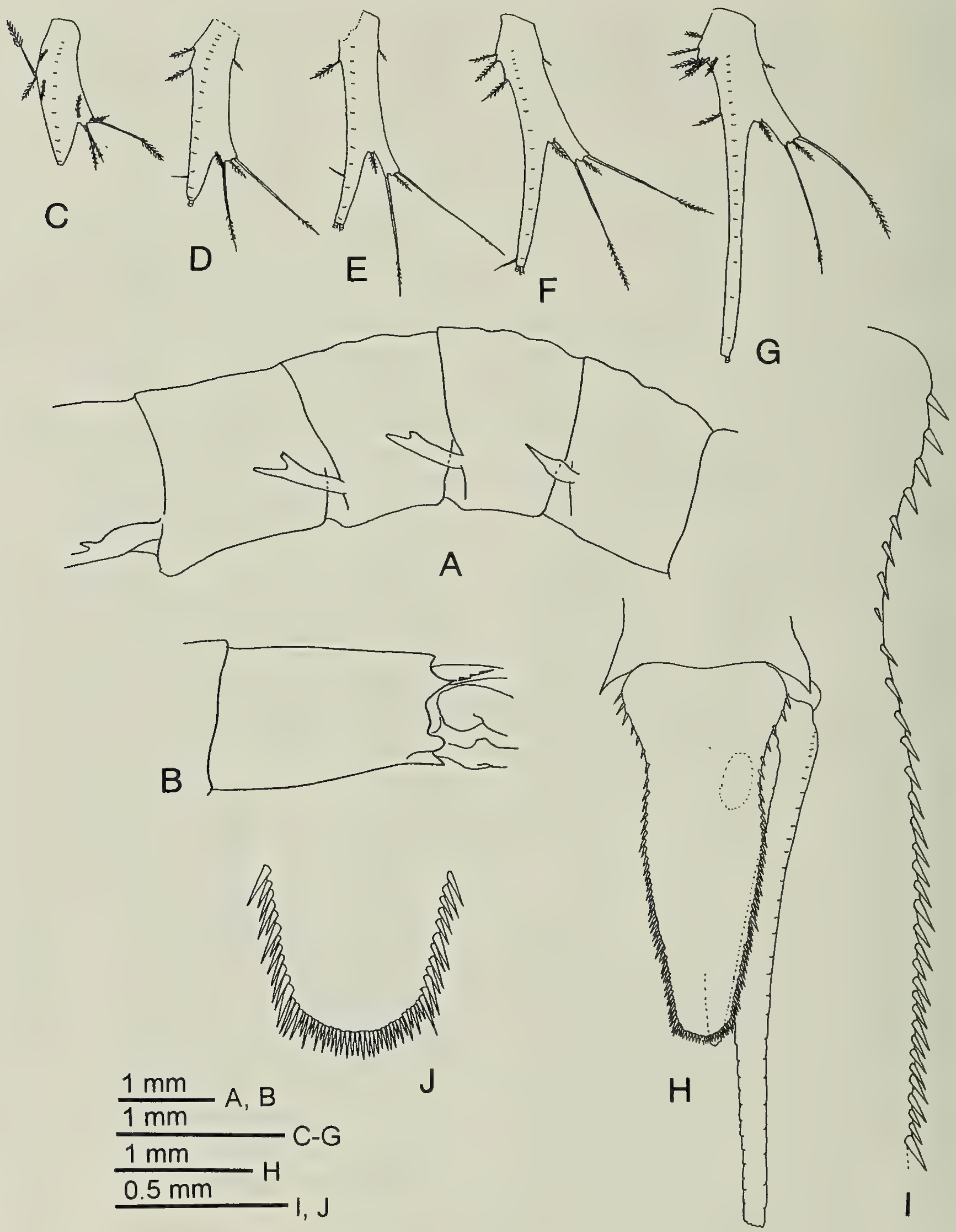

Fig. 2. *Telacanthomysis columbiae* (Tattersall, 1933), new combination. A, B, H, J: male (17.8 mm, NSMT-Cr 12980); C–G, I: female (20.2 mm, NSMT-Cr 12980). A, First to fourth abdominal somites, lateral view; B, sixth abdominal somite, lateral view; C–G, first to fifth pleopods; H, telson and uropod, dorsal view; I, proximal half of lateral margin of telson, dorsal view; J, apical part of telson, dorsal view.

sent. Labrum with acute, spiniform, frontal process. Maxillule with hump-like projection on outer margin of outer lobe. Endopod of third to eighth thoracic limbs with carpopropodus divided into 4–6 subsegments. Penis armed with several short setae on posterior margin, several inwardly curved setae on apical margin, and several plumose setae on distal half of anterior margin. Marsupium composed of 2 pairs of ordinary oostegites. All pleopods of both sexes, except fourth of male, reduced to unsegmented lobe, increasing in length posteriorly; fifth pair long; pseudobranchial lobe poorly developed. Fourth pleopod of male biramous; endopod rudimentary, unsegmented; exopod elongate, 2-segmented, distal segment long, with 2 long spiniform setae on terminal end. Endopod of uropod armed with 4 spines on inner ventral surface of statocyst region. Telson linguiform, armed with spines along entire margins, spines not arranged in groups, apex with two pairs of spines, outer pair longer than inner.

Remarks.—*Columbiaemysis* characterized by the pointed anterolateral corner of the carapace, the four- to six-subsegmented carpopropodus of the endopods of the third to eighth thoracic limbs, the elongated distal segment of the exopod of the male fourth pleopod, and the linguiform telson armed with spines along entire margins.

This genus is allied to the East Asian species group within *Acanthomysis* s. l. having the most species. All species, except *A. dimorpha* Ii, 1936, are found from the South China Sea to Japanese waters. However, *Columbiaemysis* is distinguished from the East Asian species group in the following points: the anterolateral corner of the carapace is pointed in *Columbianemysis* while rounded in the East Asian species group; in *Columbiaemysis* the distal segment of the exopod of the male fourth pleopod is so long that it occupies about ⅔ of the proximal segment in length, while in the East Asian species group it is short, $\frac{1}{20}$–$\frac{2}{5}$ of the proximal segment; and the lateral spines of the telson gradually decrease in size apically in *Columbiaemysis,* whereas in the East Asian species group these are subequal in size or arranged in groups with several small spines between larger ones.

Columbiaemysis includes only one species, *C. ignota.*

Columbiaemysis ignota Holmquist, 1982
Fig. 3

Columbiaemysis ignota Holmquist, 1982: 496, 497, figs. 12, 13. (type locality: Whiffen Spit, Sooke Harbor, south Victoria Island, Canada).—Daly & Holmquist, 1986:1208 (list).—Kathman et al., 1986:124, fig. (p. 125).—Müller, 1993: 213, 214 (list).

Acanthomysis brunnea Murano & Chess, 1987:189–192, figs. 5, 6. (type locality: Alvion Cove, California).—Müller, 1993: 190 (list).

Material examined.—3 males (22.4 mm and 2 damaged); Gulf of S. Matinus, California, 8 Dec 1978, provided by J. R. Chess (1 male: NSMT-Cr 12981). 3 females (17.8 mm and 2 damaged); California, 12 m, 21 Sep 1978, provided by J. R. Chess (1 female: NSMT-Cr 12982). 2 males (16.8 mm and 1 damaged) and 2 females (16.4 and 18.4 mm); from stomach contents of a bird, Cassin's auklet (*Ptychoramphus* sp.), Stinson Beach, California, 14 July 1995, borrowed from M. Galbraith.

Description.—Body robust. Integument not hispid. Thoracic somites without sternal process.

Carapace anteriorly produced into triangular rostral plate with pointed apex extending slightly beyond middle of first segment of antennular peduncles, lateral margin of rostrum almost straight; anterolateral corner acutely pointed; posterior margin smooth, emarginate, leaving last one or two thoracic somites exposed dorsally (Fig. 3A).

Eye extending beyond distal margin of second segment of antennular peduncle, 1.3 times as long as broad; cornea semiglobular, occupying ⅖ to half of whole eye in dorsal view; eyestalk with minute setae in basal part, without papilliform process on dorsal surface (Fig. 3A).

Antennular peduncle of male more robust than that of female, third segment slightly shorter than proximal two segments combined, 1.3 times as long as broad (Fig. 3A); in female third segment as long as first, 1.4 times as long as broad.

Antennal scale lanceolate with rounded apex, all margins setose, apical suture present. In male scale extends beyond distal margin of antennular peduncle by ⅓ of its length and slightly beyond apex of appendix masculina, 6.8 times as long as broad (Fig. 3A, B). In female scale extends beyond distal margin of antennular peduncle for half of its length, 7.6 times as long as broad. Antennal peduncle about half as long as scale in male, ⅖ as long in female (Fig. 3B). Antennal sympod with spiniform process at outer distal angle (Fig. 3B).

Labrum with frontally directed, short, acute process. Mandibular palp with second segment expanded in middle, about 2.2 times as long as broad, third segment half to ⅗ length of second. Outer lobe of maxillule armed with 13 stout spines on apical margin and 3 setae on surface, with hump-like process in middle of outer margin. Exopod of maxilla not reaching anterior margin of first segment of endopod, armed with many plumose setae on outer and apical margins; endopod with second segment narrow, 1.9–2.2 times as long as broad, without spines on outer margin.

Endopod of first thoracic limb short and robust, with preischium, ischium and merus slightly expanded inwardly. Endopod of second thoracic limb robust. Endopod of third to eighth thoracic limbs with carpopropodus divided into 5–7 subsegments, dactylus with slender terminal claw (Fig. 3C). Exopods of thoracic limbs with flagellum 8-segmented in first and eighth limbs, 9-segmented in second to seventh limbs; basal plate with outer distal corner rounded and without spines (Fig. 3C).

Penis posteriorly expanded, 1.3 times as long as broad in lateral view, armed with 6 short setae on posterior margin, 7 smooth, inwardly curved setae on apical margin, and 6 plumose setae on apical half of anterior margin (Fig. 3D).

Female with hair tuft on coxa of fourth and fifth thoracic limbs, rudimentary oostegite in sixth endopod, and ordinary oostegites in seventh and eighth endopods; oostegite of seventh limb with bailing lobe.

Abdominal somites subequal in length, smooth or with folds. In some specimens first to fourth abdominal somite with 1 or 2 transverse folds, fifth somite with 1 transverse and 1 middorsal folds, and sixth somite with 2 dorsal folds, anterior one of which is discontinuous in middorsal portion (Fig. 3E).

First to third and fifth pleopods of male reduced to unsegmented lobe, gradually increasing in size posteriorly; fifth pair 1.4 times as long as third (Fig. 3F–H, J). Fourth pleopod of male biramous; endopod reduced to unsegmented lobe; exopod elongate, extending posteriorly to middle of telson, 2-segmented, proximal segment 3 times as long as endopod, armed with a long seta at inner distal corner, distal segment rather long, about ⅔ length of proximal segment, armed with 2 unequal barbed terminal setae, longer seta ⅖ length of distal segment and 1.3 times as long as shorter one (Fig. 3I). All pleopods of female reduced to unsegmented lobes, gradually increasing in size posteriorly; fifth pair 1.5 times as long as third, 1.3 times as long as fourth. Pseudobranchial lobe of all pleopods undeveloped except in fourth pleopod of male (Fig. 3F–J).

Endopod of uropod extending to or slightly overreaching apex of telson, armed with 4 spines on inner ventral margin near statocyst, and with single small spine on dorsal surface of statocyst region (Fig. 3K, L); exopod 1.4 times longer than endopod (Fig. 3L).

Telson long linguiform, 1.6 times as long as last abdominal somite, 2.4 times as long as broad at base; lateral margin armed with

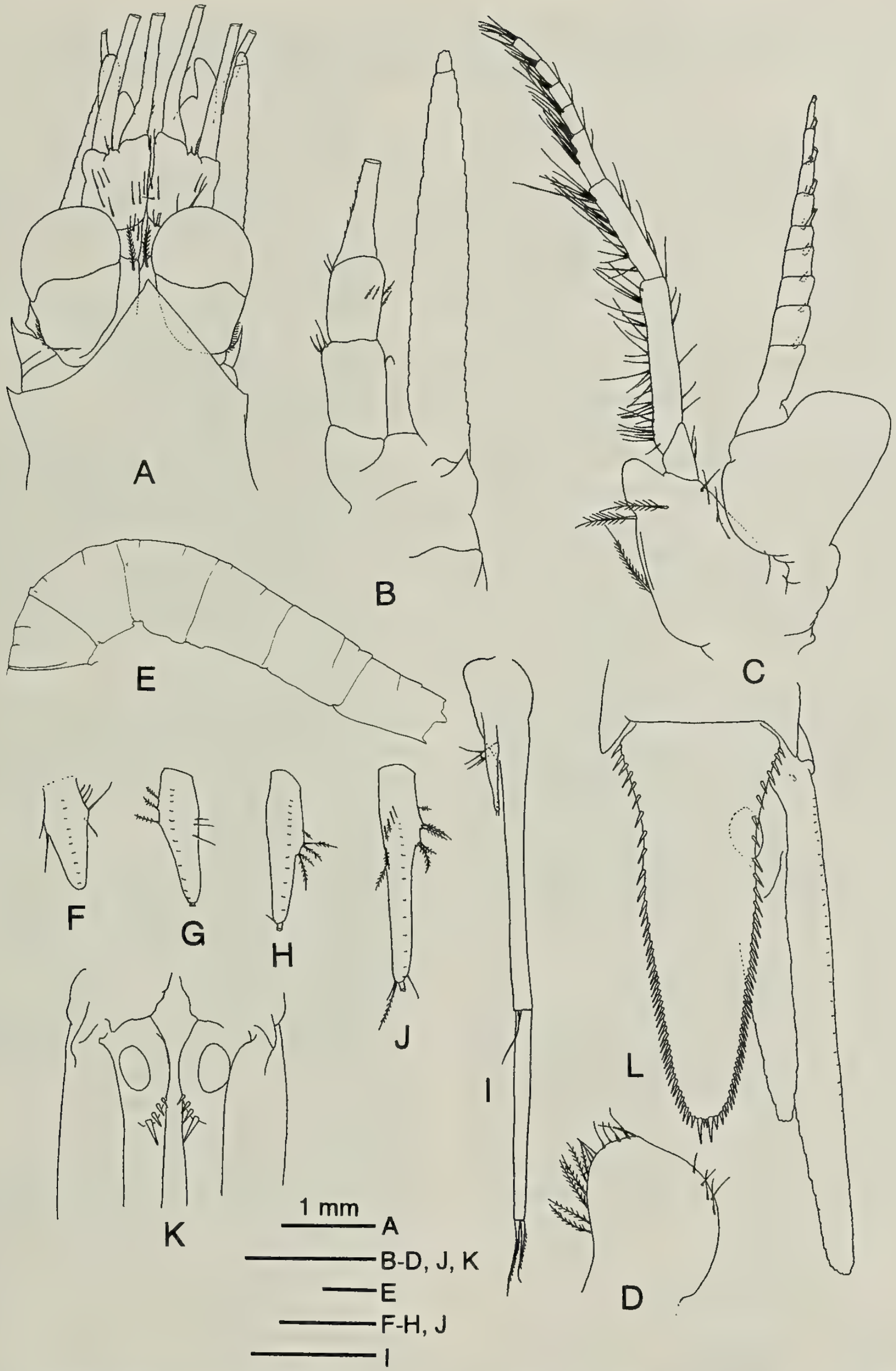

Fig. 3. *Columbiaemysis ignota* Holmquist, 1982. A–J, L: male (22.4 mm, NSMT-Cr 12981); K: female (17.8 mm, NSMT-Cr 12982). A, Anterior part of body, dorsal view; B, antenna; C, third thoracic limb; D, penis, lateral view; E, first to sixth abdominal somites, lateral view; F–J, first to fifth pleopods; K, proximal part of uropod, ventral view; L, telson and uropod, dorsal view.

about 45 spines gradually decreasing in size apically; apex with 2 pairs of spines, outer pair of spines twice as long as distalmost lateral spine, inner pair of spines about half the length of outer pair (Fig. 3L).

Remarks.—Holmquist (1982) described the abdominal somites as smooth. By contrast Kathman et al. (1986) examined a number of specimens that showed some variations with respect to the number of folds or grooves on these abdominal somites. In a reexamination of Holmquist's specimens, an incomplete groove was observed on several somites (Kathman et al. 1986). In the present specimens, one or two folds were present on all abdominal somites.

Murano & Chess (1987) established *Acanthomysis brunnea* based on specimens collected from Californian waters. *Acanthomysis brunnea* agrees with the original description of *C. ignota,* except for the abdominal somites that show intraspecific variation and which are clarified by Kathman et al. (1986). The fourth pleopod of male of *A. brunnea* agrees with the description and illustration of *C. ignota* given by Kathman et al. (1986). *Acanthomysis brunnea* is synonymous with *Columbiaemysis ignota.*

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A new species of *Ectinosoma* Boeck, 1865 (Copepoda: Harpacticoida: Ectinosomatidae) from northwestern Mexico

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Abstract.—A new species of harpacticoid copepod, *Ectinosoma mexicanum* (Harpacticoida: Ectinosomatidae), is described from a coastal lagoon in northwestern Mexico (Sinaloa state). *Ectinosoma mexicanum* appears to be allied to *E. porosum* (Wells, 1967) by sharing a robust endopod on P2 and P4 and a strong setae on the first and second endopodal segment of P2 and P4. The new Mexican ectinosomatid also has the seta next to the outermost seta of exopod of P5 barely longer than the exopod inner edge as in *E. porosum* and *E. mediterraneum* Kunz, 1975.

In 1991 a one-year study on the impact of organic enrichment on the distribution and abundance of meiofauna in a coastal lagoon in the southeastern Gulf of California (Mexico) was undertaken (Gómez-Noguera & Hendrickx, 1997). During this study 63 harpacticoid taxa were identified, most of which turned out to be new to science. Ectinosomatidae was by far the most abundant family throughout the study period (39.4%), and was represented by species of *Halectinosoma* Lang, 1965, *Hastigerella* Nicholls, 1935, *Pseudectinosoma* Kunz, 1935 and *Ectinosoma* Boeck, 1865. This contribution deals with the description of the only species of *Ectinosoma* found in the sediment samples taken in Ensenada del Pabellon lagoon (northwestern Mexico).

Materials and Methods

Quantitative triplicate sediment samples were taken in Ensenada del Pabellon lagoon (Sinaloa, northwestern Mexico). The sample strategy was described in Gómez-Noguera & Hendrickx (1997). Harpacticoids were stored in 70% ethanol prior to further investigation. Observations and drawings were made from the whole and then dissected specimen mounted in glycerin, at 1250× using a Leitz Periplan phase contrast light microscope equipped with a drawing tube. The terminology proposed by Huys & Boxshall (1991) for the general morphological description, Koomen (1992) and Seifried & Dürbaum (2000) for U-pores, Seifried (1997) and Seifried & Dürbaum (2000) for the somitic ornamentation (palisades), and Moore (1976) for hyaline frill, were adopted. Abbreviations used in the text and tables: P1–P6, first to sixth leg; EXO, exopod; END, endopod; ae, aesthetasc.

Family Ectinosomatidae Sars, 1903

Genus *Ectinosoma* Boeck, 1865

Ectinosoma mexicanum, new species

Figs. 1–6

Type material.—A single dissected female (holotype) catalogued EMUCOP-020591-17, deposited in the collection of the Institute of Marine Sciences and Limnology, Mazatlan Marine Station.

Type locality.—Ensenada del Pabellón lagoon (24°19′–24°35′N, 107°28′–107°45′W). Leg. S. Gómez, May 1991.

Diagnosis.—Ectinosomatidae. Rostrum relatively large and fused to cephalothorax. Antennule six-segmented. Armature formula of P1–P4 (EXO/END): 0.1.123/1.1.221; 1.1.223/1.1.221; 1.1.323/1.1.221; 1.1.323/1.1.221. First and second endopodal segment of P2–P4 with one strong spinulose seta. Endopod of P2–P4 robust, first endopodal segment of P2 and P3 as long as wide, first endopodal segment of P4 wider than long. Seta next to the outermost seta of exopod of P5 barely longer than inner edge of exopod. Setae I and VI of caudal rami spine-like.

Description.—Habitus (Fig. 1A–B, 2A–C), fusiform. Length 773 μm including rostrum and caudal rami. Rostrum (Fig. 1A) relatively large, fused with cephalothorax. The latter about ⅓ of total body length, with denticulate hyaline frill and sensilla; integument ornamented with tiny depressions arranged longitudinally and perforated by U-pores. Surface of third to fifth thoracic somites with tiny depressions arranged as in cephalothorax; U-pores present. Third thoracic somite without palisades, fourth and fifth thoracic somites with 2 and 4 transverse rows of palisades, respectively; third to fifth thoracic somites with denticulate hyaline frill, that of the fifth one deeper than that of the third and fourth thoracic somites. Fifth thoracic somite with 1 transverse row of small palisades and 3 transverse rows of long palisades. P5 bearing-somite (sixth thoracic somite) ornamented with 3 transverse rows of small palisades and 1 row of long palisades, and with evenly distributed tiny depressions (possibly pores) and U-pores; with denticulate hyaline frill. W:L ratio of genital double-somite, 1.19 (width measured in the proximal wider part of seventh thoracic somite); dorsal surface with remains of ancestral subdivision between seventh thoracic somite and first post genital abdominal somite (indicated in Fig. 1A–B) and ornamented with transverse rows of palisades and evenly distributed depressions and U-pores; ventral surface plain, with U-pores; P6 represented by 2 setae, genital pore located in proximal half; hyaline frill of first post genital abdominal somite as in sixth thoracic somite. Second and third post genital abdominal somites ornamented with 3 and 4 rows of palisades; second post genital abdominal somite with U-pores and with denticulate hyaline frill; third post genital abdominal somite without U-pores, with protruded pseudoperculum dorsally, reaching to distal third of anal segment, with entire striated hyaline frill ventrally (Fig. 2C). Anal segment (fourth post genital abdominal somite) with palisades and U-pores. Caudal rami about 1.5 times longer than broad, with 7 elements. Posterior dorsal edge of caudal rami terminating as an acuminate lappet; rami with 1 ventral proximal row of small palisades, and 2 sets of ventrolateral spinules at base of elements I and II; setae I and VI developed as spines.

Antennule (Fig. 3A), six-segmented. Surface of segments smooth. Armature formula 1.10.3+ae.0.3.3+ae.

Antenna (Fig. 3B): basis massive, with 2 inner long elements (indicated in Fig. 3B). Endopod two-segmented; first segment bare; second segment ornamented with strong and short proximal spinules and with longer spinules at base of 2 inner lateral spines; with 6 distal spines. Exopod three segmented; first segment as long as third and about 2.3 times longer than second one, with one seta; second segment with 1 spine; third segment with 2 spines and ornamented with subapical set of spinules, one of them markedly stronger.

Mandible (Fig. 3C): gnathobase of coxa with a strong spinulose distal spine on cutting edge, 1 strong and 4 smaller teeth; basis large with 2 long and slender inner setae and 1 thickened and spinulose inner element. Endopod one-segmented, with 8 setae, 2 each of distal 4 fused at base forming 2 pairs of elements. Exopod one-segmented, small, with 1 lateral and 2 distal setae.

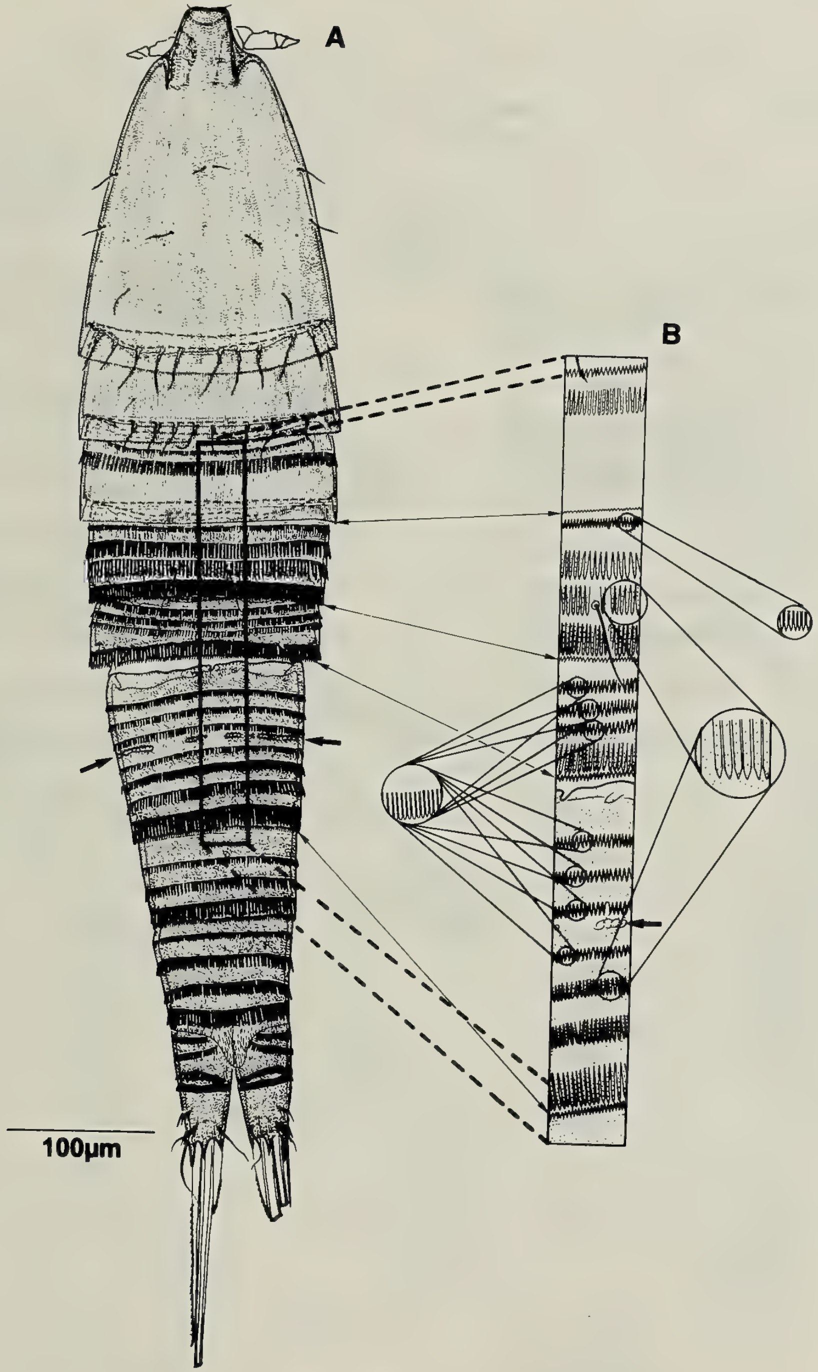

Fig. 1. *Ectinosoma mexicanum,* new species. Holotype, female, EMUCOP-020591-17. A, habitus, dorsal; B, surface ornamentation of fourth to seventh thoracic somites and first post genital abdominal somite.

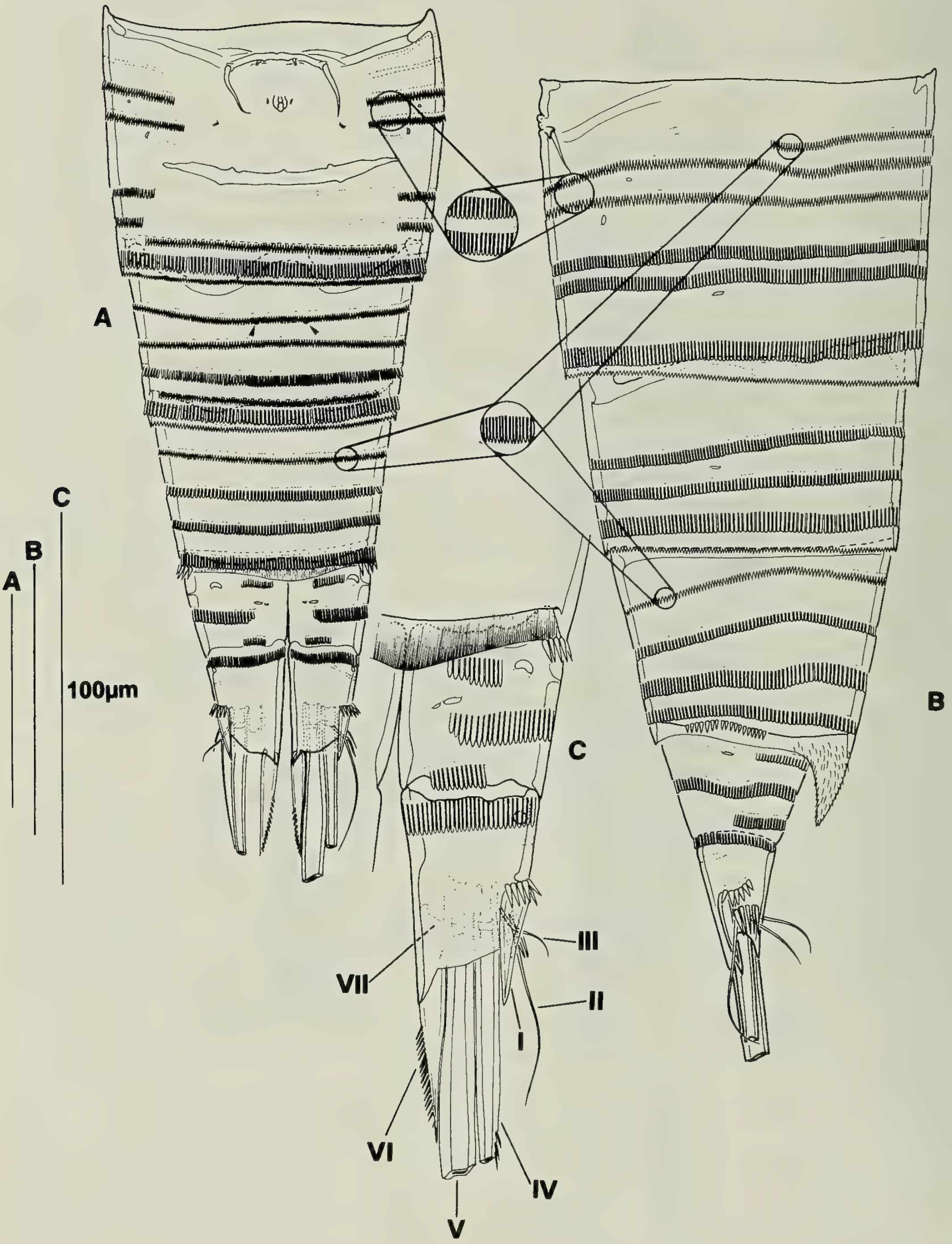

Fig. 2. *Ectinosoma mexicanum,* new species. Holotype, female, EMUCOP-020591-17. A, urosome, ventral (first urosomite omitted); B, urosome, lateral, (first urosomite omitted); C, part of anal segment and left caudal ramus, ventral.

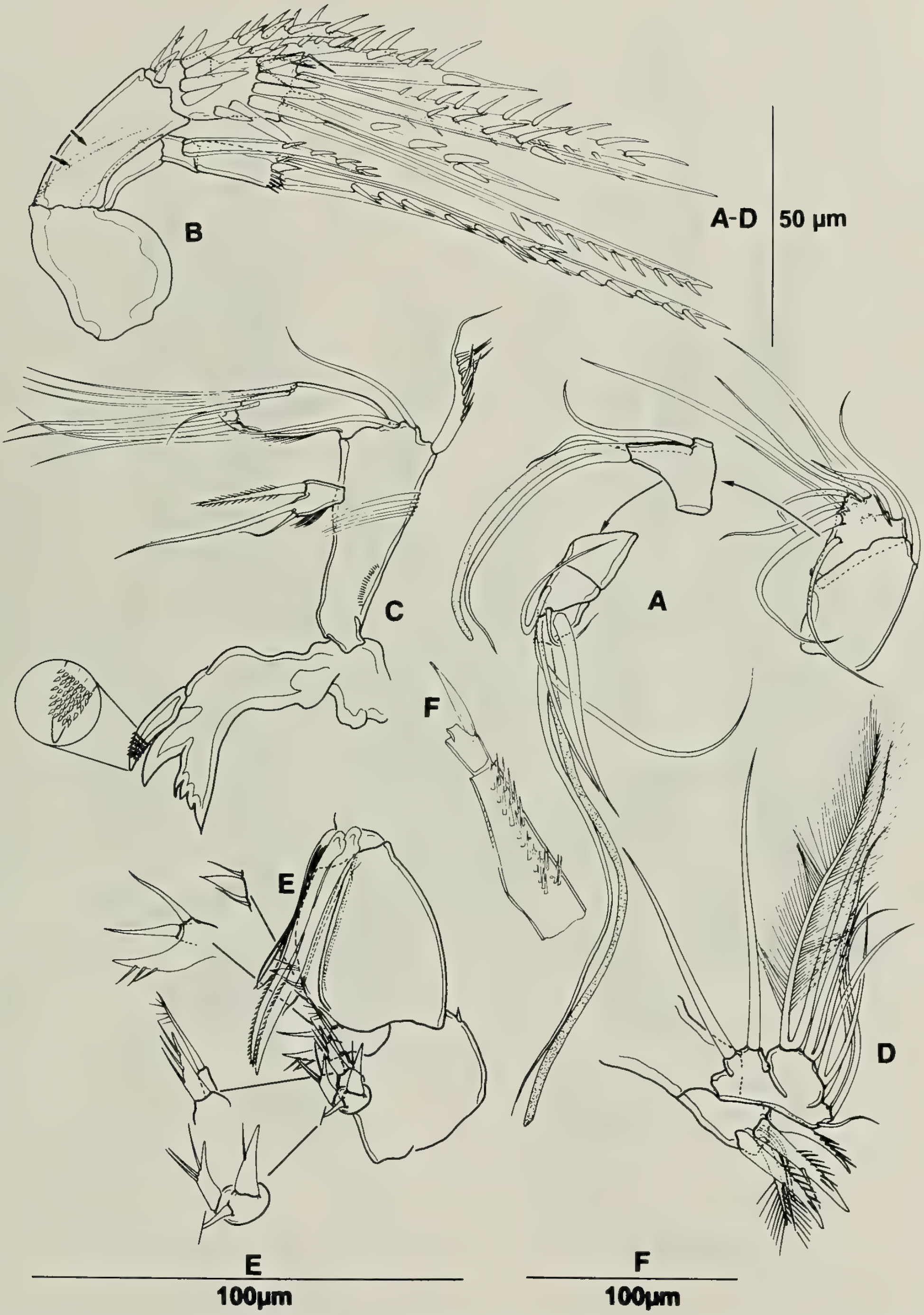

Fig. 3. *Ectinosoma mexicanum,* new species. Holotype female, EMUCOP-020591-17. A, antennule, third segment separated from second and fourth; B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped (endopodal setae lost during dissection).

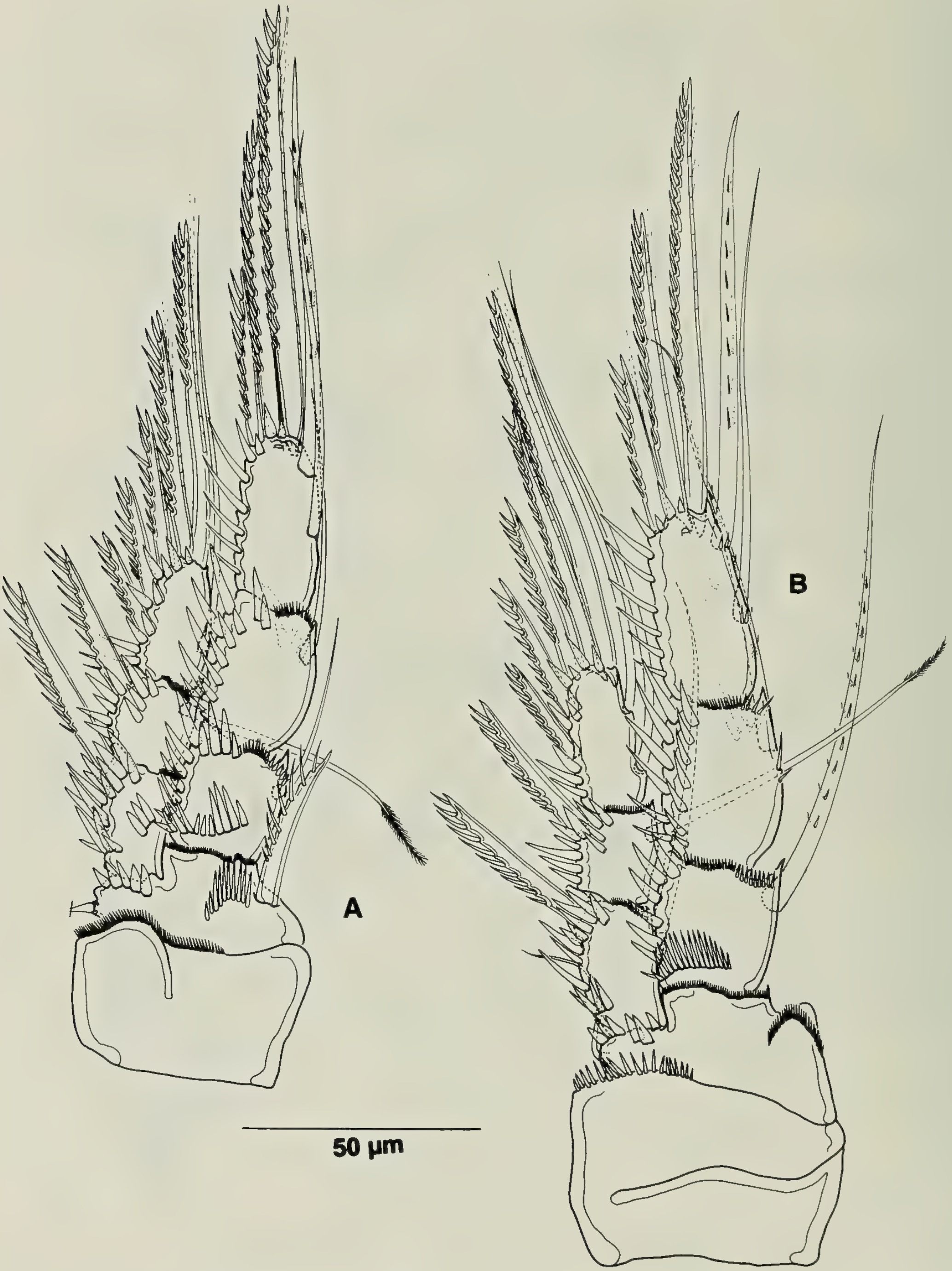

Fig. 4. *Ectinosoma mexicanum,* new species. Holotype female, EMUCOP-020591-17. A, P1, anterior; B, P2, anterior.

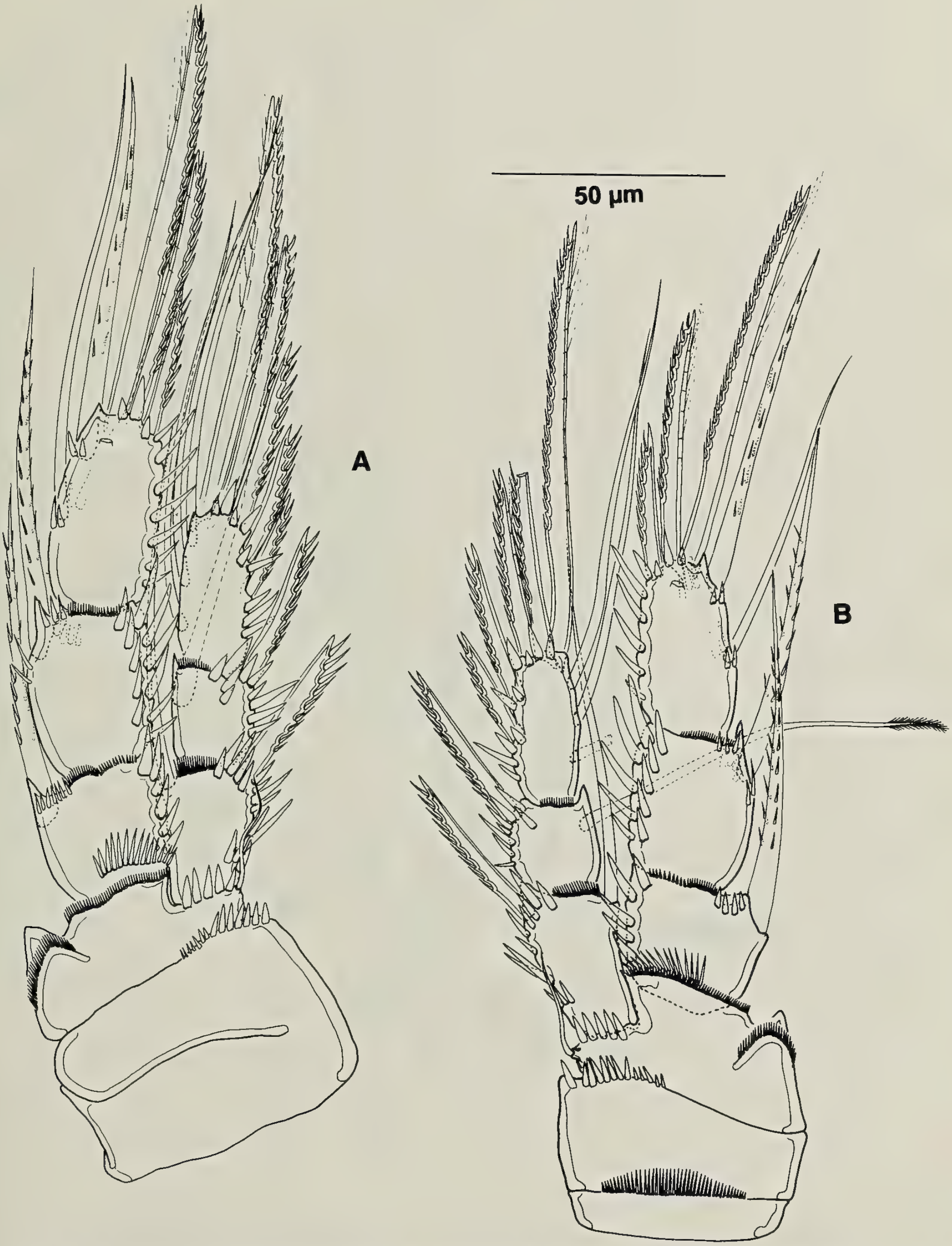

Fig. 5. *Ectinosoma mexicanum,* new species. Holotype female, EMUCOP-020591-17. A, P3, anterior; B, P4, anterior.

Fig. 6. *Ectinosoma mexicanum,* new species. Holotype female, EMUCOP-020591-17. Fifth leg, anterior.

Maxillule (Fig. 3D): arthrite of praecoxa with 4 apical spines and 2 bare setae; coxa and basis fused, the latter with 3 setae; exopod and endopod not articulating at base; exopod with 2 seta, endopod with 6 setae, 2 each fused at base to form 3 pairs of setae.

Maxilla (Fig. 3E): syncoxa with 3 en-

Fig. 7. *Ectinosoma porosum* (Wells, 1967). Holotype female, Natural History Museum (London)-1967.8.4.21. Endopod of P4.

Table 1.—Armature formula of swimming legs (P1–P4) of *Ectinosoma mexicanum.*

	EXO	END
P1	I-0; I-1; III, II, 1	0-1; 0-1; I, II, 2
P2	I-1; I-1; III, II, 2	0-1; 0-1; I, II, 2
P3	I-1; I-1; III, II, 3	0-1; 0-1; I, II, 2
P4	I-1; I-1; III, II, 3	0-1; 0-1; I, II, 2

dites, proximal endite with 3, middle endite with 2, distal one with 3 setae; allobasis with 3 setae medially. Endopod one-segmented, with 2 long spines and 5 setae.

Maxilliped (Fig. 3F): badly damaged; the endopodal setae missing. Basis with 2 parallel rows of spinules.

P1 (Fig. 4A), with massive coxa ornamented with distal spinules. Basis with outer seta and inner strong spine, with spinules at base of exo- and endopod and close to inner spine. Rami three-segmented, ornamented with strong spinules; exopod barely reaching beyond second endopodal segment. Inner seta of second endopodal segment spinulose at tip. Armature formula as in Table 1.

P2–P4 (Fig. 4B, 5A–B), with massive coxa ornamented with row of spinules in outer distal corner. Basis ornamented with strong spinules at base of exopod and with minute ones at base of endopod and in distal inner corner, the latter with dentiform process. Rami three-segmented, ornamented with spinules as in P1. Exopod of P2 barely reaching beyond second endopodal segment, of P3 and P4 reaching middle of third endopodal segment. Endopods robust; first endopodal segment of P2 and P3 as long as wide, of P4 wider than long; first and second endopodal segment of P2–P4 with strong curved setae ornamented with 2 rows of spinules. Armature formula as in Table 1.

P5 (Fig. 6): baseoendopod with 2 inner setae, innermost about 1.8 times longer than outer one; inner expansion of baseoendopod ornamented with fine spinules at base of both setae, and with strong ones along inner margin of posterior face; with 1 median anterior, and 1 distal and 1 median posterior U-pore; inner baseoendopodal expansion reaching middle of exopod. Exopod wider than long, basal limit only visible on posterior face; with 4 marginal setae and ornamented with row of long spinules in the middle and at the base of the three largest marginal elements; outermost seta about 3.5 times longer than adjacent one, the latter barely longer than inner edge of exopod; seta adjacent to innermost seta about 1.8 times longer than innermost element, the latter about 1.2 times longer than outermost seta of baseoendopod.

Remarks.—At present about 35 species of Ectinosomatidae (apart from *E. mexicanum* new species), have been attributed to the genus *Ectinosoma.* The taxonomy and phylogeny of this genus has been obscured by poor descriptions that in most cases lack sufficient detail. Moreover, no revisions of the genus are available and nothing is known about the phylogenetic relationships of this taxon (Seifried, 1997; Seifried & Dürbaum, 2000).

Ectinosoma mexicanum and *E. porosum* (Wells, 1967), seem to be related by the following synapomorphies: strong spinulose seta on the first and second endopodal segment of P2 and P4, and by the robust endopod of P2 in which the first segment is as long as wide. Unfortunately, Wells (1967) illustrated only the third exopodal segment of P3, and did not discuss the general morphology of P4. In order to check the general morphology of P3 and P4 of *E. porosum,* the only material available (Holotype 1967.8.4.21) was borrowed from the Natural History Museum (London). Unfortunately, the only slide on which the dissected holotype of *E. porosum* was mounted was badly damaged during transit and only the mouth parts, P1, P2, P4, P5 and abdomen were successfully recovered.

The general morphology of P4 of *E. porosum* (Fig. 7) showed that the robust rami constitutes a synapomorphy for *E. porosum* and *E. mexicanum.* On the other hand, the general morphology of P2–P4 of *E. mexi-*

canum shows that the robust condition of the rami and the strong spinulose seta of the first and second endopodal segment is constant in these three swimming legs. This is the case also for P2 and P4 of *E. porosum* and in all probability for the third swimming leg.

Some *Bradya* Boeck, 1872, *Pseudobradya* Sars, 1904, and *Halectinosoma* Lang, 1965 species, exhibit more robust endopods of P2–P4 than observed for most *Ectinosoma* species, but *E. mexicanum* seems to be unique within the genus *Ectinosoma* in the following derived characters: endopod of P2–P4 robust, first endopodal segment of P2 and P3 as long as wide, and first endopodal segment of P4 wider than long; first and second endopodal segment of P2–P4 with strong curved setae equipped with 2 characteristic rows of spinules; exopod of P5 wider than long (not shared by any other *Bradya, Pseudobradya, Halectinosoma* or *Ectinosoma* species), and outermost but one seta barely longer than inner edge of exopod. The latter is shared with *E. mediterraneum* Kunz, 1974, and *E. porosum.* The outermost but one seta of exopod of P5 is much shorter than the inner edge of exopod in *E. obtusum* Sars, 1920, and much longer in all other *Ectinosoma* species.

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A new species of *Monstrilla* (Crustacea: Copepoda: Monstrilloida) from Brazil with notes on *M. brevicornis* Isaac

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Abstract.—*Monstrilla pustulata* n.sp., is described from three adult females collected in the Guanabara Bay system on the coast of Brazil. The new species is similar to *M. brevicornis* Isaac in having a peculiar, conical, horn-like protuberance on the ventral surface near the antennular bases. The new species is compared with the holotype of *M. brevicornis,* from the Java Sea. *Monstrilla pustulata* can be distinguished by its body proportions and details of the antennular armature and swimming legs. However, the most striking feature of this species is its cuticular ornamentation, with a dorsal patch of small, blister-like processes on the head surface and other patches on the cephalothorax and on some pedigerous somites. The original description of *Monstrilla brevicornis* is complemented with new morphological data and is compared with *M. turgida* Scott, also from the Indonesia region. This is the first monstrilloid species described as new from the southwestern Atlantic Ocean.

Monstrilloid copepods are parasites of benthic invertebrates such as polychaetes and molluscs (Isaac 1975, Davis 1984). Adults represent the most conspicuous stage since they are free-living and are frequently captured by plankton nets. However, the group has several taxonomic and nomenclatural problems due to incomplete morphological information about the species (Huys & Boxshall 1991, Grygier 1994a). In order to make a serious revision of the taxonomic status of about 95 species included in this peculiar order of copepods, it is important to have better descriptions than has been the norm for new species and also complementary data for the previously described species. Several species have been redescribed and/or reclassified recently (Grygier 1994b, Suárez-Morales & Riccardi 1997, Suárez-Morales 1999), but much work is still needed, particularly for species in the tropical areas.

An analysis of zooplankton samples collected in 1993 and 1994 in Guanabara Bay, Brazil, yielded several specimens of monstrilloid copepods. Among them we found three females of *Monstrilla* that were identified as a new species. The new species is described herein, following the upgraded standards set by Grygier & Ohtsuka (1995), and it is compared with other related species of *Monstrilla.* The type material is deposited in the Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil.

Monstrilla pustulata, new species
Figs. 1A–F; 2A–F

Material.—Holotype adult female, preserved in ethanol, undissected. Guanabara Bay, Rio de Janeiro, Brazil (22°54.604′S, 43°08.988′E), collected 29 Sep 1994. Museu Nacional da Universidade Federal do Rio de Janeiro, Brasil, deposited under catalogue number: MNRJ 13646. Two paratype adult females, same locality, collected

9 Jun 1993, one deposited in the Museu Nacional da Universidade Federal do Rio de Janeiro, Brasil (MNRJ 13647). The other one, collected 4 Jun 1993, deposited in the zooplankton collection of El Colegio de la Frontera Sur, Chetumal, Mexico (ECO-CHZ-00518).

Description.—Female. Body length of three individuals 2.8, 2.67, and 2.83 mm (average: 2.77 mm), measured from anterior end of body to posterior margin of anal somite. Body robust, head widening gradually toward the posterior region of cephalothorax, maximum width at anterior ⅓, almost same width of posterior margin (Fig. 1A). Cephalothorax swollen ventrally in lateral view. Cephalothorax (incorporating first pedigerous somite) 54% of total body length.

Forehead flat in dorsal view, with two small, slender sensilla widely separated from each other between bases of antennules. Anteriormost part of cephalothorax with ventral, high conical protuberance pointing forward, its height (0.09 mm) similar to that of oral papilla (Fig. 1B). Another cuticular process, formed by a tranverse pattern of striations reaches halfway around the cephalothorax (see Fig. 1B). Posterior to this protuberance, and on same ventral surface. Two nipple-like processes lying below and close to conical protuberance, surrounded by patterns of short striations (Fig. 1E). Oral papilla large, protuberant, lying midventrally, about ⅓ of way from anterior edge of cephalothorax (Fig. 1B). Nauplius eye present, weakly developed, ocelli slightly pigmented on inner edge, with rounded shape. Eyes separated by a distance equal to 1.5 eye diameters.

Dorsal ornamentation of head consisting of large, branched patch of small, rounded blister-like structures arranged in tight pattern. Largest section of this patch on central portion of head, covering area between antennule bases and scattered along both sides of head where two other smaller patches are formed (Fig. 1D). Central cephalic patch extending to posterior part of cephalothorax, and forming a linear, lighter pattern reaching to posterior end of cephalothorax, where it forms a denser patch which stretches to both sides covering the posterior outer margins of the cephalothorax (Fig. 1A), and extending to a ventral patch near the coxae of the first swimming legs. Succeeding five somites (including genital double somite) bearing lateral patches of progressively smaller blisters covering mainly middle portion of outer margins.

Antennule four-segmented; distal segment comprised of segments 4–5 fused. Antennule relatively short, slightly longer than 16% of total body length and about 30% the length of cephalothorax. Proximal three antennular segments with similar length, the distal one is longest; ratio of length of antennule segments as: 18.5: 19.1: 19.2: 43.2 = 100. Armed with 0,I; 1,V; 2,I; 7,X setae (Roman numerals) and spines (Arabic numerals), plus large aesthetasc on proximal part of fourth segment (Fig. 2A). Two of these spines terminal, forming pincer-like structure (Fig. 2B). In terms of pattern described by Grygier & Ohtsuka (1995) for female monstrilloid antennular armature, setae, spines, and aesthetascs on segments 1–4 as: first (1), second ($2v_{1-3}$, $2d_{1,2}$, IId), third (3,IIIv,IIId), and fourth (4aes, $4v_{1-3}$, $4d_1$, $4d_2$, IVd, Vm, Vd, Vv, 6aes, 6_1, 6_2, b_{1-4}, b_5; setae IVv and b_6, and spine 5 not seen). Setae b_{1-3}, and b_5 dichotomously branched from distal ⅓. Seta b_5 is much bigger and more branched than in Grygier & Ohtsuka's (1995) pattern.

Cephalothorax-incorporated first pedigerous somite and 3 free succeeding pedigerous somites each bearing pair of biramous swimming legs. Intercoxal sclerites rectangular. Basis diagonally articulating with large, rectangular coxa. Basis with lateral hair-like seta on legs 1–4; on leg 3 this seta at least 2 times longer and noticeably thicker than on other legs, lightly setulated. Swimming leg setae all biserially plumose. Endopodites and exopodites of legs 1–4 triarticulated. Third exopodal segment of legs 1–4 with row of finely spiniform cu-

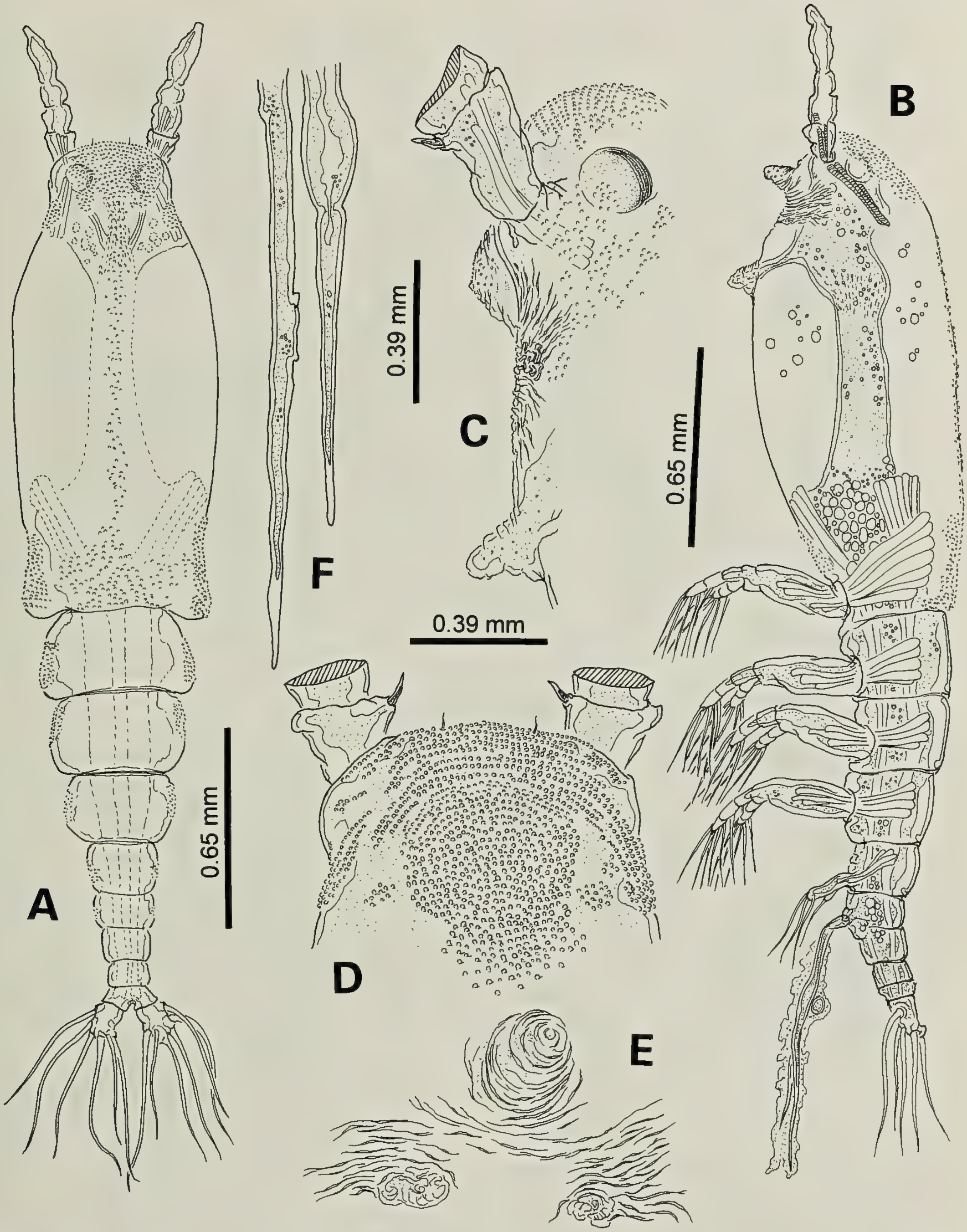

Fig. 1. *Monstrilla pustulata,* n. sp., holotype adult female: A, habitus, dorsal view; B, habitus, lateral view, lateral pustular ornamentation not shown; C, head, lateral view of paratype variant form, showing different shape of frontal cone. D, head, dorsal view, showing cuticular ornamentation; E, details of frontal conical process and related paired nipple-like ornamentations, ventral view.

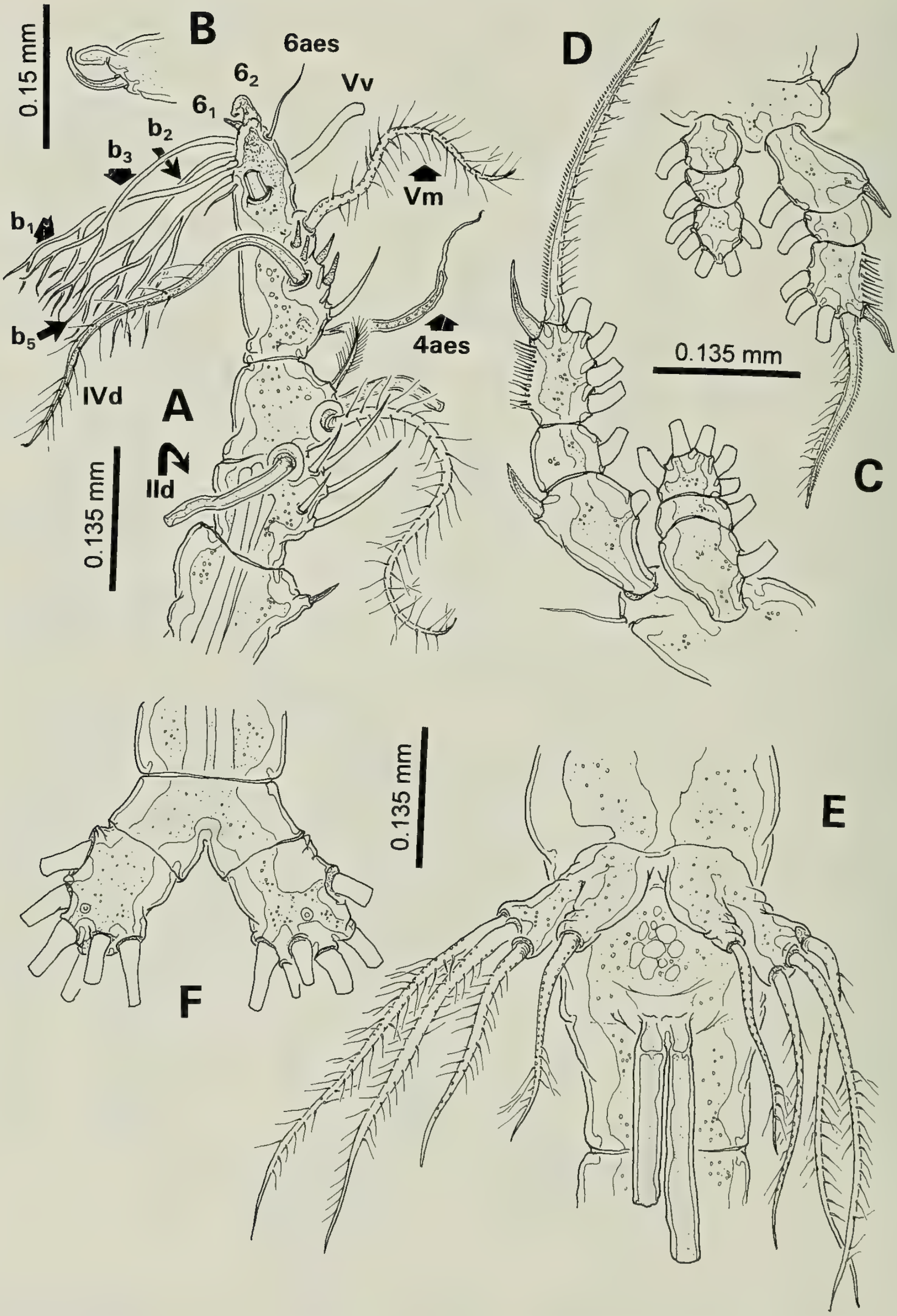

Fig. 2. *Monstrilla pustulata,* n. sp. holotype: A, left antennule, dorsal view; B, detail of pincer-like structure formed by terminal elements of antennule; C, first swimming leg, most setae cut short; D, fourth swimming leg, most setae cut short; E, fifth leg and double genital somite showing insertion of ovigerous spines, ventral view; F, caudal rami, dorsal view, setae cut short.

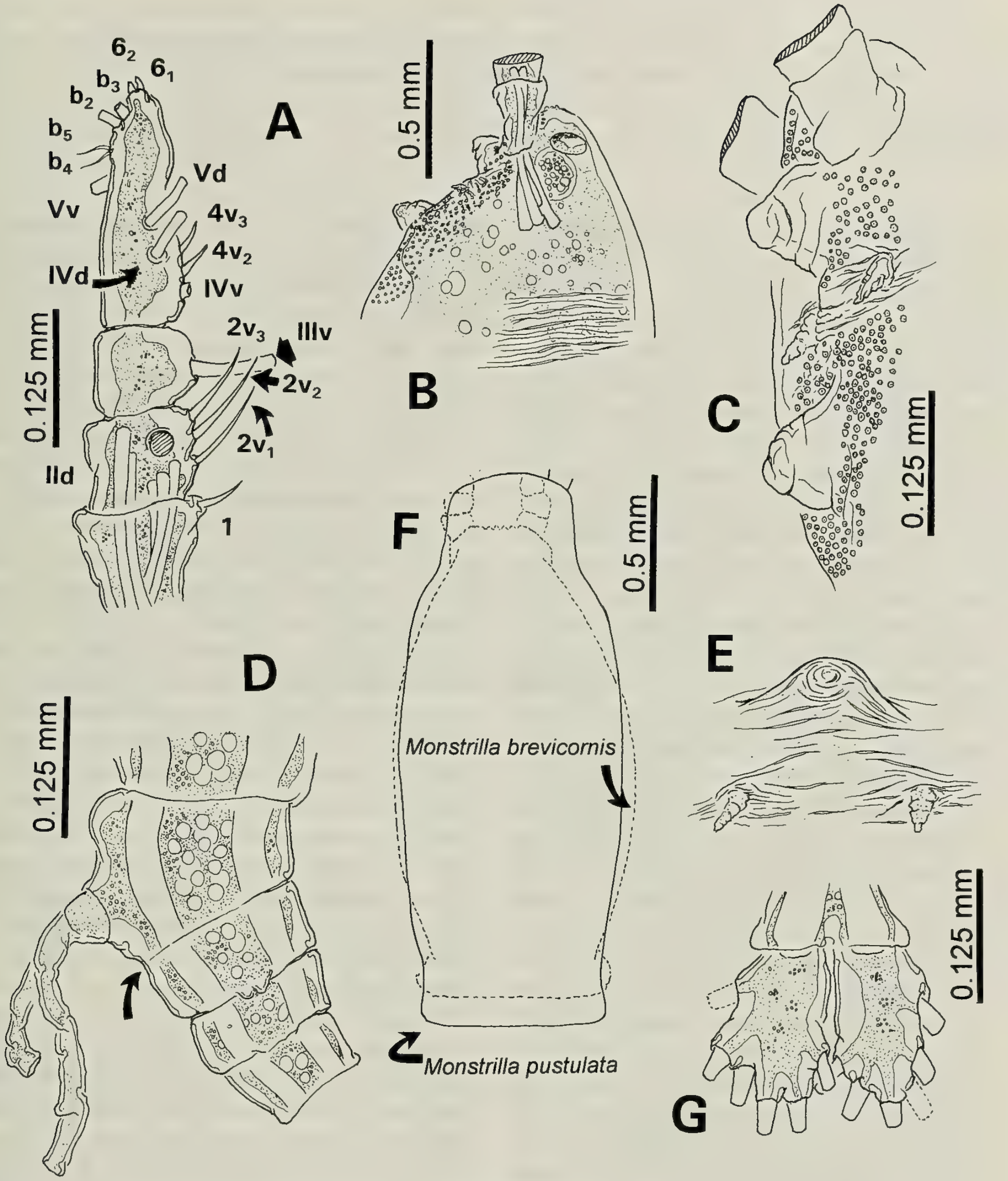

Fig. 3. *Monstrilla brevicornis,* holotype: A, left antennule, dorsal view, showing armature as nomenclature by Grygier & Ohtsuka (1995); B, head, lateral view; C, detail of head showing cuticular ornamentation; D, genital double somite, lateral view, complete suture arrowed; E, detail of ventral horn-like protuberance and nipple-like processes; F, comparative dorsal profiles of cephalothorax of *Monstrilla brevicornis* (broken line) and *M. pustulata*; G, Caudal rami, dorsal view, showing probable position of missing setae (broken lines).

Table 1.—Armature of the basis, endopodite and exopodite of *Monstrilla pustulata,* new species.

	Basis	Endopodite	Exopodite
Leg 1	1-0	0-1; 0-1; 1, 2, 2	I-1; 0-1; I, 1, 3
Legs 2–4	1-0	0-1; 0-1; 1, 2, 2	I-1; 0-1; I, 1, 2, 2

ticular processes on outer margin. Outermost terminal spiniform seta of exopod slightly curved, 2.6–3.4 times as long as bearing segment, armed with row of spines along outer margin; spines become progressively smaller toward distal part of seta, inner margin lightly setulated (Figs. 2C, D). Outer terminal spine of exopod of swimming legs 1–4 curved, relatively long, between 0.7 and 0.8 as long as bearing segment. Armature of swimming legs as in Table 1. Fifth legs bilobed, fused medially at base. Basal portion relatively short as measured from ventral anterior end of its somite. Outer lobe about 1.2 times thicker than inner lobe, armed with 3 long, lightly setulated setae, two outer ones subequal in length and breadth, innermost noticeably (34%) shorter. Inner lobe slender, cylindrical, armed with single seta as long as innermost one of outer lobe (Fig. 2E). All setae biserially setulated. Setae of fifth legs reaching about ¾ length of genital double somite.

Urosome consisting of fifth pedigerous somite, genital double somite, one free abdomina somites, and anal somite. Pedigerous somites 2–4 accounting for 26.7% of total length in dorsal view. Urosome, excluding caudal rami, accounting for 19.3% of total body length. Genital double somite with partial intersegmental division, visible in dorsal and lateral views; double somite representing less than half (38%) of length of urosome (Fig. 1B). Ratio of length of fifth pedigerous somite, genital double somite, and free abdominal somite: 30.6: 38: 14.8: 16.6 = 100. Medial portion of genital double somite flat, bearing relatively long, basally separated ovigerous spines, slender in distal one third but slightly swollen distally (Fig. 1F), one slightly longer than the other. Ovigerous spines representing about 30% of total body length, extending slightly beyond setae of caudal rami. Caudal rami short, subquadrate, about as long as wide, moderately divergent, bearing six setae: two lateral, three terminal, one dorsal (Fig. 2F).

Variability.—One (ECO-CHZ-00518) of the two paratype specimens with reduced pattern of pustular patches relative to the holotype, only about half the surface covered by the patch in the holotype is covered in the paratype. Another difference is a lower frontal cone (see Fig. 1C).

Type locality.—Guanabara Bay (Rio de Janeiro, Brazil) (22°54.604′S; 43°08.988′W). Water column. Depth average: 50 m.

Etymology.—This new species is named using an adjectival derivative of the Latin term *pustula* meaning blister or bubble, *pustulatus* meaning blistered, and using the feminine form *pustulata.* The epithet refers to the peculiar cuticular ornamentation of the species, formed by patches of minute, bubble-like processes, not reported in any other previously known species of Monstrilloida.

Remarks.—The female specimens of this new species can be easily included in the genus *Monstrilla* because of the presence of two somites between the anal and the double genital somites (Isaac 1975). This species is morphologically similar to *M. brevicornis* Isaac, 1974a, described from material collected in the Java Sea off Indonesia (Isaac 1974a), and they may be closely related. They both share a character not commonly found in any other species of *Monstrilla*: a high conical ventral process between the oral papilla and the antennular bases. Another species of *Monstrilla* with a long conical process is *M. spinosa* Park, 1967, but it differs strongly from these two species in several other important characters. The general body shape and proportions are also very much alike, and based on the draft illustrations of Isaac (1974a, 1974b), the Brazilian specimens would be identified as *M. brevicornis.* This species is not mentioned in Isaac's (1975) key to the Monstrilloida.

We have examined the adult female holotype specimen of *Monstrilla brevicornis,* collected at Bangka Strait, Java Sea, Indonesia. Plankton sample, leg. *Prinz Adalbert,* determined by M. J. Isaac, 1973. Deposited in the Museum für Naturkunde Berlin, under catalogue number 15 698.

The new species shows several characters which vary from the holotype of *M. brevicornis.* Although in both species the cephalothorax is robust, its length/width (at widest point) proportions differ: 1.9 in *M. brevicornis* vs. 2.3 in *M. pustulata.* Hence, the cephalothorax of the new taxon is more slender and longer than the clearly oblong, wider shape of *M. brevicornis* (see Fig. 3F).

The cuticular ornamentation of the head is considered to be a useful character to differentiate species of *Monstrilla* (Suárez-Morales & Gasca 1998). In the new species the ornamentation pattern is peculiar, with a large patch of blister-like processes on the dorsal surface of the cephalic region, patches on the lateral margins of the pedigerous somites (see Fig. 1), and a linear patch along the dorsal surface of the cephalothorax. In *M. brevicornis* the ornamentation is entirely different, mainly with transverse cuticular lines around the anterior ⅓ of the cephalothorax and near the oral papilla. There is also a pattern of uniformly arranged, small, button-like ornamentations on most of the antero-ventral surface; they are arranged in a tighter pattern near the oral papilla (Fig. 3C). The front is roughly corrugated in *M. brevicornis,* whereas it is covered with cuticular blisters in *M. pustulata.* In both species the conical process is as high as the oral papilla, but it seems to be located closer to the antennule bases in *M. brevicornis* than it is in the new species.

Both species have nipple-like processes on the ventral surface between the conical process and the oral papilla; however, these structures differ substantially between the two species. In *M. brevicornis* they are very long and digitiform, and they clearly protrude from the ventral surface profile in lateral view. In the new species these structures have a different cuticular pattern of ridges, are almost flat, and barely noticeable in lateral view (see Figs. 1B, C). One of the most important differences between both species is the arthrodial membrane separating the posterior the posterior thoracic somite and anterior abdominal somite. It is complete in *M. brevicornis,* whereas it is incomplete in the new species, not reaching the ventral surface.

The antennules of *M. brevicornis* represent about 18% of the body length, whereas this figure is 16% in *M. pustulata.* The terminal spines of the distal segment of the new species are clearly forming a pincer-like structure (see Fig. 2A); in *M. brevicornis* both spines are short, and they do not form such kind of structure.

In the swimming legs, the outer margin of the exopods have long hair-like cuticular processes in the new species but this margin is naked in *M. brevicornis.* The terminal spiniform seta of the distal exopodal segment is different in both: in the new species the inner margin bears thin setules (see Figs. 2C, D), whereas it is naked in *M. brevicornis.* The fifth legs of the holotype of *M. brevicornis* are incomplete, they seem to have originally had two lobes, but only the outer one is now present. Two lobes are clearly present in the new species, the inner one armed with a single seta. Due to the morphological similarity of both species, it is expected that *M. brevicornis* shares the same condition, but this can't be verified until more specimens of *M. brevicornis* become available. The terminal setae of the outer lobe of the fifth leg in *M. brevicornis* are widely separated from each other and are markedly divergent; in the new species these setae are not divergent and show a tighter placement along the terminal margin of the fifth leg. Another character in which the two species differ is the shape and proportions of the caudal rami. These are quadrate, as long as wide, in *M. pustulata* but clearly rectangular (1.85 longer than wide) in *M. brevicornis.* Although Isaac (1974a, 1974b) illustrated six setae on both furcal rami, we could only find five on the holotype; the new species bears six setae on each caudal ramus. It is probable that a seta of each side was lost during handling and or examination (see Fig. 3G).

The new species also shows some affinities with *M. turgida* A. Scott, 1909 such as the robust shape of the cephalothorax and the bilobed fifth leg with a three outer and one inner setae. However, besides the peculiar conical process shown by *M. pustulata,* these two species can be distinguished by the detailed structure of the fifth legs. In the new species the legs have a short basal part, whereas the base is much longer and slenderer in *M. turgida.* The fifth leg's inner lobe is longer than the outer lobe in *M. turgida,* but it is shorter in *M. pustulata.* The ovigerous spines in *M. turgida* are long, equal to about 60% of the total body length, whereas they are much shorter in the new species, representing around 30% of the body length. Furthermore, the ovigerous spines of *M. turgida* are distinctly pointing anteriorly; this feature was considered by Grygier & Ohtsuka (1997) to be one of the main characters to define a genus level group of species within the Monstrilloida.

As mentioned above, the original description of *M. brevicornis* is incomplete and comments are provided here as a complementary description of this species. The cephalothorax is laterally expanded in dorsal view, with a wide oblong shape, 1.9 times longer than wide (Fig. 3F). The head is relatively wide and tapers abruptly toward the posterior end. The front is coarsely corrugated and no sensillae were observed there. The cuticular ornamentation consists of a uniform pattern of minute, flat, button-like processes covering most of the dorsal and ventral surfaces of the cephalothorax. The lateral margins of the cephalothorax and the area around the oral papilla have tranverse, parallel cuticular ridges (Fig. 3B). On the ventral surface, between the oral papilla and the conical process, this species has a pair of protruding digitiform nipple-like processes surrounded by an irregular pattern of cuticular ridges (Figs. 3C, E). The genital double somite has a complete suture and a pair of lateral processes on the posterior margin of this compound somite (Fig. 3D).

The antennules represent 18.2% of the total body length, a figure different from the 14% estimated by Isaac (1974a). This difference might be due to the forward position of one of the antennules; our measurement was made on the same observation plane. Due to the generally poor condition of the holotype, most of the antennular armature is lost. Following Grygier & Ohtsuka (1995), the elements found in this specimen are: 1 (first segment); $2v_1$, $2v_2$, $2v_3$, socket of IId (second segment); IIIv (third segment); IVv, $4v_2$, $4v_3$, IVd, IVv, Vd, Vv, 6_1, 6_2, bases of b_2, b_3, and b_5, b_6 (see Fig. 3A). Isaac (1974b) mentioned only one terminal spine on the distal segment, it actually has two, but one is broken near the base.

As mentioned by Isaac (1974b), the four pairs of swimming legs show the usual armament pattern of monstrilloid copepods. Here we can add that all swimming setae are lightly and biserially plumose. The small terminal spine on the outer margin of the third exopod is clearly curved as in the new species (see Fig. 2C), and the spiniform are lightly and biserially plumose. The small terminal spine on the outer margin of the third exopod is clearly curved as in the new species (see Fig. 2C), and the spiniform seta next to it has a smooth inner margin. The fifth legs were interpreted by Isaac (1974a, 1974b) as having a single lobe with three setae; however, an inner ramus was probably present in this specimen, but it is broken. The furcal rami are rectangular and each is armed with five setae only, they are probably six of them as suggested by Isaac (1974a, 1974b) when adding the setae indicated in their corresponding positions as shown by broken lines in Fig. 3G.

This species was originally described from material collected in the Java Sea (Isaac 1974a), and basically the same brief description and illustrations were repeated by Isaac (1974b). As mentioned by Grygier (1995), Isaac (1974a, 1974b) did not compare it with *M. turgida* Scott, 1909, which he mentioned as having similarly short antennules. *Monstrilla brevicornis* differs from *M. turgida* in the shape of the cephalothorax, which is widest at its anterior one-third in the former and at the middle in the latter species. The caudal rami are nearly quadrate in *M. turgida* and clearly rectangular in *M. brevicornis.* The antennules are 35% of the cephalothorax length in *M. turgida* and 25% in *M. brevicornis.* The fifth legs are not fully comparable due to the broken inner part of the holotype of *M. brevicornis,* but the arrangement of the three setae on the fifth leg of *M. turgida* (as depicted by Scott 1909) seems to be tight, whereas they are widely separated at base in *M. brevicornis.* However, the main difference between these two species is the presence of the conical process in *M. brevicornis,* which is absent in *M. turgida.*

Previous records of *Monstrilla* in Guanabara Bay include: *M.* cf. *reticulata, M. rugosa* Davis, 1947, and *M. grandis* Giesbrecht, 1891 (Dias 1996). Thus, *M. pustulata* is the first species of *Monstrilla* described as new from this bay. *Monstrilla grandis* Giesbrecht, 1891, from off Patagonia is the other species first described as new from the southwestern Atlantic Ocean region. There are a few other scattered records of species first described from elsewhere being known in the region (Razouls 1996).

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Haplostoma kimi, a new species and a redescription of *Haplostomella halocynthiae* (Fukui) from Korea (Copepoda: Cyclopoida: Ascidicolidae)

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Abstract.—A new species of the genus *Haplostoma* associated with the ascidians *Styela clava clava* Herdman and *Amaroucium pliciferum* Redikorzev is described. The new species can be differentiated from its 13 congeners in having 4 simple spines on second segment of antenna, 3 spines and 1 seta on the exopod of legs 3 and 4, and 6 distinct projections on the posterior margin of labrum. In addition, *Haplostomella halocynthiae* (Fukui), a new record in Korean fauna is redescribed, based on the specimens collected from the ascidians, *Styela clava clava* and *Halocynthia roretzi* (von Drasche).

The subfamily Haplostomatinae, one of the eight subfamilies in the family Ascidicolidae (Illg & Dudley 1980), consists of four genera (*Haplostoma, Haplostemella, Haplostomides,* and *Haplosaccus*). Most species are known to inhabit the common test of compound ascidians, but some species have been described from the branchial sac and/or intestine of solitary ascidians (Ooishi & Illg 1977).

During the course of a survey of the Korean ascidicolid copepods, two species of Haplostomatinae from Korean waters were found, one is a new species and the other a species known only from Japan. This paper describes both species.

The specimens were cleared in lactic acid for approximately one day before taking measurements and dissecting. Drawings were made with the aid of a camera lucida.

Description

Family Ascidicolidae Thorell, 1859

Subfamily Haplostomatinae Chatton and Harant, 1924

Genus *Haplostoma* (Canu, 1886)

Haplostoma kimi, new species

Figs. 1, 2

Type material.—20 ♀ ♀ found inside intestine of solitary ascidian, *Styela clava clava* at Gangneung (approximately 37°45′N, 128°50′E) in Sea of Japan, Aug 1992. Holotype ♀ (EWNHM60258) and paratypes 14 ♀ ♀ (EWNHM60259) deposited in Natural History Museum, Ewha Womens University, Seoul, Korea. Remaining specimens (dissected) in the collection of the author.

Other material examined.—20 ♀ ♀ on common test of compound ascidian, *Amaroucium pliciferum,* collected at Hupo in Sea of Japan, on 3 Aug 1987; 5 females collected from *A. pliciferum* at Seongsanpo in Jeju Island, on 27 Jun 1987.

Female: Body (Fig. 1A–C) columnar, vermiform and grub-like. Full grown adult 2.04 mm long (holotype, from tip of cephalosome to end of caudal rami excluding setae), with slightly tapering cephalosome (Fig. 1A, B) but in dorsal view becoming gradually broadened posteriorly (Fig. 1A). Young adult with evenly rounded cephalosome and evenly wide metasome (Fig. 1C, E). Cephalosome with distinct rostrum, bearing antennule, antenna, mandible, and maxilliped. Dorsal cephalic plaque represented by 2 large sclerotized areas (Fig. 1D). Pedigerous somites demarcated from each other by moderately prominent constrictions. Each pedigerous somite bearing 1 pair of minute protrusions on dorsolateral surface. Each protrusion prominent in adults, with minute seta. Anal segment (Fig. 1F) about $\frac{1}{10}$ length of whole body, directed posteroventraly (Fig. 1B, G), consisting of rounded, broad anterior part and narrower, laterally parallel posterior part. Proximal section of anal segment with genital apparatus consisting a pair of oviducal apertures on dorsolateral sides. Oviducal aperture at each side with 3 spines (Fig. 1F). Caudal rami divergent. Each ramus as long as wide, strongly tapering, triangular, inconspicuously demarcated from anal segment, and armed with 1 lateral, 1 disterodorsal, and 1 terminal spine. Terminal spine extremely thick, triangular and claw-like.

Rostrum with a row of minute spinules on both sides (Fig. 1E). Antennule (Fig. 1H) indistinctly segmented and tapering terminally. Proximal part with 3 broad setae and 2 or 3 thin setules. Distal part incompletely divided on posterior margin into 3 segments, with 2 broad proximal setae mounted on a large elevation, 5 broad (1 being distinctly larger) and 1 slender setae in medial part, and 8 slender setae terminally. Antenna (Fig. 1I) 2-segmented. First segment broad and slightly longer than distal segment. Second segment with sclerotized margins, and bearing 3 lateral and 1 terminal spines. All spines thick and claw-like.

Labrum with 6 rounded, distinct projections on posterior margin (Fig. 2A). Mandible a lobe bearing 2 terminal setae (Fig. 2A). Maxillule and maxilla absent. Maxilliped (Fig. 2B) 5-segmented. First segment nearly as long as wide, much wider than distal segments but unarmed. Second segment as long as wide, with 1 distal and 1 subdistal setae on inner margin; location of subdistal seta varied, occasionally located in middle portion of inner margin. Third and fourth segments indistinctly segmented (sometimes fused), short and unarmed. Fifth segment a small claw, with 1 subterminal, claw-like process on inner side.

Legs 1–4 alike in general shape and becoming gradually larger from anterior to posterior. Protopod non-segmented, with thick sclerotization along posterior margin. Endopod fused with protopod and represented by large, conical protrusion. Exopods unsegmented. Exopod of leg 1 (Fig. 2C) with a trace of segmentation, armed with 1 proximal seta, 4 claw-like spines, and 1 small dentiform process. Exopod of leg 2 similar to that of leg 1, but 1 spine less (Fig. 2D). Leg 3 (Fig. 2E) and 4 (Fig. 2F) alike, protruded in the middle portion of outer margin near insertion of seta, and armed with 1 proximal seta and 3 spines. Bases of these spines with rows of minute spinules.

Leg 5 (Fig. 2G) a small tapering lobe located on dorsolateral side of last metasomal somite, bearing 1 basal and 2 terminal setae.

Male: Unknown.

Etymology.—The specific name, *kimi,* is given after Dr. Il-Hoi Kim who provided specimens of the new species.

Remarks.—There are 13 species of *Haplostoma,* with five of them bearing processes on the posterior margin of labrum. The new species has 6 processes, similar to the following three species: *H. banyulensis* (Brément, 1909), *H. eruca* (Norman, 1869), and *H. minutum* Ooishi & Illg, 1977. These three species are easily differentiated from *H. kimi,* by the armature on the exopod of legs 3 and 4, armed with either 2 (in *H. eruca* and *H. minutum*) or 4 spines (in *H. banyulensis*), instead of 3 spines and 1 seta as in *H. kimi.*

According to Ooishi (1998), *Haplostoma mizoulei* Monniot, 1962 is synonymous with *H. brevicauda* (Canu, 1886). *H. mizoulei* Monniot, 1962 is the only species that carries the same number of spines on the exopod of legs 3 and 4 as the new species (Monniot, 1962). However, *H. mizoulei*

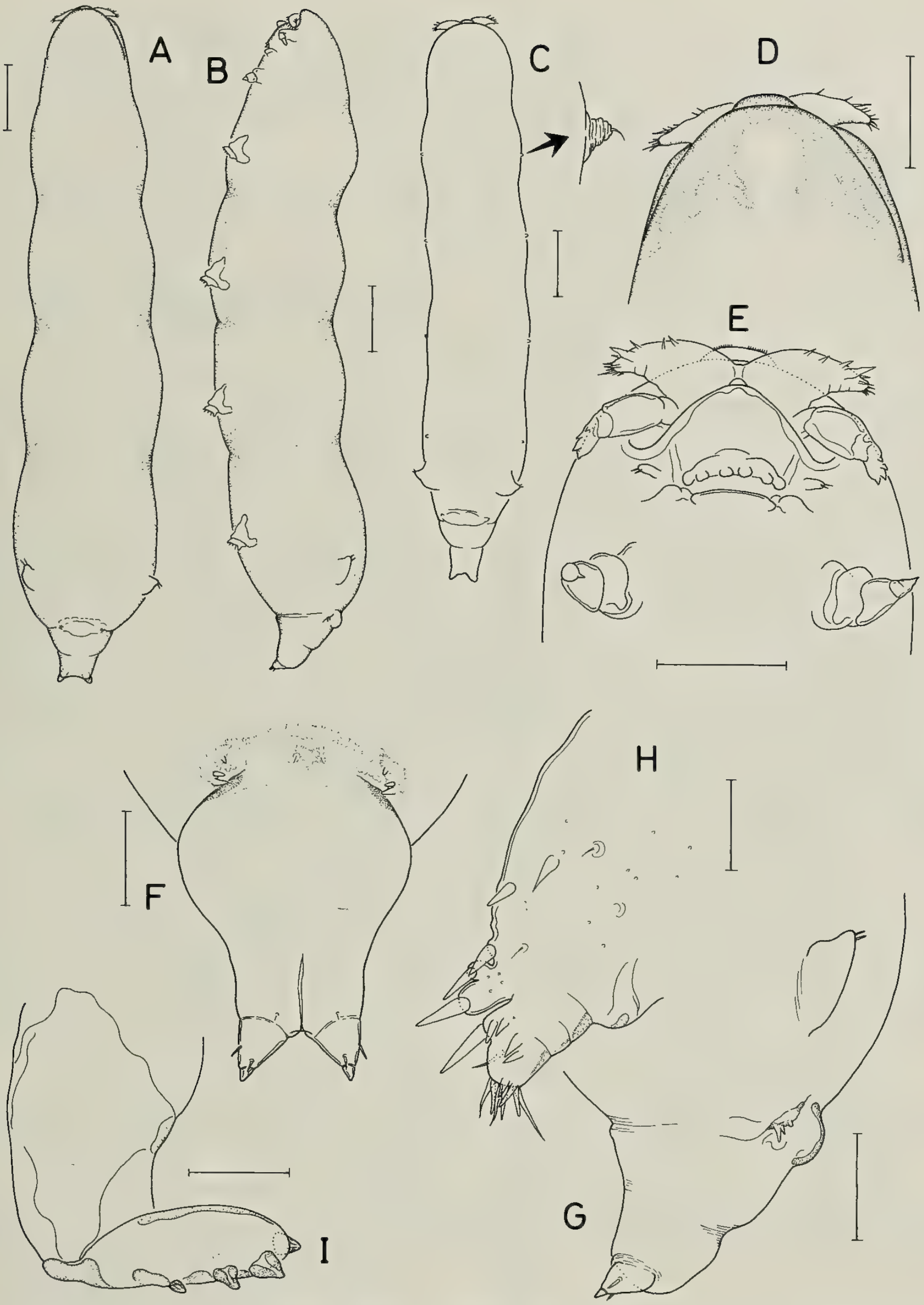

Fig. 1. *Haplostoma kimi* new species. Female. A, habitus, dorsal; B, habitus, lateral; C, habitus, protrusion of dorsal, D, cephalic plaque; E, oral area, ventral; F, anal segment and caudal rami; G, leg 5, anal segment and caudal rami. lateral; H, antennule; I, antenna. Scales : A–C = 0.2; D–G = 0.1; H, I = 0.02mm.

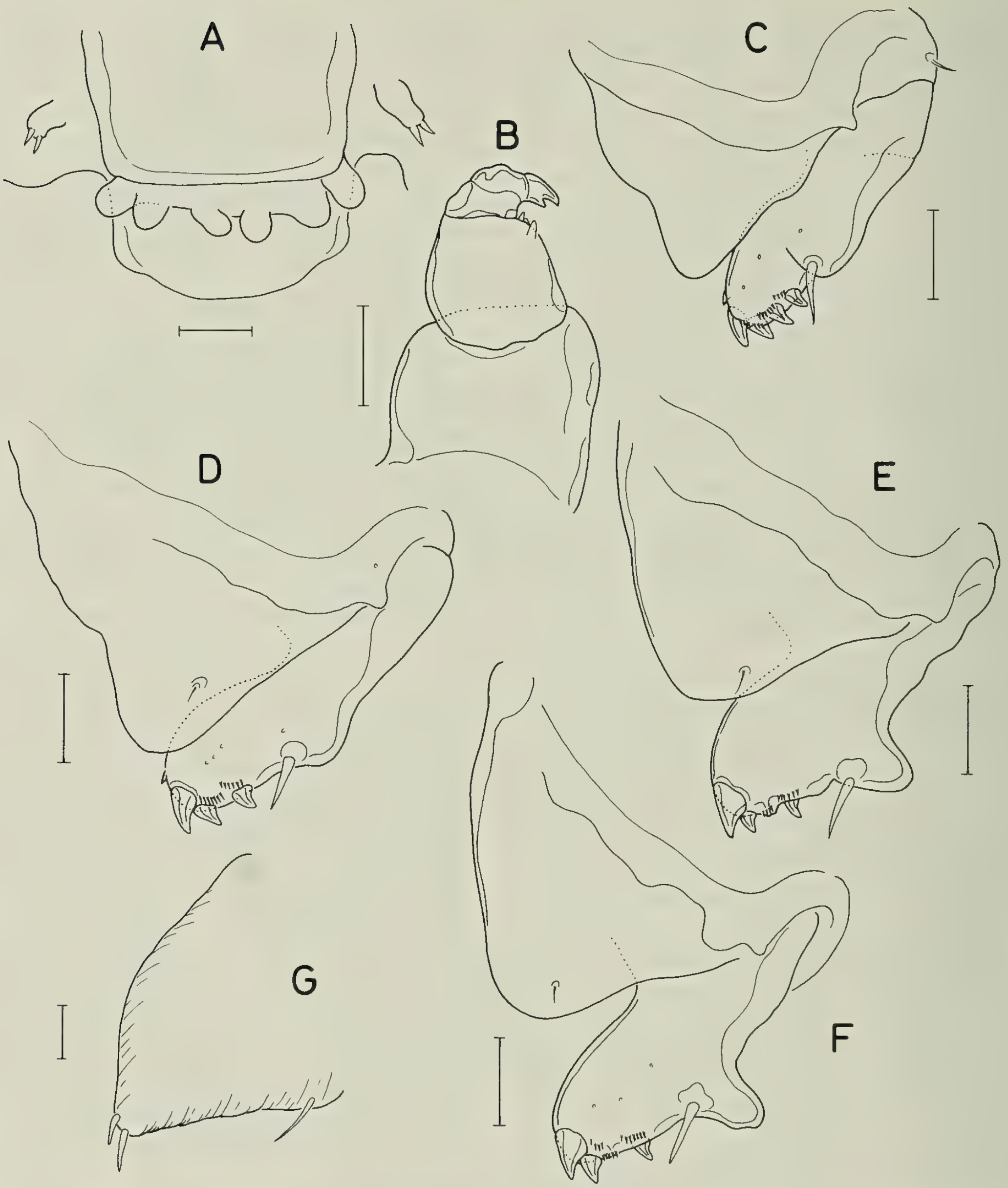

Fig. 2. *Haplostoma kimi* new species. Female. A, labrum and mandible, ventral; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 4; G, leg 5. Scales : 0.02 mm all.

differs from *H. kimi,* in having 2 spines and 2 setae instead of 1 spine and 2 setae on the caudal ramus, 3 setae instead of 2 setae on the apex of leg 5, and no subterminal process on the terminal claw of maxilliped.

Haplostoma gibberum (Schellenberg, 1922) is incompletely known but not comparable with the new species on the basis of morphology of the labrum and legs. According to Ooishi and Illg (1977), *H. gibberum* has 3 spines on the terminal segment of the antenna. This character differs from that of the new species which has 4 simple spines.

It is remarkable that although *H. kimi* is associated with both solitary and compound ascidians, specimens from either host do not show noticeable differences in morphology.

Genus *Haplostomella* Chatton and Harant, 1924

Haplostomella halocynthiae (Fukui, 1965)
Figs. 3, 4

Rhabdomorpha halocynthiae.—Fukui, 1965:61.

Haplostomella halocynthiae.—Ooishi and Illg, 1974:365, figs. 1–3.

Material examined.—From *Styela clava clava* Herdman: 2 ♀ ♀ from Busan in Tsushima Strait, on 1 Jul 1986; 2 ♀ ♀, from Busan, on 3 Nov. 1986; 1 ♀ from Gangneung in Sea of Japan, on 3 Nov 1979. From *Halocynthia roretzi* (von Drasche): 1 ♀ from Yeosu in Tsushima Strait, on Feb 1993.

Female: Body elongate, 10.3 mm long, non-segmented and vermiform. Segmentation in some cases identifiable by lateral constrictions. Body roughly divided into 3 sections: cephalosome, metasome and urosome, with length proportion of 1 : 21 : 7.4. Ventral surface of body, especially around legs, with numerous rows of minute spinules as in Fig. 4C; each row consisting of 4 to 15 spinules. Cephalosome small, with discernible cephalic shield. Metasome indistinctly 5-segmented, with 5 pairs of legs. Each metasomal somite with a pair of suboval dorsal plates (Fig. 3A). Urosome tapering, without any trace of segmentation, about 20% as long as body. Oviducal aperture (Fig. 4D) located dorsolaterally on genital somite, with hood-like semicircular projection armed with 4 dorsal denticles, outermost denticle 3 or 4 small points. Caudal rami widely separated from each other (Fig. 3C), 167 × 81 μm, 2.06 times as long as wide, armed with 5 setae (Fig. 3D). Egg sac elongate, 5.0 mm long.

Rostrum not discernible. Antennule (Fig. 3F) tapering, with 17 setae and several setules, and 2 traces of segmentation in distal portion. Antenna (Fig. 3G) curved, consisting of 2 parts. Basal part comprises 75% length of antenna, with 1 inner distal seta. Distal part armed terminally with 1 blunt process and 3 setae; innermost seta globular and tipped with a setule.

Labrum unarmed, posterior margin with round medial projection. Mandible (Fig. 3H) fringed with a hyaline layer, armed in distal half with 2 rows of ±10 denticles. Maxillule not identified. Maxilla (Fig. 3I) indistinctly 2-segmented. First segment robust. Second segment distinctly narrower, about twice as long as wide, and half as long as first segment; protruded postero distally and tipped with a small tubercle (sometimes absent), in addition to bearing 1 large antero distal, spiniform seta. Maxilliped (Fig. 4A, B) 3-segmented stout and massive. First segment unarmed. Second segment with many rows of spinules on outer dorsal surface and 2 unequal processes on inner margin, with larger one distally. Terminal segment represented by a strong pointed claw, with its tip inserting between two processes on second segment.

Legs 1–4 uniform in shape. Protopod indistinctly demarcated from body surface, represented by sclerotized integument covered by rows of spinules and hairs. Exopod divided into ventral and dorsal lobes ventral lobe claw-like and smaller, dorsal one tipped with a setule. Body surface near exopod with 4 prominent digitiform processes. Endopod fused to protopod, represented by posterior bilobed bulge and covered by rows of spinules (Fig. 4C). Leg 5 (Fig. 4F) represented by 2 setae and 2 or 3 minute setules.

Male: Unknown.

Remarks.—*Haplostomella halocynthiae* has so far been known only from *Halocynthia roretzi* in Japan. The Korean specimens of *H. halocynthiae* are very similar in morphology to the Japanese specimens. Therefore, the present record adds another ascidian host, (*Styela clava clava*) from another

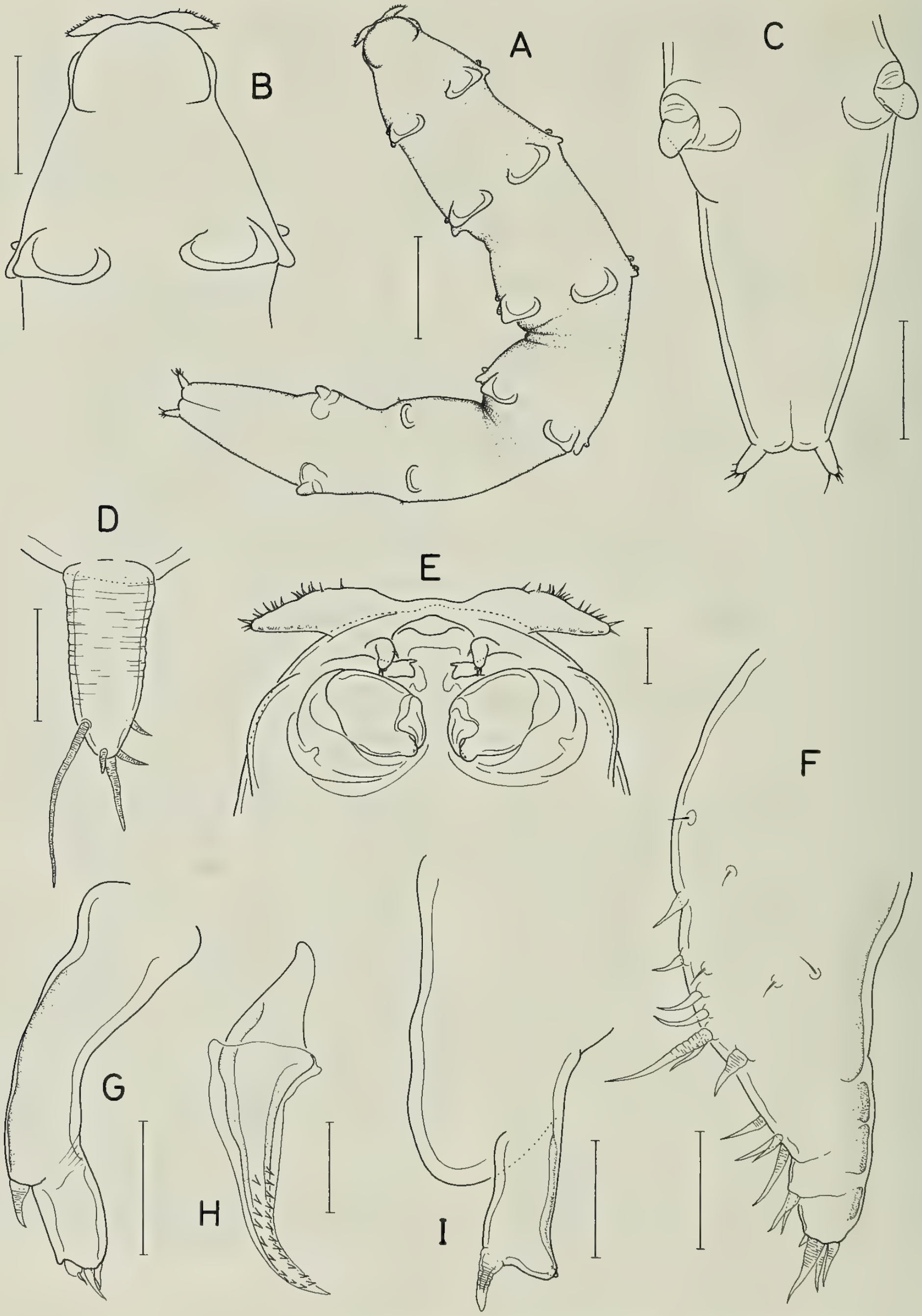

Fig. 3. *Haplostomella halocynthiae* (Fukui). Female. A, habitus, dorsal; B, cephlosome, dorsal; C, urosome, dorsal; D, caudal ramus; E, oral area, ventral; F, antennule; G, antenna; H, mandible; I, maxilla. Scales : A = 1; B, C = 0.5; D, E = 0.1; F, G, I = 0.05; H = 0.02mm.

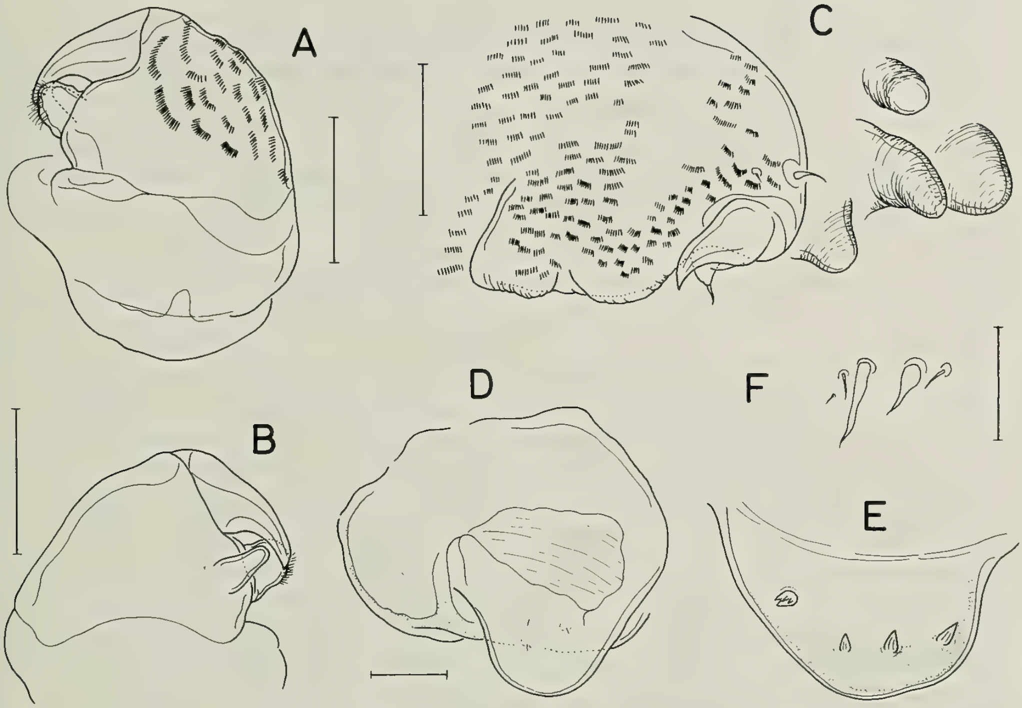

Fig. 4. *Haplostomella halocynthiae* (Fukui), Female. A, maxilliped, outer; B, maxilliped, inner; C, leg 1; D, oviducal aperture, dorsal; E, oviducal aperture, ventral; F, leg 5. Scales : A–E = 0.1; F = 0.05 mm.

country. This species was thoroughly redescribed by Ooishi and Illg (1974); it is redescribed herein as one of its hosts, *H. roretzi,* is the most important ascidian cultured along the Korean coast.

Acknowledgement

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Nauplii and copepodids of *Scottomyzon gibberum* (Copepoda: Siphonostomatoida: Scottomyzontidae, a new family), a symbiont of *Asterias rubens* (Asteroidea)

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Abstract.—Naupliar and copepodid stages of *Scottomyzon gibberum* (Scott & Scott, 1894) associated with the starfish *Asterias rubens* Linnaeus, 1767 in the North and White Seas were collected from the host or reared in the laboratory. There are six copepodid stages and four naupliar stages. Changes in size and proportions of the prosome of adult females result from an expansion of unsclerotized integument along the margins of the shield of the cephalothorax and tergites of the second and third thoracic somites. The monotypic genus *Scottomyzon* Giesbrecht, 1897 is transferred to a new family Scottomyzontidae on the basis of a 3-segmented abdomen for adults of both sexes, paired dorsolateral gonopores near the posterior margin of somite, paired ventral copulatory pores near the middle of somite, and sexual dimorphism in oral siphon.

Scottomyzon gibberum (Scott & Scott, 1894) currently is the only species in the monotypic genus *Scottomyzon* Giesbrecht, 1897 of the Asterocheridae. The copepod is associated with the starfish *Asterias rubens* Linnaeus, 1767 in the North Sea and the White Sea, and with many different species of starfishes in the Sea of Japan (Humes 1986, Kim 1992, Smurov 1993). In slightly more then 100 years since its description, this "highly interesting copepod" (Bresciani & Luetzen 1962:381) has been redescribed by Roettger (1969) and by Kim (1992). Roettger considered the unusual variability among mature females. Smurov & Ivanenko (1993) and Ivanenko & Smurov (1995, 1996) discussed growth of the adult female, morphology and settlement of the first copepodid stage, and bacterial infestation of the exoskeleton of White Sea specimens.

Descriptions of postembryonic development of siphonostomatoids associated with invertebrates are not as numerous as those of siphonostomatoids parasitizing fishes. Naupliar and copepodid stages of invertebrate symbionts are described for the cancerillid *Cancerilla tubulata* Dalyell, 1851 by Carton (1968) and the asterocherid *Asterocheres simulans* (Scott, 1898) by Murnane (1969), although some incorrect schematic illustrations and errors in identification of copepodid stages limit the use of these data. Development of parasitic nicothoids have been reported by Bowman & Kornicker (1967), Boxshall & Lincoln (1983), and Heron & Damkaer (1986). Knowledge about changes in morphology of adult parasitic copepods is not as well known as changes in adult free-living crustaceans (Freeman 1993), and there are only a few studies of growth of the siphonostomatoid females (Kabata 1979, Smith & Whitfield 1988, Piasecki 1989). We present here the first detailed description of the complete postembryonic development, including morphological changes in adult females, of *S. gibberum,* a siphonostomatoid associated with an invertebrate.

Methods

Specimens of the starfish *Asterias rubens* were isolated in plastic bags during SCUBA dives near the Marine Station of Moscow State University on the White Sea. Individual starfishes were washed in freshwater and then the washwater was filtered through a fine-mesh net. Copepodid stages of *Scottomyzon gibberum* were picked from the residue and fixed with 4% formaldehyde in sea water.

Naupliar stages and the first copepodid stage of *S. gibberum* were cultured at the White Sea Marine Station (September 1993) by the senior author, following the general methods of Izawa (1986). The ovigerous females were isolated under stereomicroscope with a pipette from gall-like tissue extensions of starfishes with radius exceeding 5 cm. The nauplii obtained from eggs were reared in petri dishes to the first copepodid stage at 11–13°C; water was changed two or three times daily.

All measurements and dissections were made for the copepods from the White Sea. Specimens were cleared in lactic acid following the method of Humes & Gooding (1964), and stained by adding a solution of chlorazol black E dissolved in 70% ethanol/ 30% deionized freshwater (Ferrari 1995). Drawings were made with a camera lucida.

To remove the debris and lipid drops from the exoskeletal surface for SEM observations, specimens from the White Sea were placed in a dilute solution (three drops in 100 ml of distilled water) of a detergent (Tween-80) for 30 min (Felgenhauer 1987), after which the copepods were actively shaken and washed in five changes of distilled water. Specimens then were fixed in OsO4 for four hours, dehydrated through graded ethanol dilutions, critical point dried, mounted on aluminium stubs, coated with gold, and viewed with a scanning electron microscope HITACHI S-405 A.

Naupliar stages are N1–N4; copepodid stages are CI–CVI. Somites are numbered according to their relative developmental age following Hulsemann (1991); trunk somites, except the most posterior anal somite, increase in age and decrease in numeral designation anteriorly. The first thoracic somite bears the maxilliped, and the genital openings are found on the seventh. The anal somite bearing caudal rami is designated as the first and the oldest abdominal somite, the anterior abdominal somite is the second with the third and fourth following in order posteriorly. Dorsoventral thickness of the body is measured at the level of ventral projection between maxilliped and leg 1.

Ramal segments of swimming legs 1–4 (thoracopods 2–5) are referred to by their appearence during development (Ferrari 1995). The terms "seta" and "spine" are used for articulating cuticular elements connected by an arthrodial membrane to an appendage segment; setae appear to be less rigid than spines. In the leg spine and setal formula, Roman numerals indicate spines, Arabic numerals are setae; left numerals indicate lateral elements, middle numerals are terminal elements, and right numerals are medial elements; an asterisk (*) indicates that the segment is absent. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite.

Siphonostomatoida Burmeister, 1835

Scottomyzontidae, new family

Diagnosis.—The following derived character states differentiate this family from the remaining genera of the Asterocheridae: abdomen 3-segmented in both sexes; paired dorsolateral gonopores near posterior margin of somite; paired ventral copulatory pores near the middle of somite; oral siphon sexually dimorphic.

Type and only genus.—*Scottomyzon* Giesbrecht, 1897.

Remarks.—Giesbrecht (1899) proposed

the name Asterocheridae to replace Ascomyzontidae Giesbrecht, 1895 after he had determined that *Ascomyzon* Thorell, 1860 was a synonym of *Asterocheres* Boeck, 1859. The family Asterocheridae now consists of 45 genera, most of which are listed in Ivanenko (1999). *Kolocheres* Johnsson, 1998 and *Ophiurocheres* Humes, 1998 were proposed since the list of Ivanenko (1999) was compiled. The monotypic genus *Madacheres* Humes, 1996 had been separated from other asterocherids based on the state of a 2-segmented mandibular palp, but this state is common for a number of species from the type genus *Asterocheres*; *Madacheres* was interpreted as junior synonym of *Asterocheres* Boeck, 1859 by Ivanenko (1999). *Scottomyzon* is moved herein to its own new family.

Species of the family Asterocheridae have been differentiated from other families of Siphonostomatoida by four character states (Stock 1987, Ivanenko 1999): mandibular palp present (except *Scottocheres* Giesbrecht, 1897 and some species of *Collocheres* Canu, 1893, *Collocherides* Stock, 1971, and *Glyptocheres* Humes, 1987); distal articulating segment of female antennule without proximal aesthetasc (except *Onychocheres* Stock & Gooding, 1986); antennule with a short, articulating segment bearing six or eight setae (except *Cystomyzon* Stock, 1981); the articulating segment bearing six or eight setae separated by six to eight articulating segments, with up to two setae each, from the proximal segment bearing a lateral aesthetasc. However, these four states are not apomorphies within the Siphonostomatoida, but can be shared with many species of Entomolepididae Brady, 1899. In addition, the exceptional genera *Cecidomyzon, Cystomyzon, Hammatimyzon,* and *Oedomyzon* share a synapomorphy of three groups of setae, corresponding to three segments which lack arthrodial membranes, distal to the articulating segment with six or eight setae. These data suggest that upon removal of *Scottomyzon* to a new family, the Asterocheridae still may not be a monophyletic group.

Thorell (1860) often is identified as the author of the ordinal name Siphonostomatoida (e.g., Huys & Boxshall 1991). However, Burmeister (1835:45) included and diagnosed five families of parasites within the diagnosed taxon Siphonostoma. He cited Latreille, without a date of publication, as the author of that name. Latreille (1829: 189) used Siphonostoma like a family group name. Milne Edwards (1830) diagnosed the order Siphonostome in an unpaginated table following page 356, but he did not indicate which families, genera or species belonged in the order (Damkaer electronic mail). We believe Burmeister (1835) should be considered the author of Siphonostomatoida because he apparently intended to create a taxon above the family category, he diagnosed this taxon, and he diagnosed its constituent families. Our date of publication for Thorell (1860) follows Vervoort (1988).

Scottomyzon Giesbrecht, 1897

Diagnosis.—Basis of leg 1 without an inner seta. Distal segment of endopod of leg 4 with 1 short, lateral seta, 2 long, terminal setae and no medial seta.

Type species.—*Scottomyzon gibberum* (Scott & Scott, 1894).

Remarks.—Giesbrecht (1897) placed the genus *Scottomyzon* in Asterocheridae. Neither Gooding (1957) nor Bresciani & Luetzen (1962) explained their decision to remove the species to Dyspontiidae Sars, 1915. Incorrect descriptions of urosome and leg 1 compromise the analyses of Sewell (1949) and Stock (1981), as well as the keys of Stock (1987) and Gotto (1993), although Roettger (1969) had mentioned the absence of an inner seta on the basis of leg 1 and 3-segmented abdomen in females described earlier by Giesbrecht (1899) and Sars (1918). However, Roettger's (1969) first form female with one pair of long and one pair of short posterolateral setae on the last thoracic somite was mistakenly interpreted as an adult. This is a CV; adult females bear only a short seta. The smallest adult female described here has the dorsoventrally flattened prosome with a cowl-like overlay in the anterior part of the marginal area. All adult females studied by us have a 3-segmented abdomen, and there is no reduction in abdominal somites during subsequent growth of the female, contrary to Roettger's statement suggesting a decrease in the number of abdominal somites in the adult female.

Scottomyzon gibberum (Scott & Scott, 1894)

Figs. 1–12

Dermatomyzon gibberum.—Scott & Scott, 1894:144, pl. 9, figs. 10–14.—Scott, 1894:260, pl. 10, figs. 26–34.—Scott & Scott, 1895:357, pl. 17, fig. 14.

Scottomyzon gibberum.—Giesbrecht; 1897: 5–6.–1899:80–81, pl. 3, figs. 46–55, pl. 10, fig. 19.—Sars, 1918:212–214, pl. 116.—Roettger, 1969:146–147, 153–165, 183, figs. 1–24, 34.—Kim, 1992:62–66, figs. 3–4.

Material.—Nauplius 1 - 2 specimens; Nauplius 2 - 2 specimens; Nauplius 3 - 2 specimens; Nauplius 4 - 2 specimens; copepodid I - 2 specimens; reared September 1993. Copepodid II - 3 specimens; copepodid III - 3 specimens; copepodid IV - 5 females, 3 males; copepodid V - 2 females, 2 males; copepodid VI - 11 females, 10 males; 26 August 1994, from *Asterias rubens* L., 3–18 m, Kandalaksha Bay (near White Sea Marine Station of Moscow State University); 66°31′N, 33°07′W, coll. VNI. (USNM 296404). Copepodid I - 7 specimens; copepodid II - 11 specimens; copepodid III - 6 specimens; copepodid IV - 7 specimens; copepodid V - 3 specimens; copepodid VI - 2 females, 13 males; 25 June 1966, off Helgoland, North Sea, coll. Rudolf Roettger. (USNM 296405).

CVI female (Fig. 1A, B, D–E).—Body length 0.48–0.65 mm; maximum width 0.18–0.43 mm; greatest dorsoventral thickness 0.29–0.58 mm; length of prosome 0.37–0.53 mm; length of urosome 0.10–0.12 mm; ratio of length to width of prosome 2.6:1–1.6:1; ratio of length of prosome to that of urosome 3.6:1–4.4:1. Genital segment length 0.42–0.45 mm; width 0.09–0.10 mm. Numerous pores and sensillae present (n = 45 specimens).

Prosome (Figs. 1A, B, D–F, 12A, B): 4 articulated sections; first a complex of 5 cephalic somites plus thoracic somites 1 and 2; sections 2–4 are articulated thoracic somites 3–5. Smallest females dorsoventrally flattened with cowl-like overlay in anterior part of marginal area (Fig. 1A). Prosome of largest females spherical (Fig. 1E, F) without cowl-like overlay.

Urosome (Figs. 1E, 2A, B): 5 somites; anterior somite is thoracic somite 6, followed by thoracic somite 7 (or genital somite) and 3 abdominal somites. Copulatory pore and oviducal openings separate; oviducal openings with 2 minute setae dorsally on posterior corners of somite; copulatory pore ventral near middle of somite.

Egg sacs: paired, ovoid with up to 9 eggs; eggs 0.12–0.15 mm. Largest females with larger number of eggs.

Rostrum (Fig. 1B): beak-like laterally, slightly overlapping oral siphon.

Oral siphon (Fig. 12C) short and robust, comprised of labrum and labium connected laterally. Siphonal opening formed by thin, straight distal margins of both labrum and labium. One row of cuticular petal-like extensions; each extension separated from others on distal margin of labrum and labium. Labrum with area of epicuticular extensions near distal notch. Labium with pores lateral to mandibular insertion into siphon.

Antennule (Fig. 2D, E): 18 articulated segments with 1, 2, 6, 2, 2, 1, 8, 2, 2, 2, 2, 2, 2, 2, 2, 2 + aesthetasc, 2, and 12 setae. All setae smooth.

Antenna (Fig. 2F): coxa and basis without setae. Exopod 1-segmented with 3 setae. Endopod 2-segmented; first segment

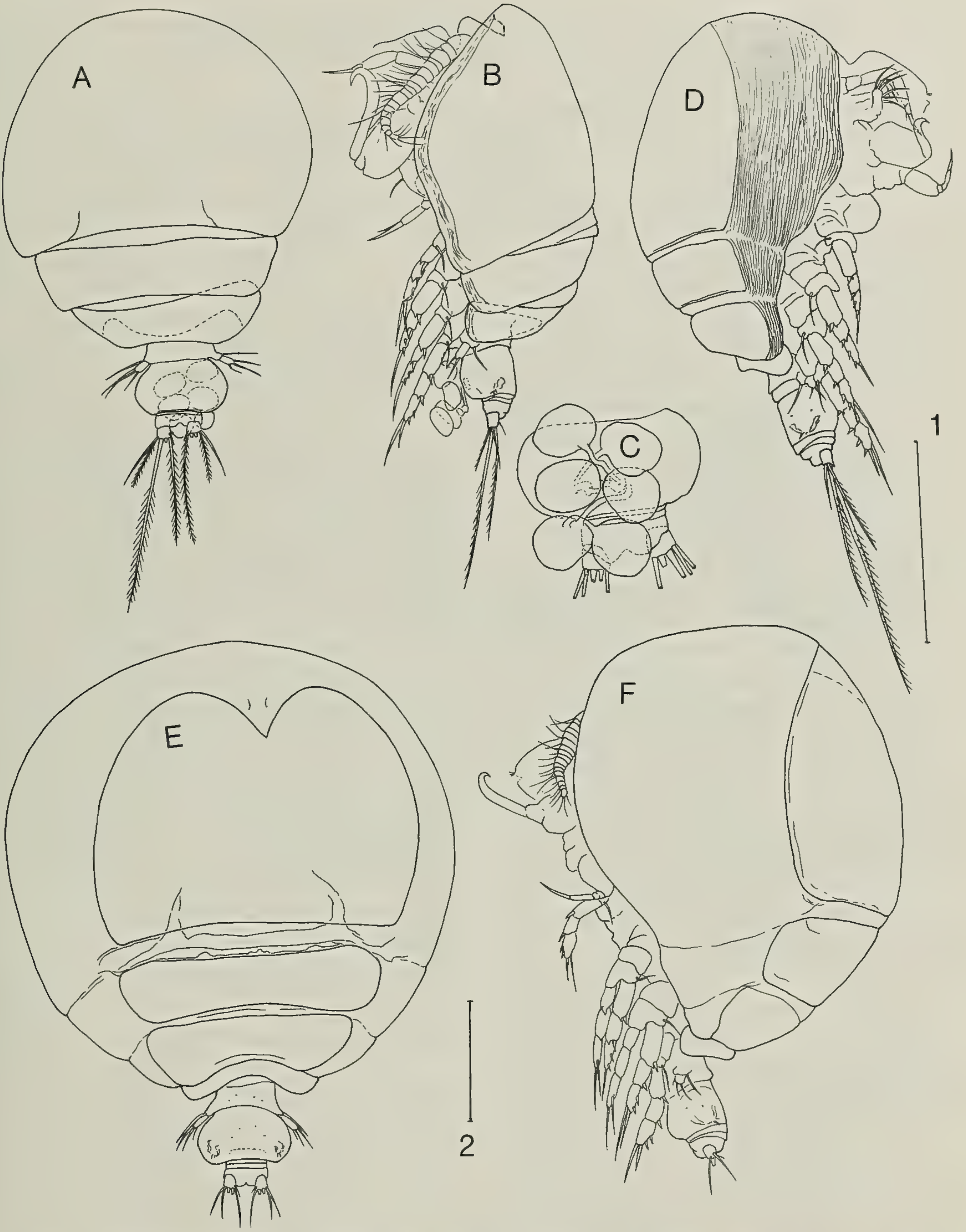

Fig. 1. *Scottomyzon gibberum* (Scott & Scott, 1894), CVI female: A, habitus, dorsal; B, habitus, lateral; C, 3 pairs of spermatophores attached to the genital somite; D, habitus, lateral; E, habitus, dorsal; F, habitus, lateral. Scale line 1 is 0.1 mm for C; line 2 is 0.1 mm for A, B, D–F.

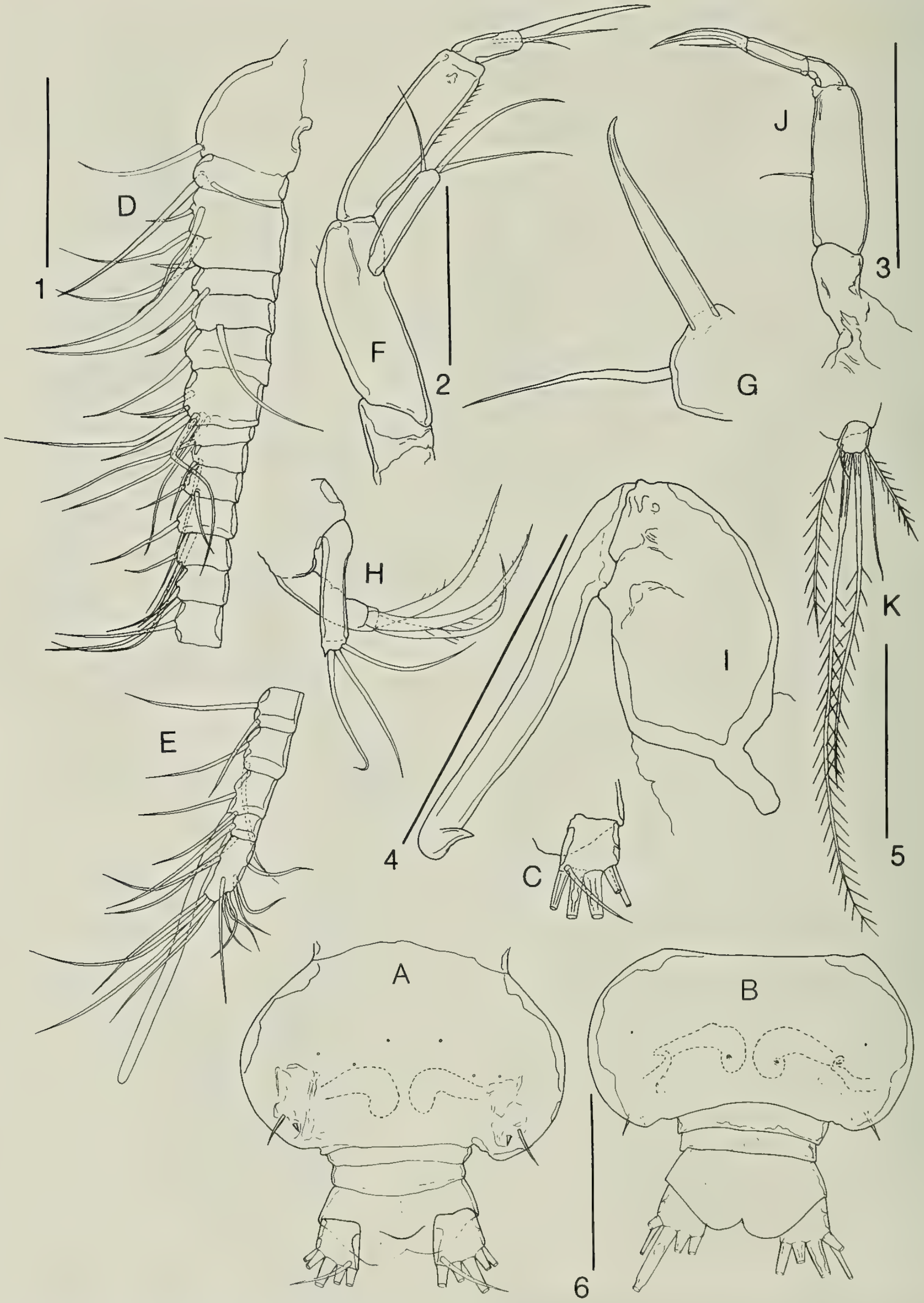

Fig. 2. *Scottomyzon gibberum* (Scott & Scott, 1894), CVI female: A, genital and abdominal somites, dorsal; B, genital and abdominal somites, ventral; C, caudal ramus, dorsal; D, antennule, segments 1–14; E, antennule, segments 14–18; F, antenna; G, mandible; H, maxillule; I, maxilla; J, maxilliped; K, setae of caudal ramus. Scale line 1 is 0.05 mm for D, E; line 2 is 0.05 mm for F; line 3 is 0.1 mm for J; line 4 is 0.1 mm for H, J, I; line 5 is 0.05 mm for C and 0.1 mm for K; line 6 is 0.05 mm for A, B.

with outer row of spinules, second segment with 3 setae including a large, thick terminal claw.

Mandible (Fig. 2G): apparently 1-segmented palp with 1 smooth seta.

Maxillule (Fig. 2H): inner lobe armed with 3 setae bearing short lateral setules; outer lobe articulating proximally with small, attenuated point medially and 3 smooth setae terminally.

Maxilla (Fig. 2I): subchela apparently 2-segmented; first segment broad and flattened; second segment curved and pointed distally.

Maxilliped (Fig. 2J, 12 E, F): short, unarmed syncoxa, longer basis with 1 inner seta near middle of medial margin. Endopod with proximal, short section apparently subdivided and with long, distal segment. Proximal section laterally with 2 distally polarized setae and 1 medially polarized seta; distal segment with 2 terminal setae, one seta large, thick and claw-like.

Legs 1–4 (Fig. 3A, B, F): biramous, with 3-segmented rami. Intercoxal sclerite and 2-segmented protopods in all legs. Spine and setal formula in Table 1. Legs 1–3 with lateral pores in middle part of middle (third) segment of exopod. Lateral seta of distal endopodal segment of leg 1 twice as long as length of segment from point of setal origin to outer attenuate tip of segment. Lateral seta of endopod of leg 2 extending beyond distolateral spine (Fig. 3F). Tip of lateral seta of endopod of leg 3 ending near the tip of terminal spine.

Leg 5 (Fig. 3G): 1-segmented; basis fused with somite and bearing a lateral seta; articulated segment elongate with 3 setae.

Leg 6 (Fig. 2A): uniramal leg bud with 2 minute setae near oviducal pores.

Caudal ramus (Fig. 2C, K): subquadrate with 4 plumose terminal setae and 2 smooth dorsolateral setae, all of differing lengths. Distal setae of large ovoid females broken proximally on all specimens.

Spermatophores (Fig. 1C) found on only 1 small female (Fig. 1A, B); 3 pairs of ovoid spermatophores with neck attached ventrally to copulatory pores.

Color (living specimens): brick-red pigmentation expressed in prosome dorsally and tips of setae of largest, ovoid specimens.

CVI male.—Differs from female CVI as follows (Fig. 4A, B): length 0.44–0.49 mm; maximum width 0.24–0.27 mm; greatest dorsoventral thickness 0.17–0.21 mm; ratio of length to width 1.6:1; length of prosome 0.33–0.35 mm; urosome 0.11–0.13 mm; ratio of length of prosome to that of urosome 2.8:1. (n = 10 specimens).

Urosome (Fig. 4C): thoracic somite 7 with copulatory pore ventrolaterally.

Oral siphon (Fig. 12D) relatively smaller than female. Siphonal opening with margins of labrum and labium turned out; inner surface of margins with rows of numerous minute protuberances. Several rows of petal-like structures framing margins of oral siphon joined proximally. Area of epicuticular extensions in distal notch of labrum less developed than female.

Antennule (Fig. 4F, G): 16 articulated segments with 1, 2, 6, 2, 2, 1, 8, 2, 2, 2, 2, 2, 2, 2, 2 + aesthetasc, and 12 setae. Geniculation between 15th and 16th articulating segments.

Antenna (Fig. 4H) as illustrated.

Maxillia: with constriction towards distal part of claw (Fig. 4J).

Maxilliped: slightly thinner and longer (Fig. 4I) than female.

Leg 1: lateral seta of the distal endopodal segment less than twice length from point of setal origin to outer attenuate tip of segment.

Leg 2: lateral seta of the distal endopodal segment not projecting beyond distolateral spine (Fig. 3E).

Leg 3: tip of lateral seta of distal endopodal segment reaching to two-thirds length of terminal spine (Fig. 3C).

Leg 4 (Fig. 3D) as illustrated.

Leg 5: shorter articulating segment (Fig. 4K).

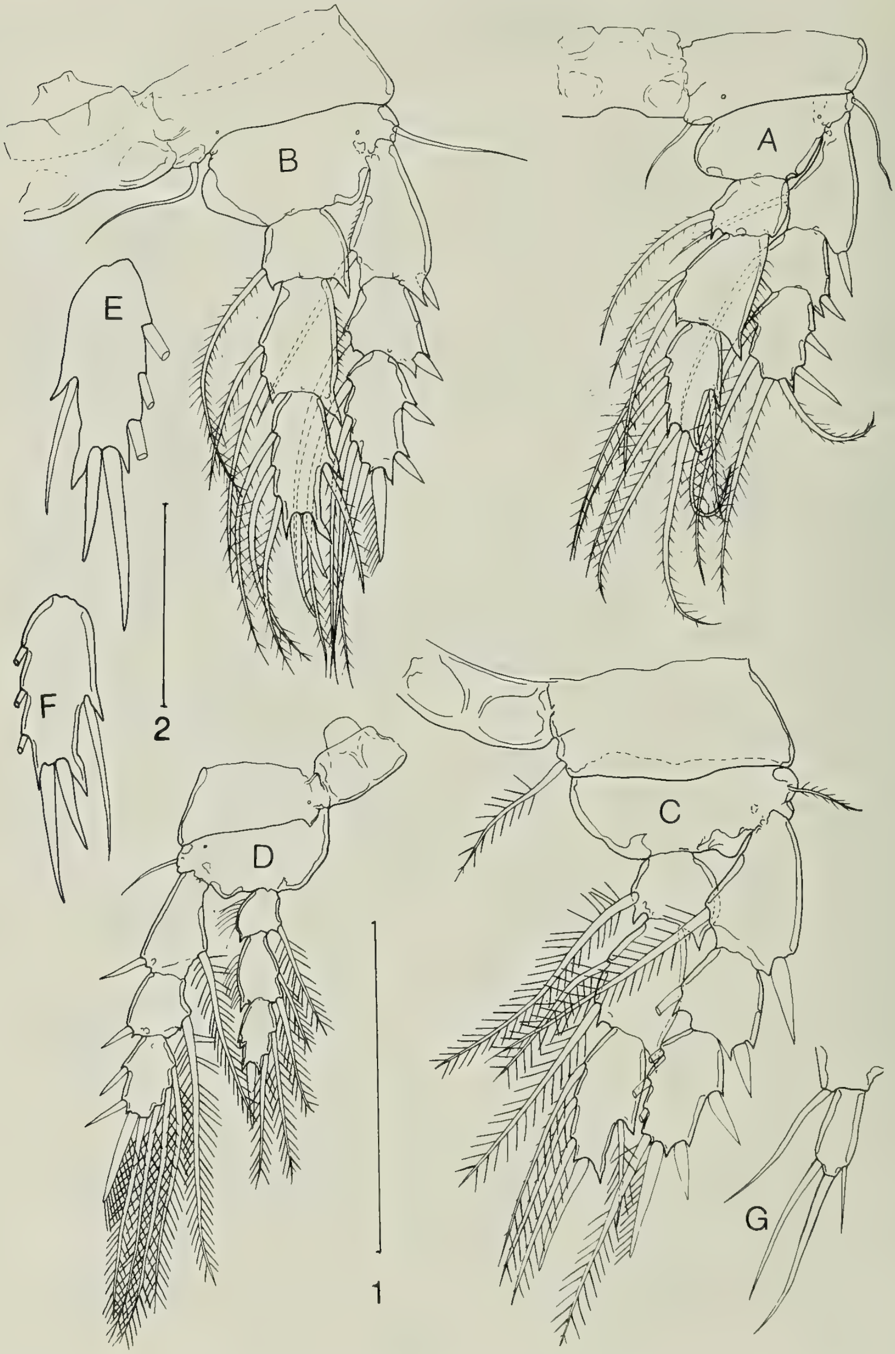

Fig. 3. *Scottomyzon gibberum* (Scott & Scott, 1894), CVI: A, female leg 1, anterior; B, female leg 2, anterior; C, male leg 3, anterior; D, male leg 4, anterior; E, male leg 2, anterior, distal segment of endopod; F, female leg 2, distal segment of endopod, anterior; G, leg 5. Scale line 1 is 0.1 mm for A–D; line 2 is 0.05 mm for E–G.

Table 1.—Spines and setae on legs 1–4 of adult female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-1	1-0	I-1; I-1; II, 1, 3	0-1; 0-2; 1, 2, 3
Leg 2	0-1	1-0	I-1; I-1; II, 1, 4	0-1; 0-2; 1, II, 3
Leg 3	0-1	1-0	I-1; I-1; II, 1, 4	0-1; 0-2; 1(0), I, 3
Leg 4	0-0	1-0	I-1; I-1; II, 1, 4	0-1; 0-2; 0, I, 2

Leg 6 (Fig. 4C): 2 posterolateral setae relatively longer.

Caudal ramus: with pointed posterolateral extension (Fig. 4D, E).

Color: unpigmented and semitransparent.

CV female.—Differs from CVI female as follows (Fig. 5A, B): length range 0.41–0.45 mm; maximum width 0.22–0.27 mm; greatest dorsoventral thickness 0.18–0.19 mm; length of prosome 0.32–0.34 mm, urosome 0.09–0.10 mm; ratio of length to width 1.8:1; ratio of length of prosome to that of urosome 3.3:1. No pores and sensillae observed (*n* = 2 specimens).

Urosome (Fig. 5F): no copulatory pore or oviducal openings.

Antennule (Fig. 5D) as illustrated.

Color: unpigmented and semitransparent.

CV male.—Differs from CV female as follows (Fig. 5E): length 0.39–0.46 mm; maximum width 0.20–0.26 mm, greatest dorsoventral thickness 0.15–0.18 mm; length of prosome 0.30–0.35 mm; urosome 0.09–0.12 mm; ratio of length to width 1.8:1; ratio of length of prosome to that of urosome 3:1 (*n* = 3 specimens).

Urosome: width of 7th thoracic somite narrower (Fig. 5C).

Antennule (Fig. 5G): fourth articulating segment from the distal segment less sclerotized than CV female.

CIV female.—Differs from female CV as follows: length 0.35–0.41 mm; maximum width 0.15–0.22 mm; greatest dorsoventral thickness 0.12–0.16 mm; length of prosome 0.27–0.30 mm, urosome 0.08–0.11 mm; ratio of length to width 2.1:1; ratio of length of prosome to that of urosome 2.9:1 (*n* = 7 specimens).

Prosome (Fig. 6A–B): 4 articulated sections; first a complex of 5 cephalic somites plus thoracic somites 1 and 2; thoracic somite 1 and 2 separated but not well-articulated. Remaining articulated sections are thoracic somites 3–5.

Urosome (Fig. 6D): 4 somites; thoracic somites 6, 7 and abdominal somites 2, 1 articulated.

Antennule (Fig. 6C): 17 articulated segments with 1, 1, 3, 2, 1, 3, 1, 2, 2, 2, 2, 2, 2, 2, 2 + aesthetasc, 2, and 12 setae.

Legs 1–4 (Fig. 7A–D): biramous, with 2-segmented rami. Intercoxal sclerite and 2-segmented protopods in all legs. Spine and setal formula in Table 2.

Leg 6 (Fig. 6D): with 1 seta.

CIV male.—Differs from CIV as follows (*n* = 2 specimens): fourth articulating segment from distal segment of antennule less sclerotized.

CIII.—Differs from female CIV as follows (Fig. 7 E, F): length 0.32–0.39 mm; maximum width 0.12–0.17 mm; greatest dorsoventral thickness 0.09–0.16 mm; length of prosome 0.21–0.28 mm; length of urosome 0.08–0.10 mm; ratio of length to width 2.3:1; ratio of length of prosome to that of urosome 3:1 (*n* = 13 specimens).

Urosome (Fig. 8A): 3 somites; thoracic somites 6, 7 and abdominal somite 1 articulated.

Antennule (Fig. 8B): 11 articulated segments with 1, 3, 2, 1, 1, 4, 1, 1, 1 + aesthetasc, 2, and 12 setae.

Antenna (Fig. 7G), Mandible (Fig. 7H), Maxillule (Fig. 7I), and Maxilla (Fig. 7J) as illustrated.

Maxilliped (Fig. 7K): proximal section of endopod with 1 distally polarized seta, 1

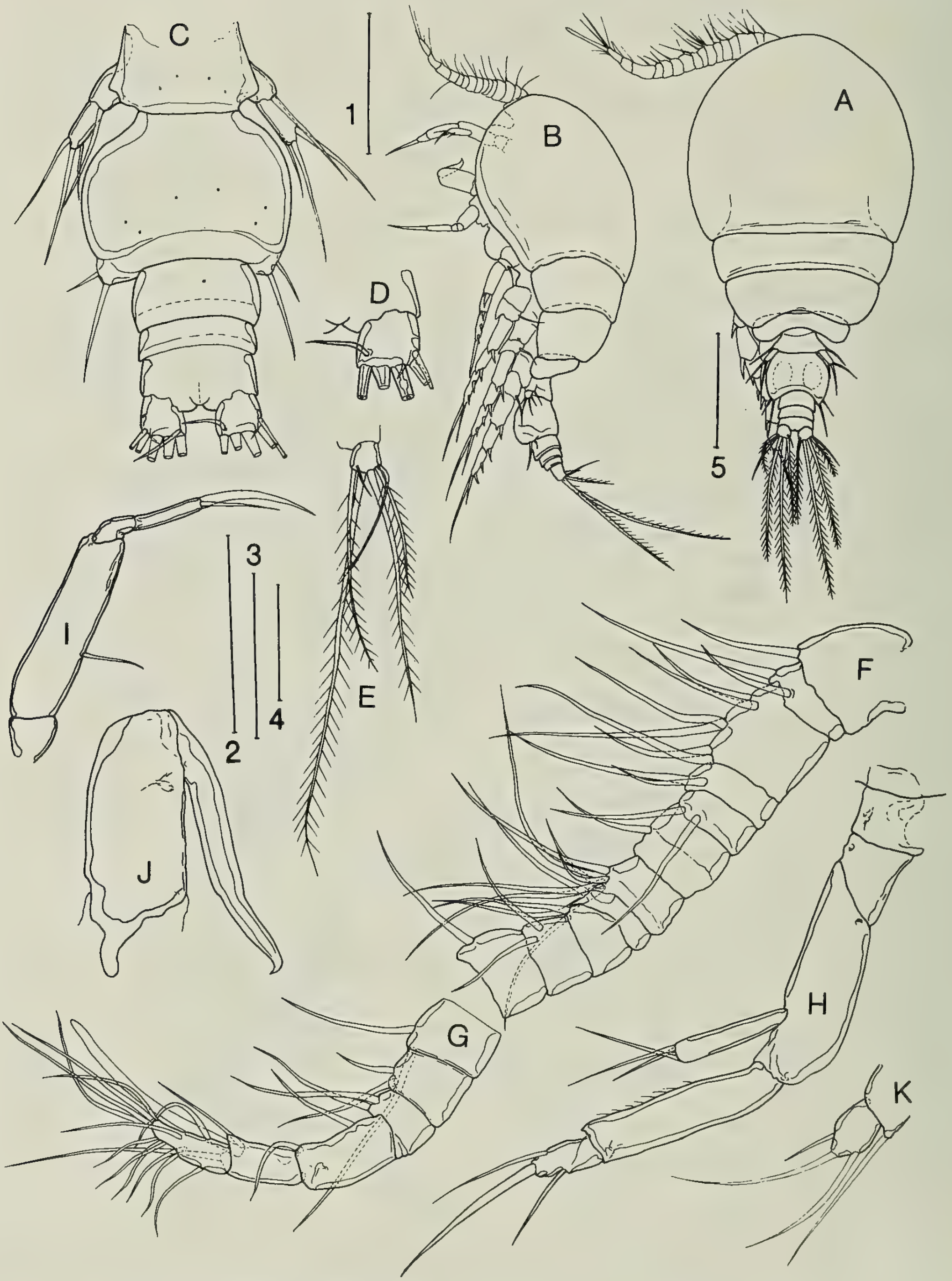

Fig. 4. *Scottomyzon gibberum* (Scott & Scott, 1894), CVI male: A, habitus, dorsal; B, habitus, lateral; C, urosome, dorsal; D, caudal ramus, dorsal; E, setae of caudal ramus; F, antennule, segments 1–11; G, antennule, segments 11–16; H, antenna; I, maxilliped; J, maxilla. Scale line 1 is 0.05 mm for C, F, G; line 2 is 0.05 mm for D, K, H; line 3 is 0.1 mm for J; line 4 is 0.05 mm for I; line 5 is 0.1 mm for A, B.

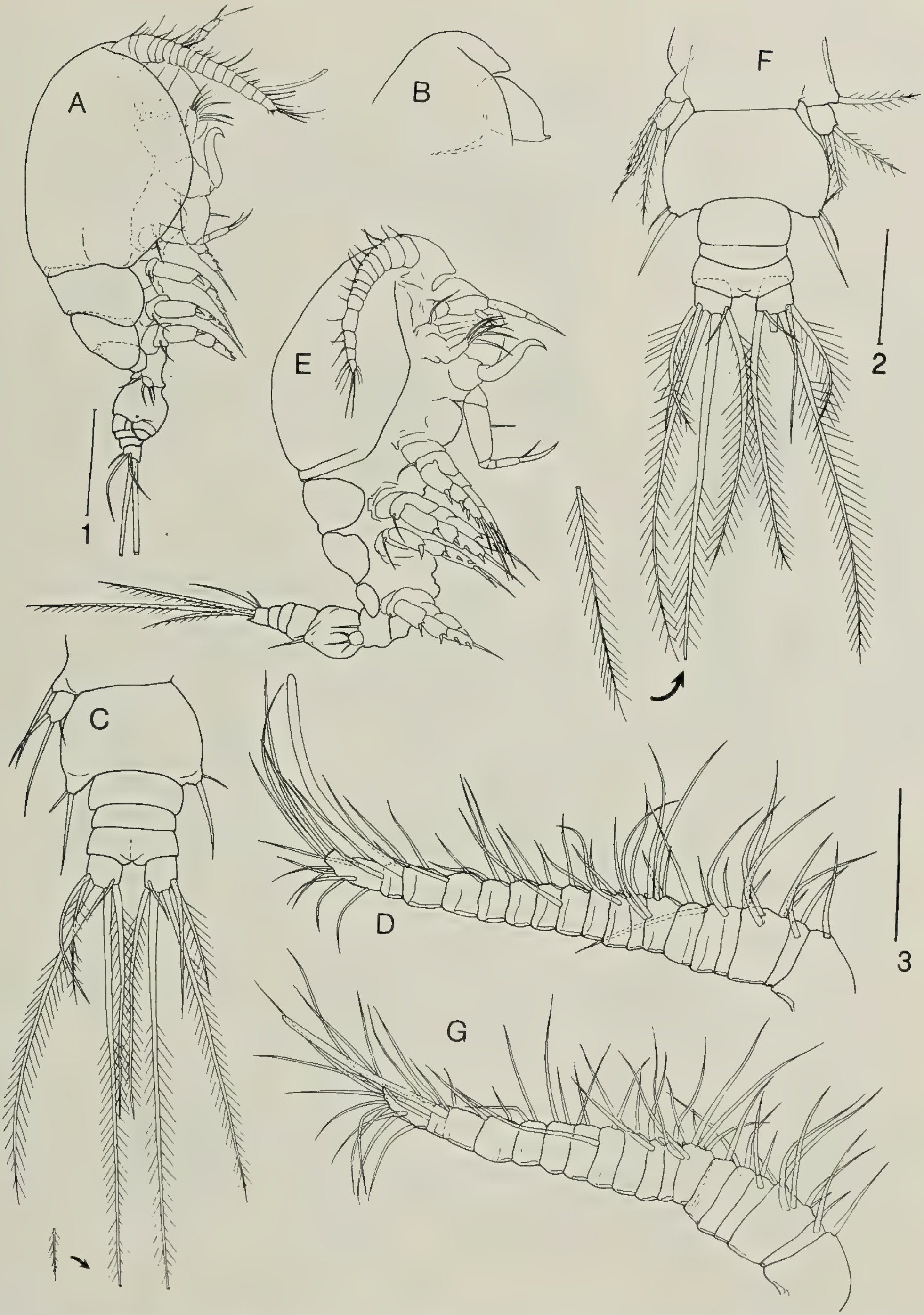

Fig. 5. *Scottomyzon gibberum* (Scott & Scott, 1894), CV: A, habitus of female, lateral view; B, rostrum of female, lateral; C, urosome of male, dorsal; D, antennule of female; E, habitus of male, lateral view; F, urosome of female, dorsal; G, antennule of male. Scale line 1 is 0.1 mm for A, B, E; line 2 is 0.05 mm for C, F; 3 is 0.05 mm for D, G.

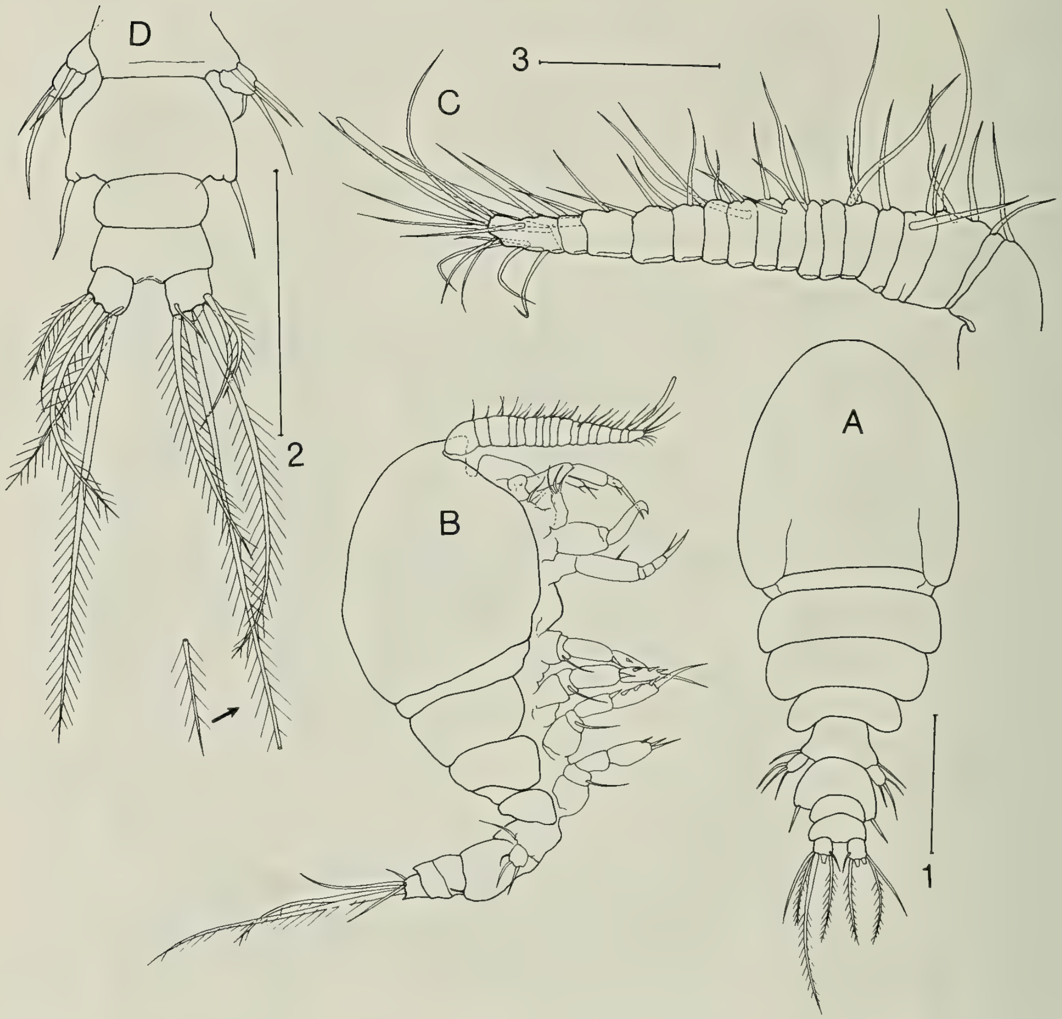

Fig. 6. *Scottomyzon gibberum* (Scott & Scott, 1894), CIV female: A, habitus, dorsal view; B, habitus, lateral view; C, antennule; D, urosome, dorsal. Scale line 1 is 0.1 mm for A, B; line 2 is 0.05 mm for D; line 3 0.05 mm for C.

medially polarized seta and 1 medial seta; distal segment with 2 terminal setae.

Legs 1–4 (Fig. 8C–F): biramous; leg 1–3 with 2-segmented rami, leg 4 with 1-segmented rami. Intercoxal sclerite and 2-segmented protopods in all legs. Spine and setal formula in Table 3.

Leg 5 (Fig. 8A): unilobe lateral bud with 2 posterior setae.

Leg 6: absent.

CII.—Differs from CIII as follows: length 0.30–0.34 mm; maximum width 0.11–0.16 mm; greatest dorsoventral thickness 0.11–0.12 mm; length of prosome 0.21–0.24 mm; of urosome 0.09–0.11 mm; ratio of length to width 2.4:1; ratio of length of prosome to that of urosome 2.3:1 (*n* = 8 specimens).

Prosome (Figs. 8G, 9A): 3 articulated sections; 1st a complex of 5 cephalic somites plus thoracic somites 1 and 2; thoracic somite 2 separated from thoracic somite 1, but not articulated; thoracic somites 3–4 articulated.

Urosome (Fig. 8G, 9B): 3 somites; thoracic somites 5, 6 and abdominal somite 1

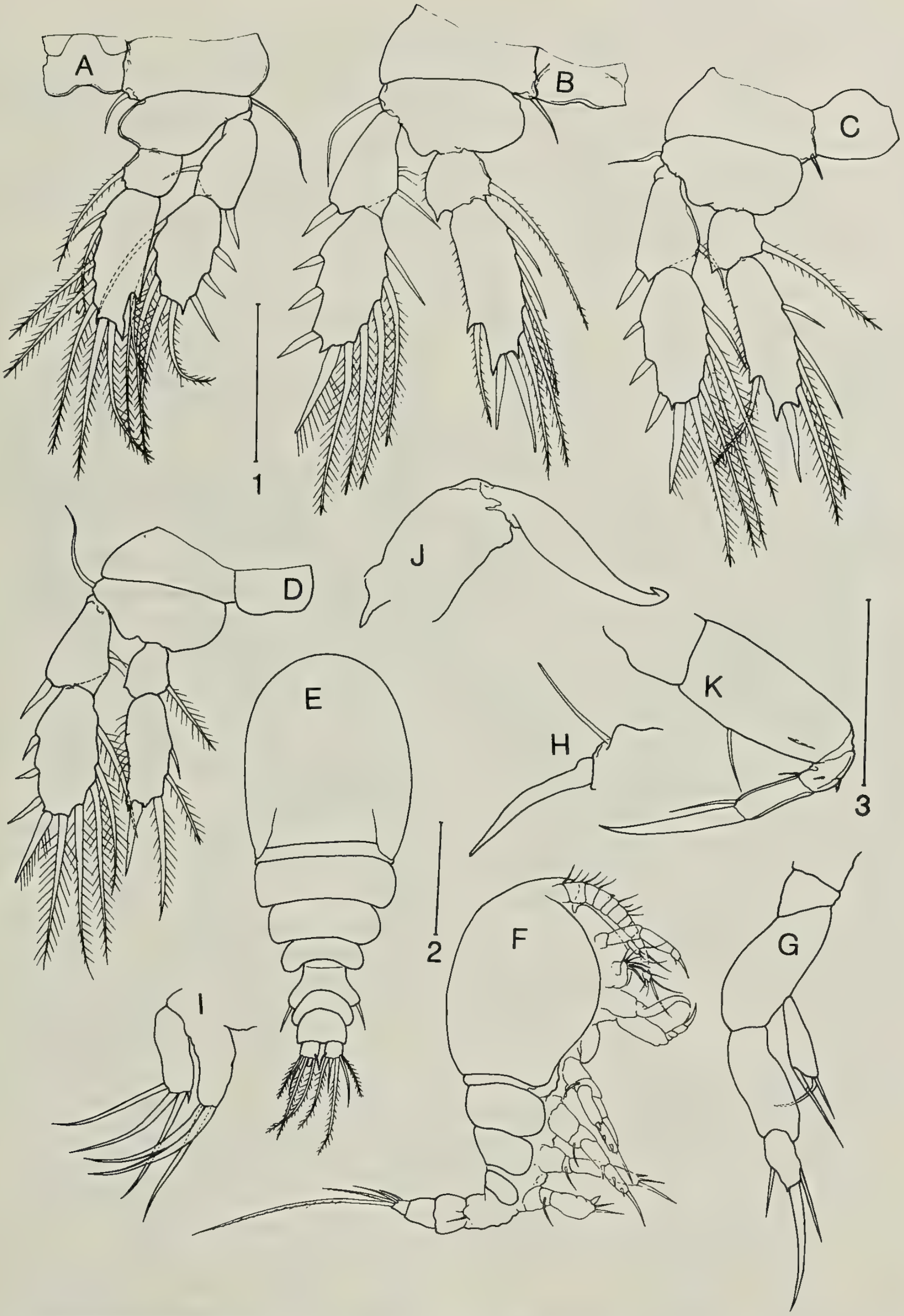

Fig. 7. *Scottomyzon gibberum* (Scott & Scott, 1894), CIV: A, leg 1; B, leg 2; C, leg 3; D, leg 4. *Scottomyzon gibberum,* CIII: E, habitus, dorsal view; F, habitus, lateral view; G, antenna; H, mandible; I, maxillule; J, maxilla; K, maxilliped. Scale line 1 is 0.05 mm for A–D; line 2 is 0.1 mm for E, F; line 3 is 0.05 mm for G–K.

Table 2.—Spines and setae on legs 1–4 of CIV female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-1	1-0	I-1; *; III, 1, 4	0-1; *; 1, 2, 5
Leg 2	0-1	1-0	I-1; *; III, 1, 5	0-1; *; 1, II, 5
Leg 3	0-1	1-0	I-1; *; III, I, 5	0-1; *; 1, I, 4
Leg 4	0-0	1-0	I-0; *; III, I, 5	0-1; *; 0, I, 3

articulated; thoracic somite 5 with lateral and medial lobes.

Antennule (Fig. 9D): 11 articulated segments with 1, 1, 1, 1, 1, 1, 1, 1, 1 + aesthetasc, 2, 4, and 8 setae.

Antenna (Fig. 9E), Mandible (Fig. 9F) as illustrated.

Maxillule (Fig. 9G): inner lobe with 2 setae; outer lobe with 3 long and 1 small setae.

Maxilla (Fig. 9H) as illustrated.

Maxilliped (Fig. 9I): syncoxa with 1 seta, basis with 1 proximal seta along medial margin; proximal section of endopod with 1 distally polarized seta and 1 medial seta; distal segment with 2 terminal setae.

Leg 1–3 (Fig. 9J–L): biramous, leg 1–2 with 2-segmented rami, leg 3 with 1-segmented rami; all three with intercoxal sclerite and 2-segmented protopod. Spine and setal formula in Table 4.

Leg 4 (Fig. 9B): a bilobe bud; dorsal lobe with 2 posterior setae and ventral lobe with a tiny seta.

Leg 5 absent.

CR (Fig. 9B, C) as illustrated.

CI.—Differs from copepodid stage II as follows: length 0.29–0.32 mm; maximum width 0.10–0.14 mm; greatest dorsoventral thickness 0.08–0.11 mm; length of prosome 0.15–0.20 mm; of urosome 0.09–0.14 mm; ratio of length to width 2.8:1; ratio of length of prosome to that of urosome 1.5:1 (*n* = 10 specimens).

Prosome (Fig. 10A, B): 1st articulating section a complex of 5 cephalic somites plus thoracic somite 1; thoracic somites 2 and 3 articulated.

Urosome (Fig. 10C): 3 somites; thoracic somites 4, 5, and abdominal somite 1 articulated.

Antennule (Fig. 10E): 5 articulated segments with 1, 1, 1, 5 + aesthetasc, and 8 setae.

Antenna (Fig. 10F), Mandible (Fig. 10G), Maxillule (Fig. 10H), Maxilla (Fig. 10I) as illustrated.

Siphon: without ornamentation.

Maxilliped (Fig. 10J): syncoxa and basis unarmed; endopod with 2 distinct segments; proximal segment with 1 medial seta and distal segment with 2 setae.

Leg 1–2 (Fig. 10K, L): biramous; with intercoxal sclerite, 2-segmented protopods and 1-segmented rami. Spine and setal formula in Table 5.

Leg 3 (Fig. 10C): a bilobe bud; dorsal lobe with 2 posterior setae and ventral lobe unarmed.

Caudal ramus (Fig. 10C, D): 3 terminal, 1 lateral and 2 dorsal setae; 2 inner-terminal setae plumose; innermost seta is longest.

N4.—length 0.21–0.23 mm; width 0.10–0.12 mm (Fig. 11A); anal opening present (*n* = 3 specimens).

Antennule (Fig. 11B): 2 articulating segments; distal segment with 4 long terminal setae and a small seta; middle of proximal segment with 1 seta on ventral side.

Antenna (Fig. 11C): coxa not separated from basis, both unarmed; proximal segment of exopod fused to basis and 4 distal articulated segments with 1, 1, 1, and 2 setae. Distal segment of 2-segmented endopod with 3 terminal setae and 1 seta in the middle; proximal segment unarmed.

Mandible (Fig. 11D): coxa indistinctly separated from basis; both unarmed; prox-

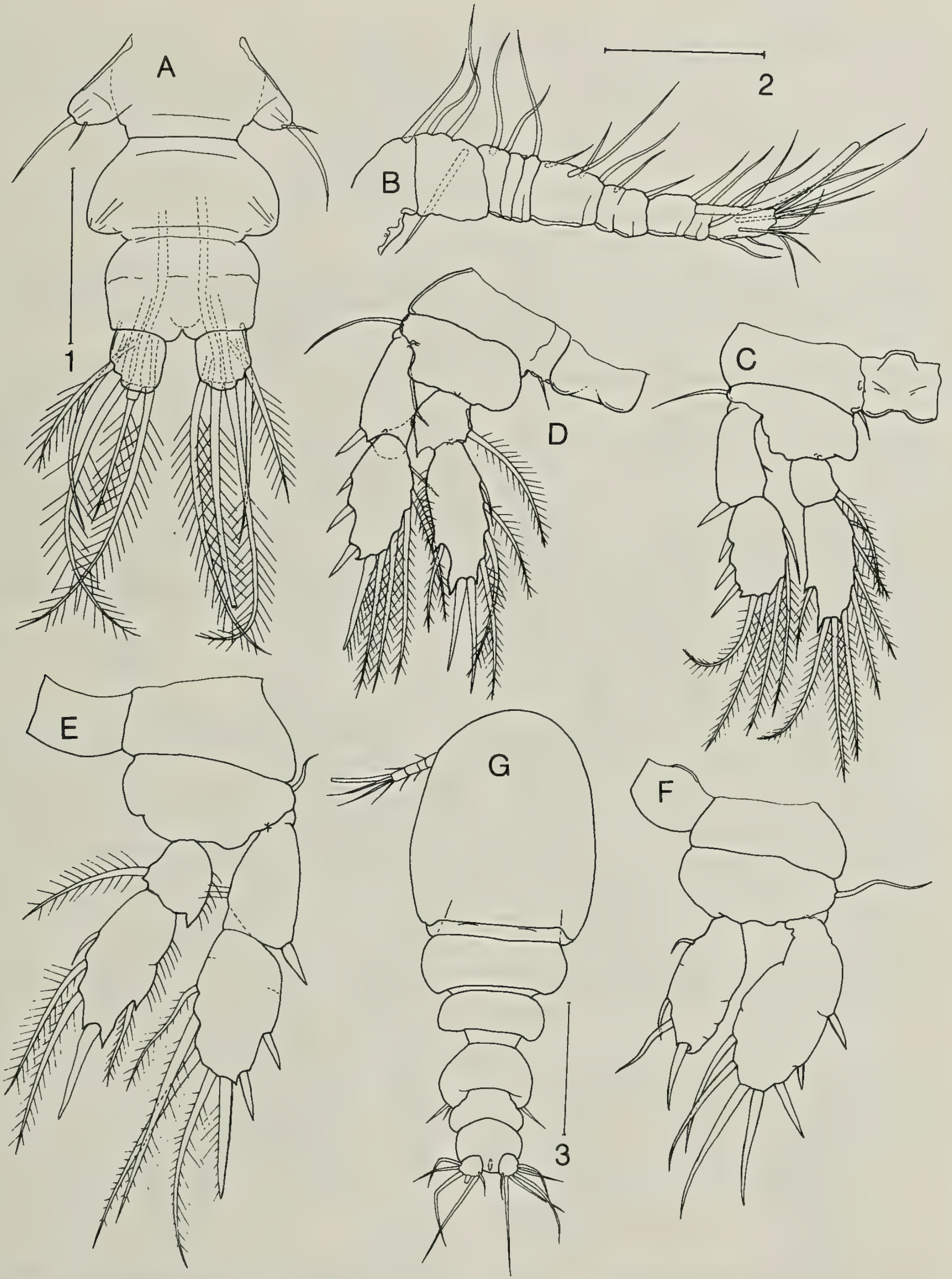

Fig. 8. *Scottomyzon gibberum* (Scott & Scott, 1894), CIII: A, urosome, ventral; B, antennule; C, leg 1; D, leg 2; E, leg 3; F, leg 4. *Scottomyzon gibberum,* CII: G, habitus, dorsal view. Scale line 1 is 0.05 mm for A; line 2 is 0.05 mm for B–F; line 3 is 0.1 mm for G.

Table 3.—Spines and setae on legs 1–4 of CIII.

	Coxa	Basis	Exopod	Endopod
			2nd; 3rd; 1st	2nd; 3rd; 1st
Leg 1	0-1	1-0	I-1; *; III, 1, 4	0-1; *; 1, 2, 5
Leg 2	0-1	1-0	I-1; *; III, I, 5	0-1; *; 1, II, 4
Leg 3	0-0	1-0	I-0; *; III, 4	0-1; *; 1, I, 3
Leg 4	0-0	1-0	*; *; III, 3	*; *; 0, I, 3

imal segment of exopod fused to basis and with inner seta, and 3 articulated segments with 1, 1, and 2 setae respectively; endopod an articulated segment with 3 terminal setae and 1 seta in the middle.

Maxillule: a bilobe bud with inner lobe attenuate.

Maxilla: not present.

Maxilliped: not present.

Leg 1 (Fig. 11A): bilobe bud; dorsal lobe (presumptive exopod) with 4 setae; ventral lobe (presumptive endopod) with 2 setae.

Leg 2 (Fig. 11A): bilobe bud; dorsal lobe (presumptive exopod) with 3 setae; ventral lobe (presumptive endopod) with 2 setae.

Caudal ramus (Fig. 11E): not articulated with somite; margin armed with 3 pairs of long setae and 2 pairs of short spinules.

N3.—Differs from N4 as follows (Fig. 11F): body length 0.19–0.22 mm; width 0.10–0.12 mm (*n* = 12 specimens).

Antennule (Fig. 11G), Antenna (Fig. 11I), Mandible (Fig. 11H) as illustrated.

Buds of maxillule and legs 1–2 absent.

CR: margin armed with 1 pair of long setae.

N2.—Differs from N3 as follows: body length 0.18–0.20 mm; width 0.11–0.12 mm (*n* = 5 specimens).

Antennule (Fig. 11J): distal segment with 3 terminal setae.

Antenna (Fig. 11K), Mandible (Fig. 11L) as illustrated.

N1.—Differs from naupliar N2 as follows (Fig. 11M): body length 0.18–0.20 mm; width 0.10–0.12 mm (*n* = 5 specimens).

Antennule (Fig. 11N): with rows of fine protuberances on anterior surface.

Antenna (Fig. 11O): with rows of fine protuberances on anterior surface. Mandible (Fig. 11P): with rows of fine protuberances on anterior surface.

Remarks.—We agree with the characterization by Sars (1918:213) of *S. gibberum* as "an easily recognizable form, which cannot be confounded with any of the other Ascomyzontidae" (a synonym of Asterocheridae). We did not find differences in specimens from the White Sea and North Sea, and agree that this copepod also can be found in the Sea of Japan (Kim 1992).

Discussion

We report six copepodid stages and four naupliar stages of *S. gibberum.* A six stage copepodid phase of development is common among copepods. Carton (1968) differentiated six naupliar stages based on body shape and size of the siphonostomatoid *Cancerilla tubulata,* an invertebrate symbiont. A four stage naupliar phase of development has not been reported for siphonostomatoids. Usually the naupliar phase for siphonostomatoids consists of at most two stages, an orthonauplius and a metanauplius.

The last nauplius of *S. gibberum* has buds of swimming leg 1 and 2; it apparently corresponds to a sixth stage nauplius. The remaining nauplii are more difficult to relate to a six stage phase. In podoplean copepods with a six stage naupliar phase like *Dioithona oculata* (Farran, 1913), whose buds of the maxilla and the maxilliped fail to appear during the naupliar phase, changes in the setation of the bud of maxilla 1 and the caudal ramus provide useful information to separate stages and to determine

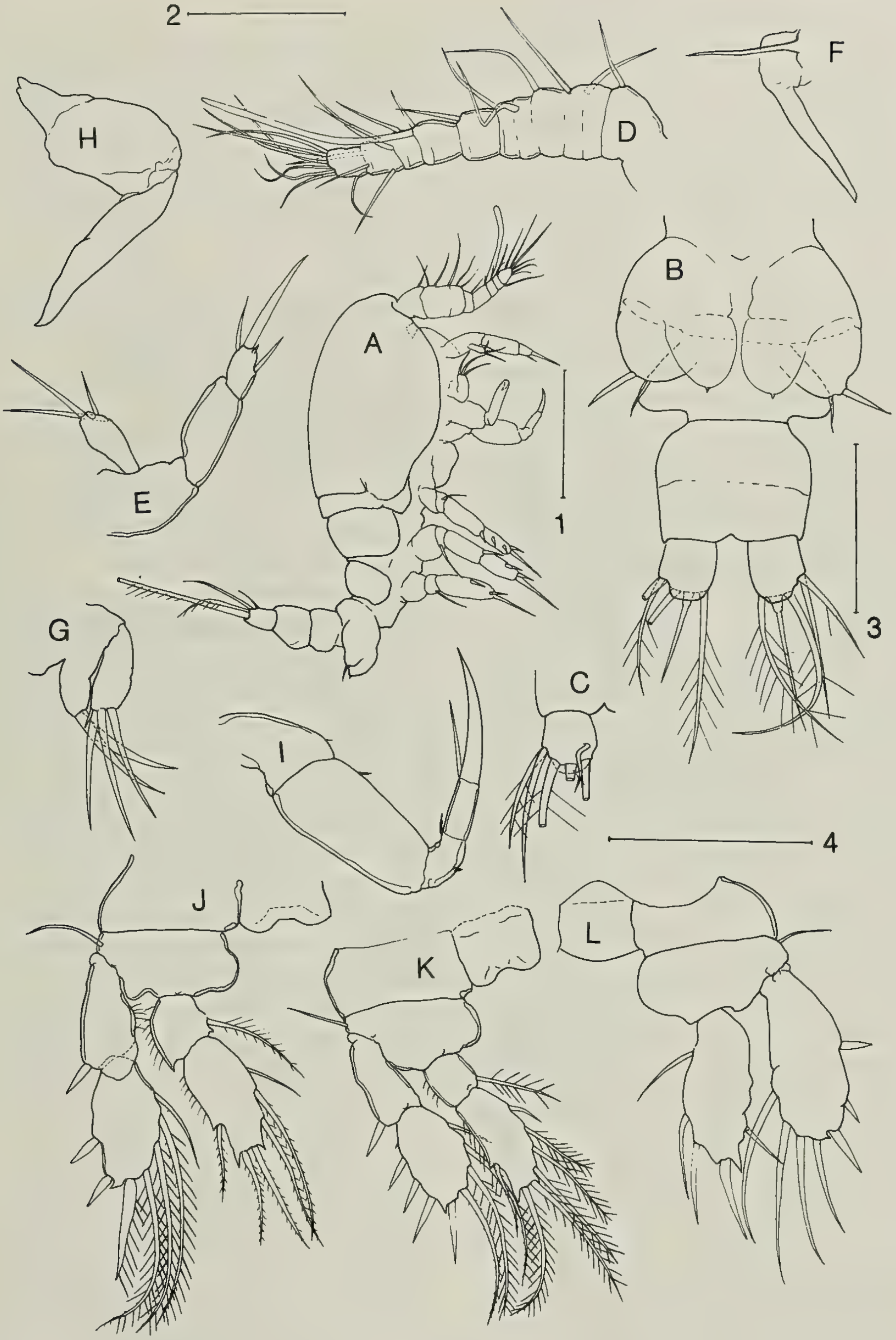

Fig. 9. *Scottomyzon gibberum* (Scott & Scott, 1894), CII: A, habitus, lateral; B, urosome ventral; C, caudal ramus, dorsal; D, antennule; E, antenna; G, maxillule; F, mandible; H, maxilla; I maxilliped; J, leg 2; K, leg 1; L leg 3. Scale line 1 is 0.1 mm for A; line 2 is 0.05 mm for D, J, K, L; line 3 is 0.05 mm for B, C; line 4 is 0.05 mm for E, F, G, I, M.

Table 4.—Spines and setae on legs 1–3 of CII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-0	1-0	I-0; *; III, 1, 4	0-1; *; 1, 2, 4
Leg 2	0-0	1-0	I-0; *; II, I, 4	0-1; *; 1, II, 3
Leg 3	0-0	1-0	*; *; II, I, 4	*; *; 1, I, 3

their correspondence (Ferrari & Ambler 1992). The first three naupliar stages of *S. gibberum* do not express buds of the maxillule; these stages were differentiated on the basis denticular protuberences of the appendages of N1 and appendage setation of N2 and N3. These three stages may correspond to the orthonauplius and two metanauplii, for which the appearance of the bud of maxilla 1 has been suppressed in this siphonostomatoid.

The two forms of adult male of *S. gibberum,* which were noted but not illustrated by Roettger (1969), were not encountered here. However, the adult females of *S. gibberum* show significant variablity in size and proportions of the prosome as a result subsequent expansion of folds of poorly sclerotized cuticle in an area between the tergal and pleural margins of cephalothorax and the two anterior somites (Fig. 12A, B). The folded cuticle is clearly present in smaller and presumably younger females, but is absent in specimens in which the apparently unfolded cuticle results in a greatly expanded cephalothorax and less expended thoracic somites 3 and 4 of larger, presumably older, females. We do not believe this significant variablity in size and proportions of the female prosome is the result of additional copepodid stages in female development, as was mentioned by Roettger (1969) because we found no changes in the number of serially repeated elements such as somites, appendage segments or setae, which usually differentiate stages in copepod development. Cuticular folds also have been reported for the urosome of *Lernaeocera branchialis* (Linnaeus, 1767) by Smith & Whitfield (1988). In *S. gibberum* the expansion of the prosome resulting from the unfolded cuticle may provide a larger area for an expanding gut or oviduct. Poorly sclerotized cuticle of thoracic somite 2 of the unrelated copepod *Benthomisophria palliata* Sars, 1909 has been explained as a way of expanding the prosome to allow an increase in the area occuppied by the gut (Boxshall 1982).

The following polymorphisms were found for the swimming legs: distal segment of right exopod of leg 4 of adult females with dense set of denticles instead of a long seta; distal segment of the endopod of right leg 3 of adult females without a lateral seta; distal segment of the endopod of left leg 3 of adult females without a distolateral spine-like attenuation; coxa of right leg 2 of adult females with a seta bifurcated near its base. Polymorphisms of the male swimming legs appear similar to those of females and include: distal segment of the endopod of leg 2 with medial seta half as long as the same setae in all other specimens; proximal segment of the endopod of right leg 4 with a second inner seta, weakly developed and plumose, located near the middle of the segment; distal segment of endopod of leg 4 with asymmetrical indentations. In addition, the distolateral margin of endopod of leg 4 of adult females, adult males, CV's and CIV's may appear asymmetrical due to presence of one or two indentations to the margin; the shape of these indentations is variable.

The number and homologies of the abdominal somites of *S. gibberum* is important in separating this genus from the remaining asterocherid genera. During the copepodid phase of development of many co-

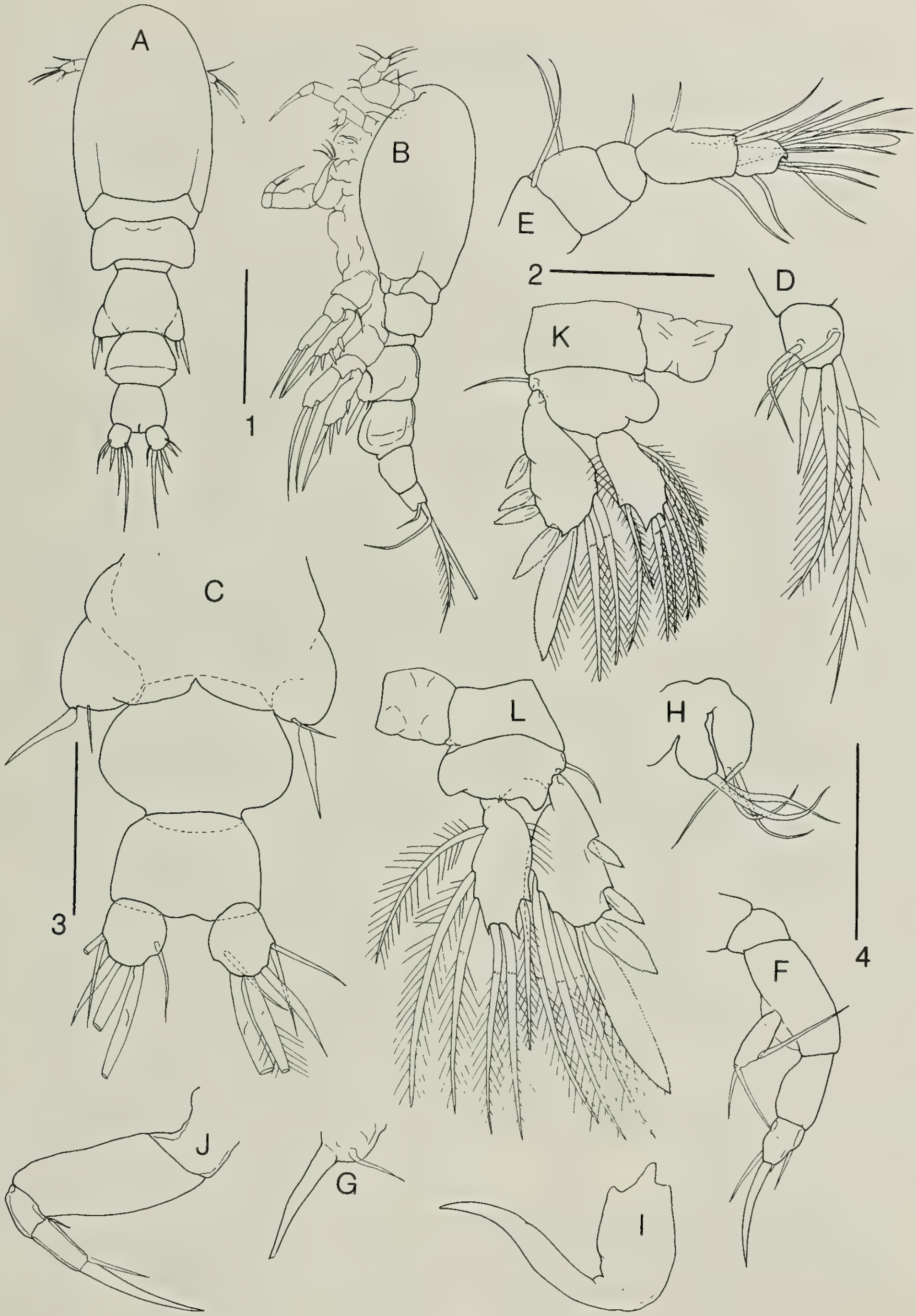

Fig. 10. *Scottomyzon gibberum* (Scott & Scott, 1894), CI: A, habitus, dorsal; B, habitus, lateral; C, urosome ventral; D, caudal ramus, dorsal; E, antennule; F, antenna; H, maxillule; G, mandible; I, maxilla; J maxilliped; K, leg 1; L, leg 2. Scale line 1 is 0.1 mm for A, B; 2 is 0.05 mm for E, K, L; 3 is 0.05 mm for C, D; 4 is 0.05 mm for F-J.

Table 5.—Spines and setae on legs 1–2 of CI.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0-0	1-0	*; *; IV, I, 3	*; *; 1, 2, 4
Leg 2	0-0	1-0	*; *; III, I, 3	*; *; 1, 2, 3

pepods, one articulating body somite usually is added at each copepodid stage, immediately anterior to the posterior somite bearing the caudal ramus. Secondary fusion of the seventh thoracic somite with the second abdominal somite occurs late in development of most copepods (Hulsemann 1991). A setose limb bud appears posteriorly one stage after the formation of each new thoracic somite (Ferrari 1988). In *S. gibberum* at CI all cephalic somites and thoracic somite 1 are fused; thoracic somites 2–5 and abdominal somite 1 articulate; a thoracic somite 2 which articulates with thoracic somite 1 has not been reported for siphonostomatoids. After each molt from copepodid stage I to V, the number of somites of *S. gibberum* increases by one as thoracic somites 6 and 7 are added, with their limb buds one stage out of register, and abdominal somites 2 and 3 are added in register; an arthrodial membrane separates each somite. At CIV-CVI the arthrodial membrane separating thoracic somite 1 and 2 fails to form. A fourth abdominal somite either fails to form or fails to separate from the posterior, first abdominal somite during the molt to CVI, resulting in three abdominal somites for the adults of both sexes.

A posterior position for leg 6 of females of *S. gibberum* is unusual for adult female siphonostomatoids and other adult female copepods in which the seventh thoracic somite is fused with the second abdominal somite. In cases of this fusion, leg 6 is located ventrally or laterally toward the middle of the segmental complex. A posterior position for leg 6 has been described for adult females of the eudactylinid siphonostomatoids *Bariaka* by Cressey (1966) and *Jushyus* by Deets & Benz (1987). Huys & Boxshall (1991) have interpreted this morphology as indicating that the genital somite, thoracic somite 7, is separated from the second, and most anterior, abdominal somite, a conclusion with which we concur. If thoracic somite 7 fails to fuse with abdominal somite 2 to form a genital complex, the bud of leg 6 can be expect to be found in a posterior position on thoracic somite 7. Thus the number and homology of somites comprising the urosome is the same for both genders of adult *S. gibberum.*

The endopod of the maxilliped of adult *S. gibberum* is interpreted as a distal articulating segment and a proximal segment complex of three segments. At CI, the endopod of the maxilliped has two articulating segments; the proximal segment with a single seta has two muscles inserting at the base of the distal segment. The distal segment, without muscles, has two setae; the larger forms a subchela or claw with the distal segment. This segment conformation agrees with the usual situation for copepods; the proximal segment always bears a single formation seta and the distal segment may bear up to four setae, depending upon the species, but that number does not change during the copepodid phase of development (Ferrari & Dahms 1998). The distally polarized seta added to the proximal segment at CII and the medially polarized seta added at CIII, respectively, are presumed to be homologous to the formation seta of a third and a fourth segment of the endopod. At CIV the formation seta of the second segment fails to form, and a second distally polarized seta is added to the proximal or third segment. Loss of the formation seta of the second segment at CIV appears to be unique for *S. gibberum*; poecilostome copepods loose the formation seta of the second segment at CII (Ferrari & Dahms 1998).

The segmentation patterns during development of swimming legs 1–4 follow the common pattern for copepods which is presumed to be ancestral (Ferrari 1988) with

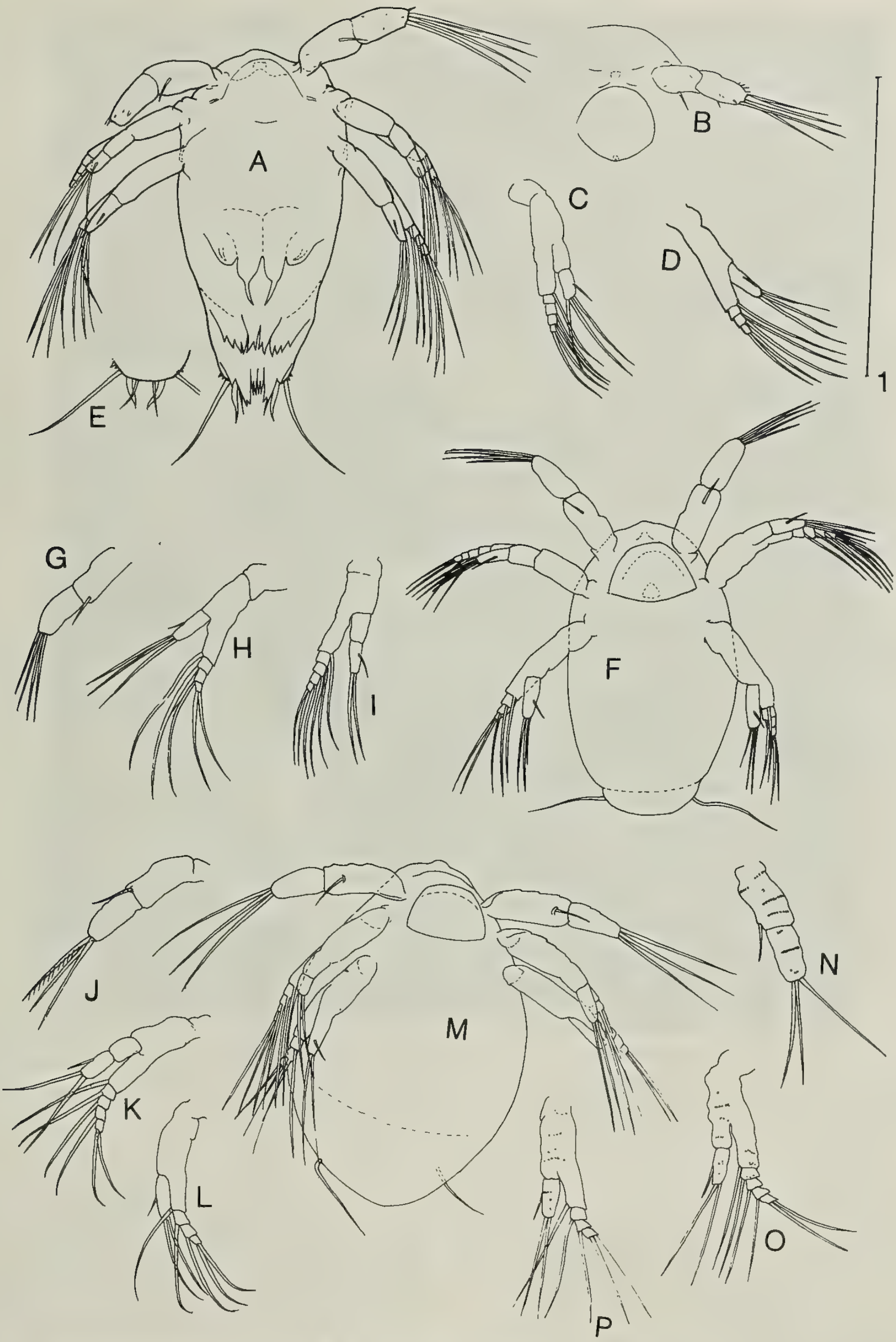

Fig. 11. *Scottomyzon gibberum* (Scott & Scott, 1894), naupliar stages: A, habitus of N4, ventral; B, antennule, N4; C, antenna, N4; D, mandible, N4; E, caudal margin, N4; F, habitus of N3, ventral; G, antennule, N3; H, mandible, N3; I, antenna, N3; J, antennule, N2; K, antenna, N2; L, mandible, N2; M, habitus of N1, ventral; N, antennule, N1; O, antenna, N1; P, mandible, N1. Scale line is 0.02 mm for A–O.

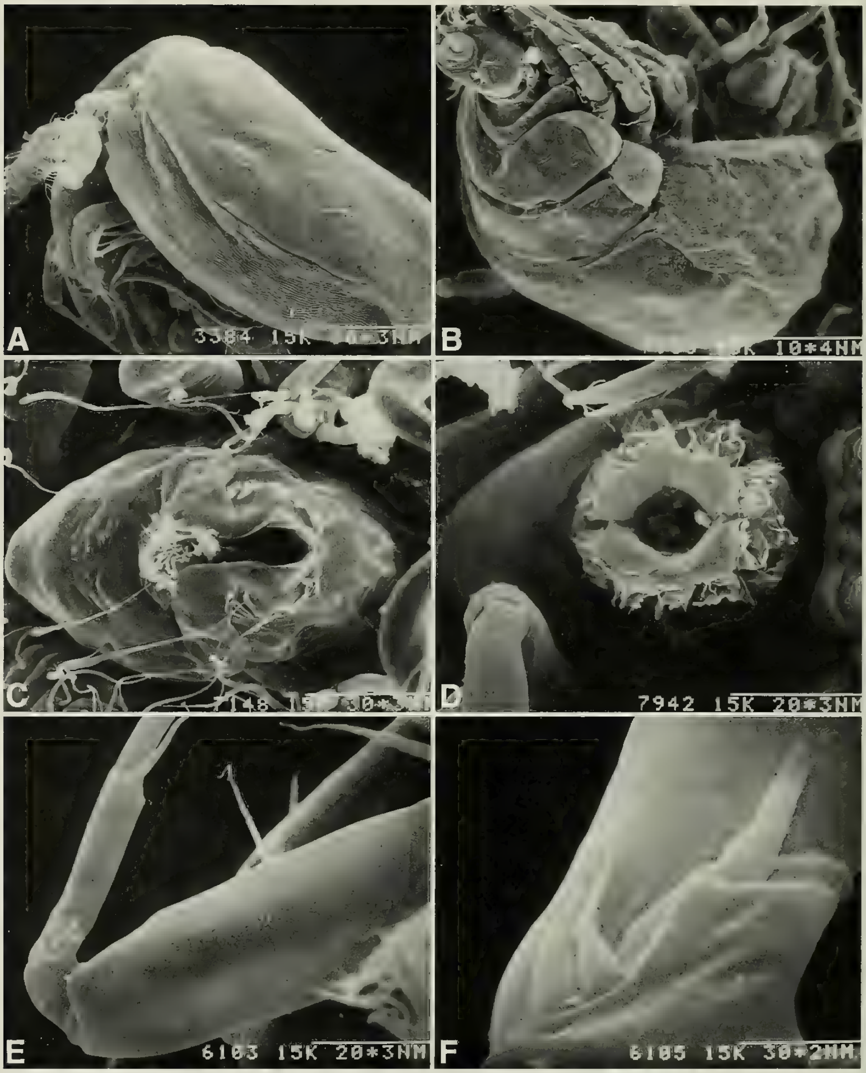

Fig. 12. *Scottomyzon gibberum* (Scott & Scott, 1894), adult female: A, prosome, with folded marginal area of growth, lateral view; B, prosome, with marginal area of intercalate growth, lateral view; C, siphon, female, maxilliped, posterior; D, siphon, male, proximal part of maxillipedal endopod, posterior. Scale line is: 90 microns for A; 100 microns for B; 30 microns for C; 20 microns for D, E; 3 microns for F.

the 3-segmented rami of legs 1–4 appearing at stage V. This is the first report of that pattern for siphonostomatoids.

Sexual dimorphism in adults is most pronounced in general body shape, the antennule, the oral siphon. Sexual dimorphism of oral siphon of adult *S. gibberum* was described previously by Roettger (1969) using light microscopy. We agree with his conclusion that this dimorphism probably reflects a divergence in feeding between genders. The male antennule is geniculate at CVI and the number of the articulating segments is reduced from 18 to 16. Articulating segments 14 and 15 of the male are elongate and bear 2 setae. Sexual dimorphism is expressed at CV in morphology of thoracic somite 7 and sclerotization of the fourth articulating segment from the distal segment of the antennule. Sexual dimorphism of CIV is expressed only in sclerotization of the fourth articulating segment from the distal segment of the antennule.

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A new species of *Onychocamptus* Daday, 1903 (Copepoda: Harpacticoida: Laophontidae) from northwestern Mexico

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Abstract.—A new species of harpacticoid copepod, *Onychocamptus fratrisaustralis* (Harpacticoida: Laophontidae), is described from a coastal lagoon in northwestern Mexico (Sinaloa state). *Onychocamptus fratrisaustralis* appears to be related to *O. krusensterni* Schizas & Shirley, 1994, by the unusual formula of the P4 exopod. *Onychocamptus anomalus* (Ranga Reddy, 1984) shares the same formula of the P4 exopod, but differs from *O. fratrisaustralis* and *O. krusensterni* in the A2 exopod (with 4 setae in *O. krusensterni* and *O. fratrisaustralis*; with 1 seta in *O. anomalus*) and female P5 exopod (with four setae in *O. anomalus*; with three setae in *O. krusensterni* and *O. fratrisaustralis*). *Onychocamptus besnardi* Jakobi, 1954, also possesses a P4 exopod with two outer spines, but lacks the inner seta of the same segment. After thorough analysis of the type material of *O. krusensterni* (USNM259322), a number of subtle differences was found between this species and *O. fratrisaustralis*: armature of the antennal exopod, length/width ratio of caudal rami, dorsal ornamentation of the genital double-somite and fourth urosomite, relative length of the inner setae of second and third exopodal segments and the two innermost setae of second endopodal segments of P2–P3, relative length of the second endopodal segment of P4, general morphology of baseoendopod and relative length of the proximal setae of the endopodal lobe of P5, and relative length of the lateral outer seta of the last antennular segment.

As for many other harpacticoid taxa, the genus *Onychocamptus* Daday, 1903 has been subject to several changes which have led to a better understanding of relationships of the species within the genus. In the most recent redefinition of the genus, Lee & Huys (1999:319) recognized *O. krusensterni* Schizas & Shirley, 1994, *O. taifensis* Kikuchi, Dai & Itô, 1993, *O. bengalensis* (Sewell, 1934), *O. mohammed* (Blanchard & Richard, 1891), *O. vitiospinulosa* (Shen & Tai, 1963), *O. besnardi* Jakobi, 1954, formerly considered by Lang (1965) as a form of *O. mohammed,* as a distinct species, and *O. anomalus* (Ranga Reddy, 1984).

A new species closely related to *O. krusensterni* from Cape Krusenstern, Alaska, is described here. It was found in 1991 during a survey of the distribution and abundance of meiofauna in a coastal lagoon in the mouth of the Gulf of California.

Methods

Quantitative triplicate sediment samples were taken in Ensenada del Pabellón lagoon (Sinaloa, northwestern Mexico), using a plastic corer of 7.06 cm^2 (see Gómez-Noguera & Hendrickx 1997). Meiofauna was separated from macrofauna using 500 and 63 μm sieves. Harpacticoids were sorted under a dis-

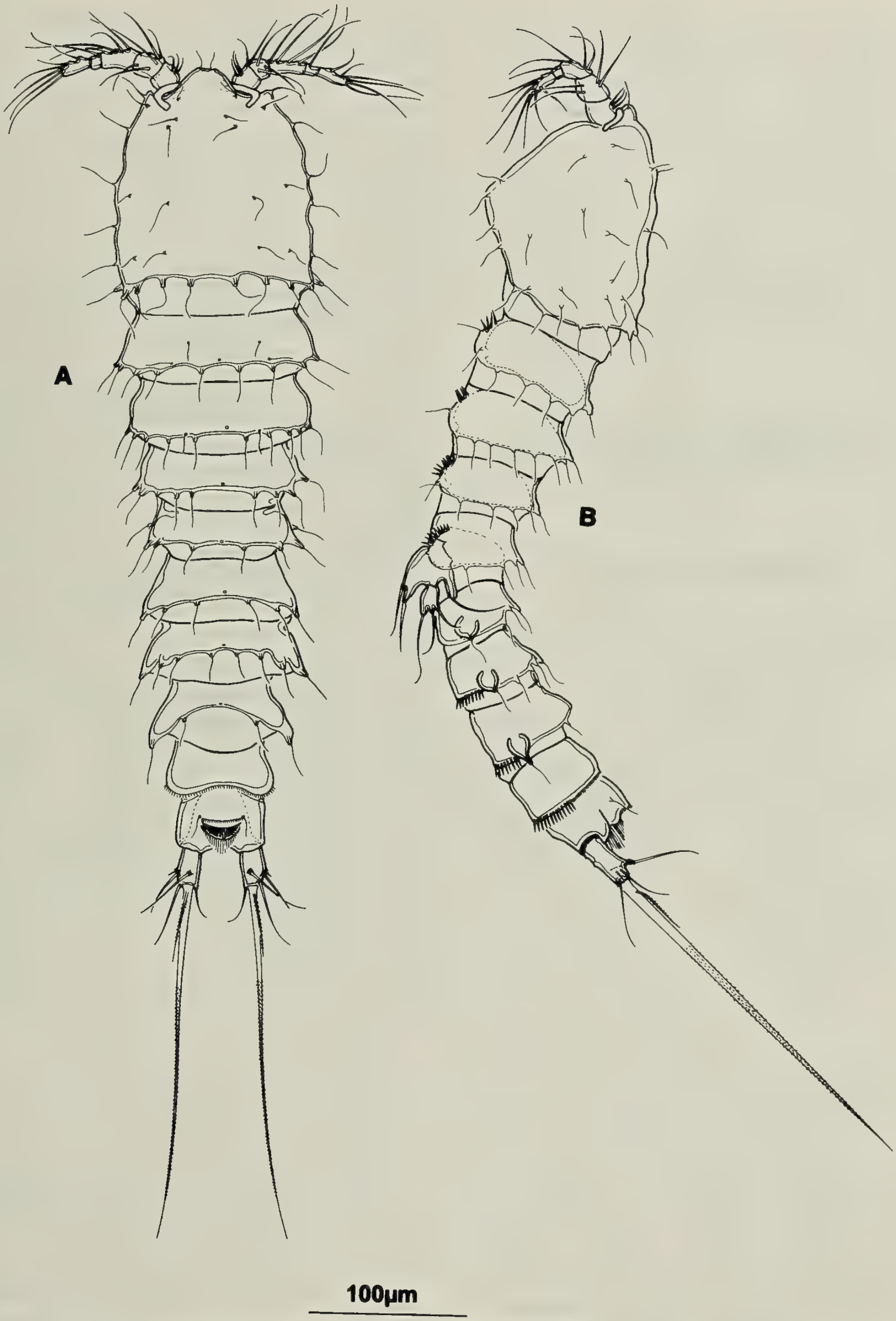

Fig. 1. *Onychocamptus fratrisaustralis,* new species. Holotype, female, EMUCOP-300392-25. A, habitus, dorsal; B, habitus, lateral.

secting microscope, counted, and preserved in 70% ethanol. Observations and drawings were made from whole and dissected specimens mounted in glycerin, at 1000× using a phase-contrast light microscope equipped with a drawing tube. In order to assure the identity of this new taxon, the type material of *O. krusensterni* (USNM259322) was thoroughly reanalysed. Terminology proposed by Huys & Boxshall (1991) was adopted. Abbreviations used in the text and tables: P1–P6, first to sixth leg; EXP, exopod; ENP, endopod.

The type material has been deposited in the collection of the Instituto de Ciencias del Mar y Limnología, Unidad Académica Mazatlán.

Family Laophontidae T. Scott, 1905

Genus *Onychocamptus* Daday, 1903

Onychocamptus fratrisaustralis, new species

Figs. 1–5

Holotype.—Dissected female, EMUCOP-300392-25, collected in May 1991 by Samuel Gómez in Ensenada del Pabellón lagoon (24°19′–24°35′N, 107°28′–107°45′W), Sinaloa, (southeastern Gulf of California), Mexico.

Paratype.—One female preserved in 70% ethanol (EMUCOP-020591-18).

Type locality.—Ensenada del Pabellón lagoon (24°19′–24°35′N, 107°28′–107°45′W), Sinaloa, Mexico.

Etymology.—The specific name is derived from the Latin *frater* (brother) (*fratris* is the genitive form) and *australis* (southern) and alludes to the close relationship of the new species with *O. krusensterni* Schizas & Shirley, 1994, of which the new Mexican laophontid is a southern relative.

Diagnosis.—Laophontidae. Antennule 5-segmented; outer lateral seta of last segment as long as segment. Armature formula of P1–P4 (EXP/ENP): P1-[I-0;III,2,0/0-0;0,I,1], P2-[I-0;I-1;III,I1,1/0-0;0,2,2], P3-[I-0;I-1;III,I1,1/0-0;I,2,3], P4-[I-0;I-1;II,I1,1/0-0;1,1,1]. Antennal exopod with 4 setae, lateral seta shorter, sub-apical seta slightly longer than exopod. Caudal rami as long as anal somite; about 2 times longer than wide. Middle seta of female P5 baseoendopod about 1.3 times longer than exopod.

Description.—Total body length of holotype 527 μm, measured from anterior margin of rostrum to posterior margin of caudal rami. Greatest width measured at posterior margin of cephalothorax. Urosome gradually tapering posteriorly (Figs. 1A, 2A). Cephalothorax nearly ¼ total body length, with surface sensilla, and with sensillar tubercles along posterior margin. Pedigerous somites ornamented like cephalothorax, dorsally with anterolateral sets of spinules (Fig. 1B). Genital double-somite wider than long (Figs. 1A, B, 2A, B), with sensillar tubercles middorsally and laterally and along posterior margin dorsally; P6 represented by one smooth element and genital field in anterior half, ornamented with small spinules along posterior margin. Fourth urosomite with 4 sensillar tubercles along posterior margin dorsally, ventrally as preceding somite. Penultimate somite with fragile spinules along posterior margin dorsally, without sensilla, ventrally as preceding somite. Anal somite as long as preceding somite, with rounded dentate operculum, and with minute spinules along posterior margin ventrally. Caudal rami as long as anal somite, about 2 times longer than wide, with 7 setae (Fig. 2A, B).

Antennule (Fig. 3A): 5-segmented. Surface of segments smooth except for 2 spinular rows on first segment. Armature formula 1-[1], 2-[8], 3-[7+ae], 4-[1], 5-[11].

Antenna (Fig. 3B): 3-segmented, comprising coxa, allobasis, and 1-segmented endopod. Allobasis ornamented with longitudinal row of spinules along inner margin, with inner seta on distal half. Exopod 1-segmented; ornamented with transverse row of small spinules; with 4 setae, lateral seta as long, subapical seta slightly longer than exopod, apical setae clearly longer than exopod (one of them longer and thicker than the other). Endopod ornamented

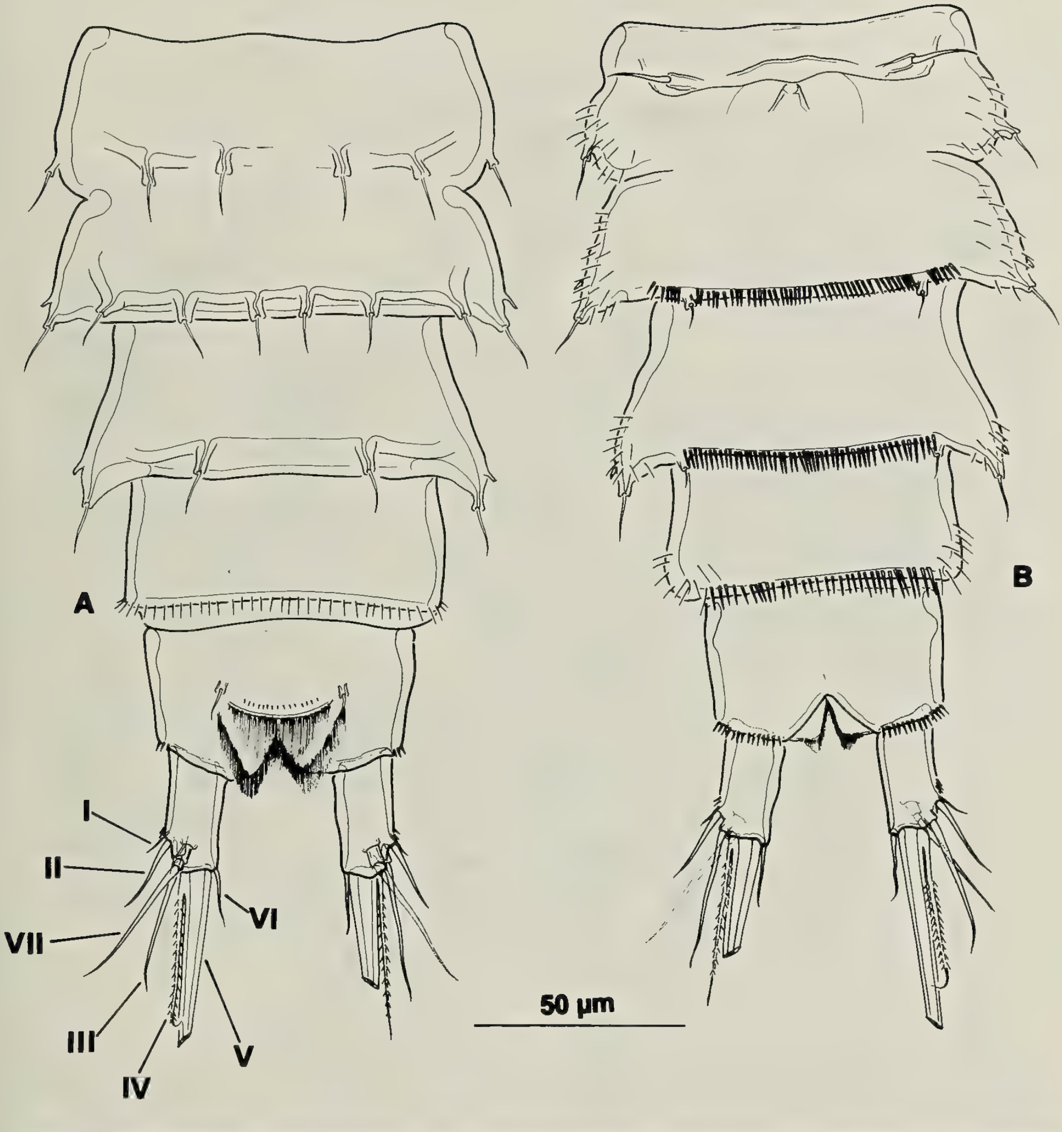

Fig. 2. *Onychocamptus fratrisaustralis,* new species. Holotype, female, EMUCOP-300392-25. A, urosome, dorsal; B, urosome, ventral.

with strong spinules along lateral margin; with 1 strong spine and 1 slender seta (the latter arrowed in Fig. 3B); with 6 distal elements (outermost 2 fused).

Mandible (Fig. 3C, D): With well developed gnathobase bearing several multicuspidate teeth around distal margin; with 1 pinnate spine and 1 naked seta. Palp small, with 5 slender setae.

Maxillule (Fig. 3E): Praecoxa with spinules at base of coxa and along outer margin. Arthrite well developed, with 6 distal elements, and 1 spine on inner margin of arthrite. Coxa with cylindrical endite bearing 1 naked and 1 curved seta. Basis with cylindrical endite bearing 3 setae, with spinular row around inner distal margin and at base of endopod. Endopod and exopod incorporated in basis, the former with 3, the latter with 2 setae.

Maxilla (Fig. 3F): Syncoxa with 2 endites; with 1 proximal inner row of small spinules

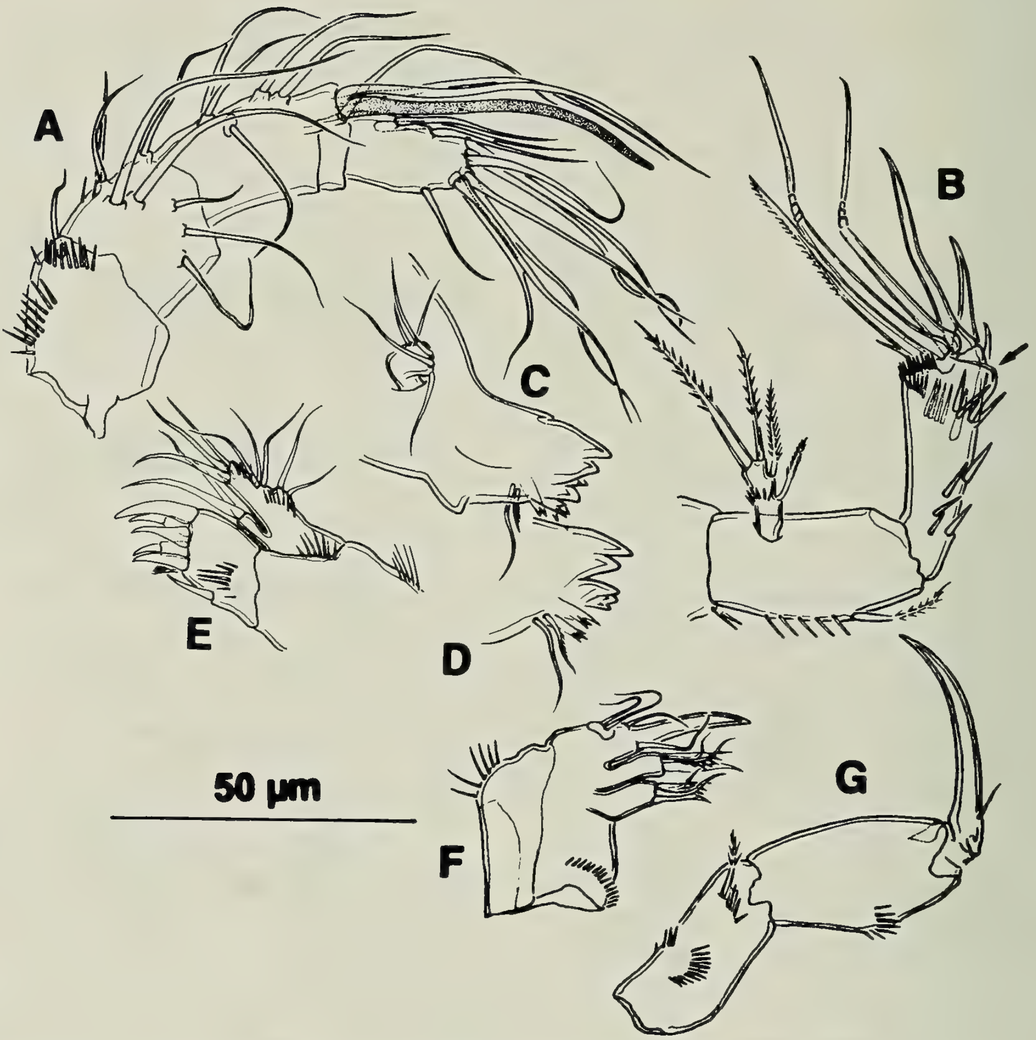

Fig. 3. *Onychocamptus fratrisaustralis,* new species. Holotype, female, EMUCOP-300392-25. A, antennule; B, antenna; C, mandible; D, gnathobase of mandible, another view; E, maxillule; F, maxilla; G, maxilliped.

and some long spinules along outer margin; both endites with 3 naked setae (2 of them slender) and 1 pinnate seta. Allobasis drawn out into strong, naked claw; accessory armature consisting of 2 slender, naked setae. Endopod represented by 2 setae.

Maxilliped (Fig. 3G): With 1 plumose seta and several patches of spinules on syncoxa. Basis with transverse row of spinules on outer margin. Endopod drawn out into long, naked claw, with 1 accessory seta anteriorly.

P1 (Fig. 4A): Praecoxa with some median spinules. Coxa large, with spinules along outer margin. Basis with 1 plumose seta on distal pedestal, long setules on proximal inner margin, and strong bipinnate outer spine with patch of short spinules at its base. Exopod 2-segmented, reaching proximal third of first endopodal segment. Endopod 2-segmented; first segment about 5.2 times longer than wide, with setular row along inner margin; second segment small, slightly longer than wide, with 1 slender naked inner seta and 1 long, naked claw. Armature formula as in Table 1.

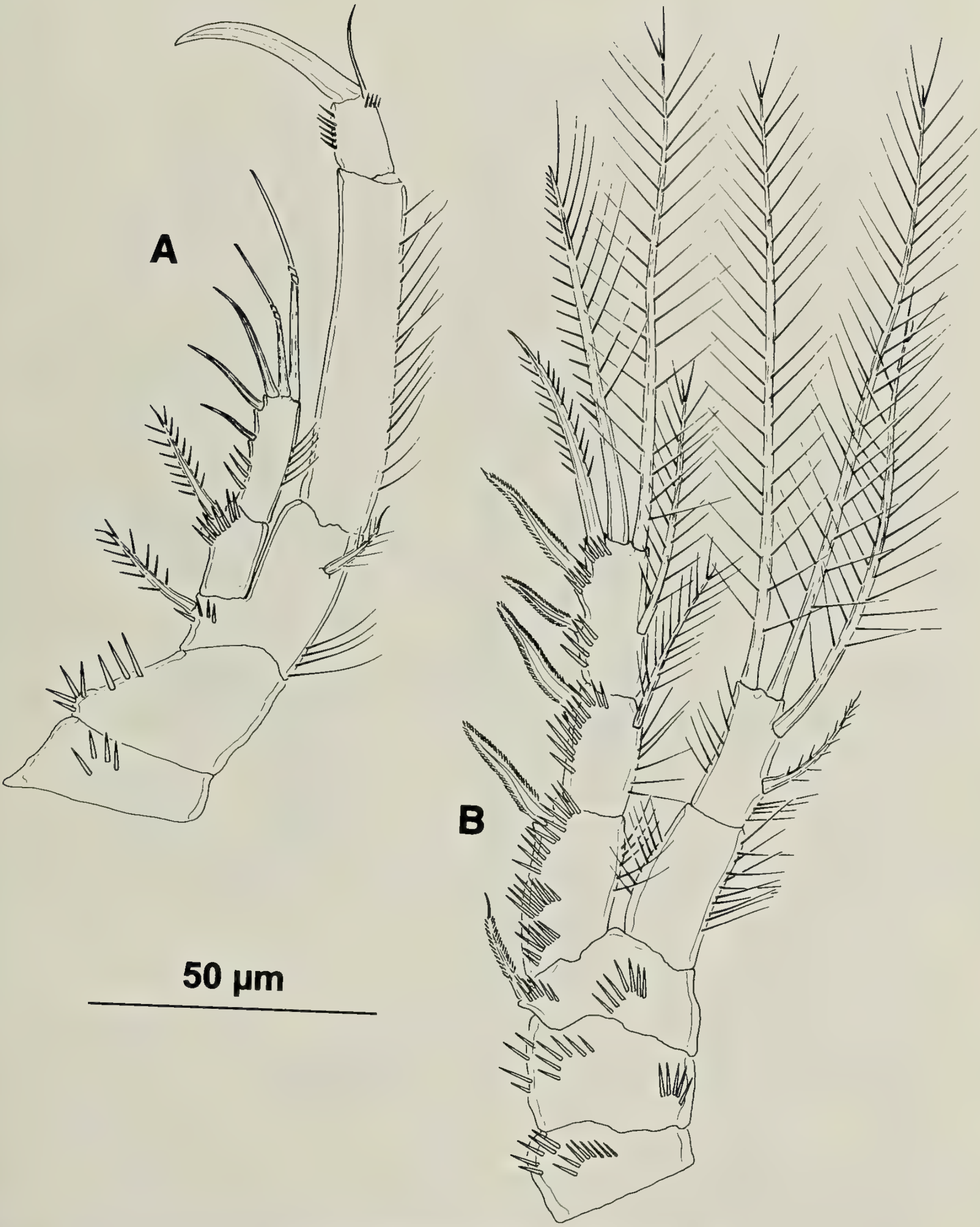

Fig. 4. *Onychocamptus fratrisaustralis,* new species. Holotype, female, EMUCOP-300392-25. A, Pl; B, P2.

P2–P4 (Fig. 4B, 5A, B): Praecoxa, coxa and basis ornamented with spinular rows as figured. Basis of P2 with outer bipinnate spine; basis of P3 and P4 with slender naked outer seta. Exopod 3-segmented. Inner seta of second exopodal segment of P2 hardly reaching tip of third exopodal segment; inner seta of third exopodal segment of P2 clearly longer than supporting segment; outer spines of third exopodal segment of P4 shorter than supporting segment. Endopod 2-segmented. Endopod of

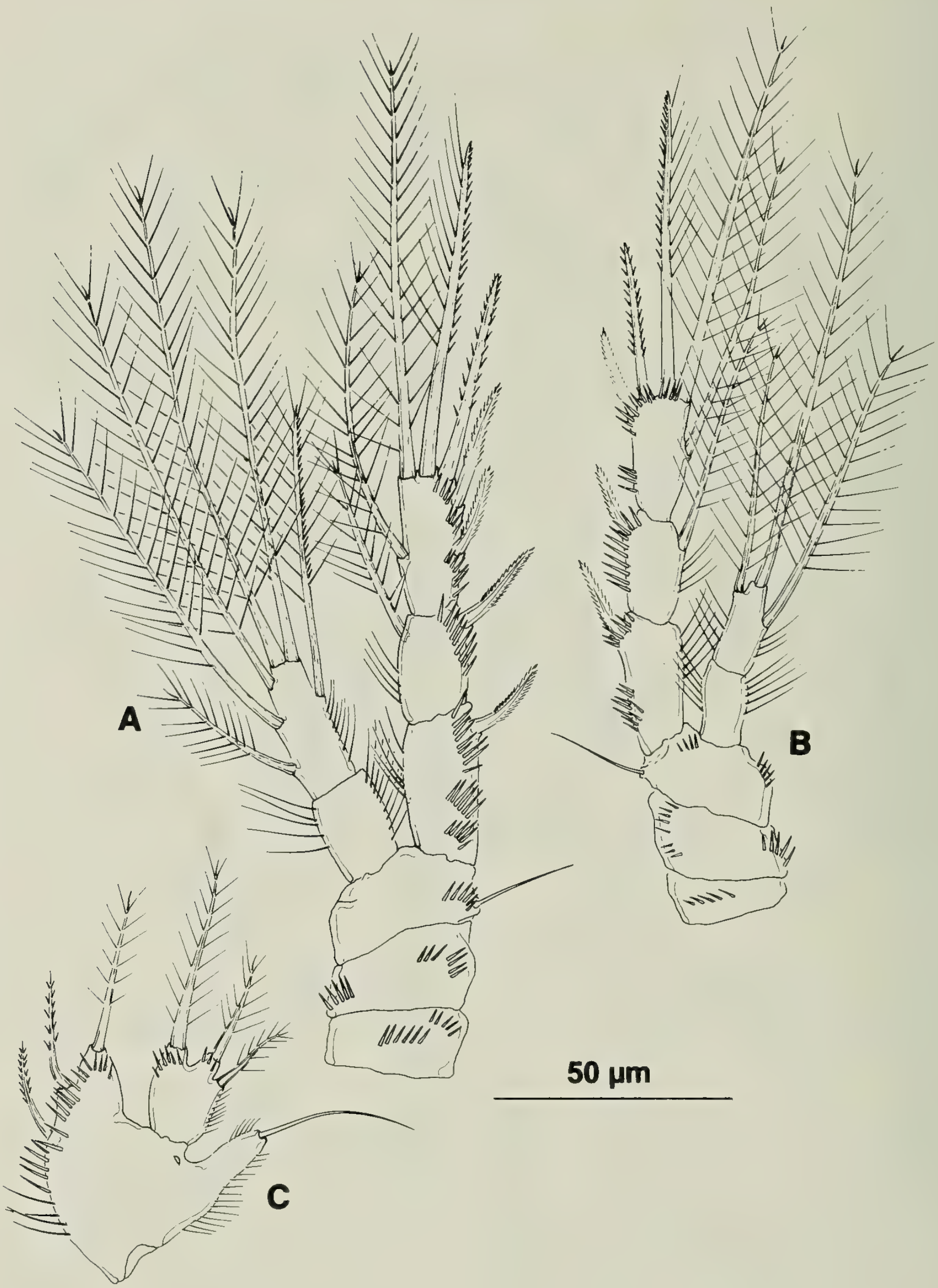

Fig. 5. *Onychocamptus fratrisaustralis,* new species. Holotype, female, EMUCOP-300392-25. A, P3; B, P4; C, P5.

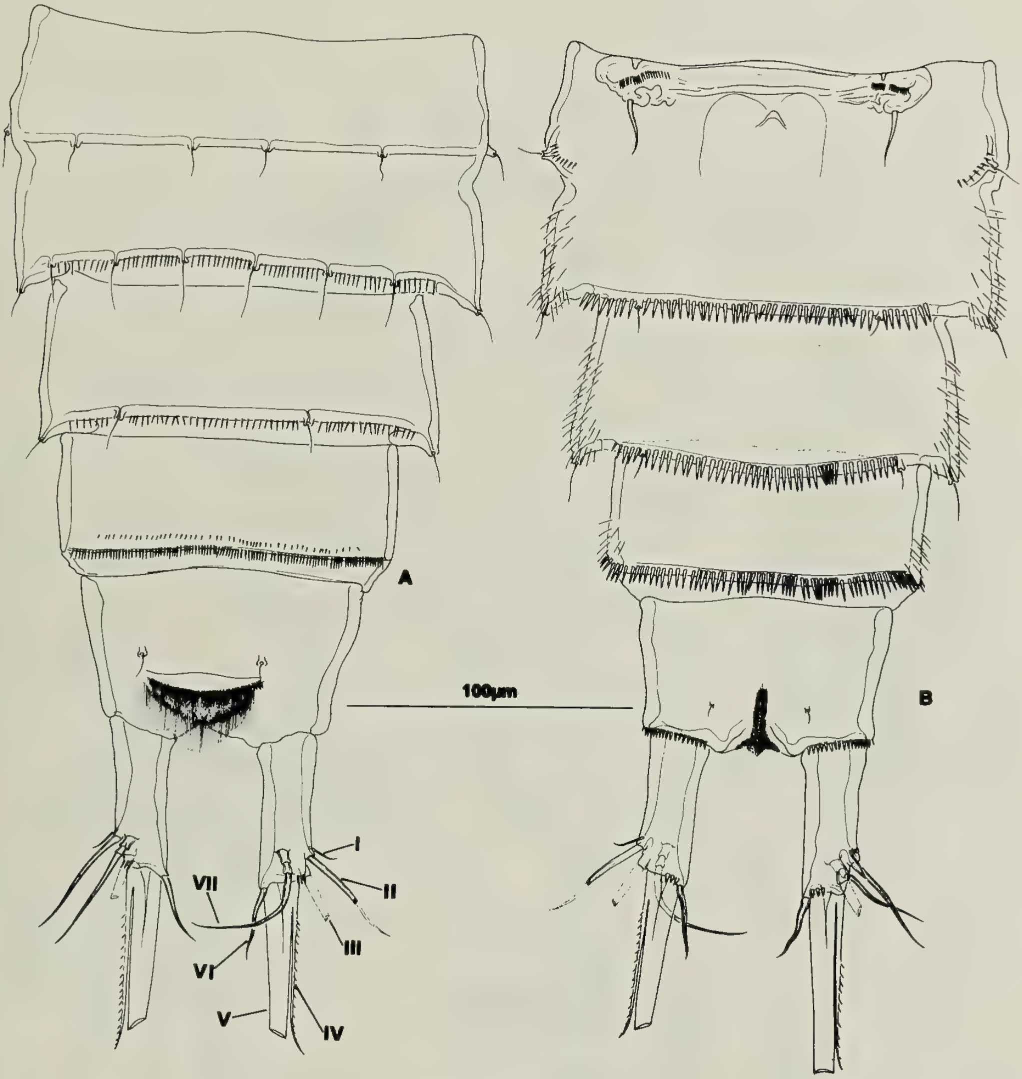

Fig. 6. *Onychocamptus krusensterni* Schizas & Shirley, 1994. Paratype, female, USNM 259322. A, urosome, dorsal; B, urosome, ventral.

P2 slightly beyond second exopodal segment, of P3 hardly reaching distal third of second exopodal segment, of P4 hardly reaching distal half of second exopodal segment. Armature formula as in Table 1.

P5 (Fig. 5C): Baseoendopod forming long outer setophore bearing basal seta and setular rows. Endopodal lobe extending almost to tip of exopod, with 1 apical seta and 2 spiniform inner elements (proximal as long as exopod), and ornamented with proximal inner set of long setules and spinular row. Exopod nearly as long as wide, with 3 setae, ornamented with setules along outer margin and with small spinules at bases of 2 innermost setae.

Male unknown.

Remarks.—The new Mexican laophontid, *Onychocamptus fratrisaustralis,* proved closely related to *O. krusensterni* found in Krusenstern Lagoon (Alaska) in 1994 (Schizas & Shirley 1994). After thorough analysis of the species and after further dissection and analysis of the type material of

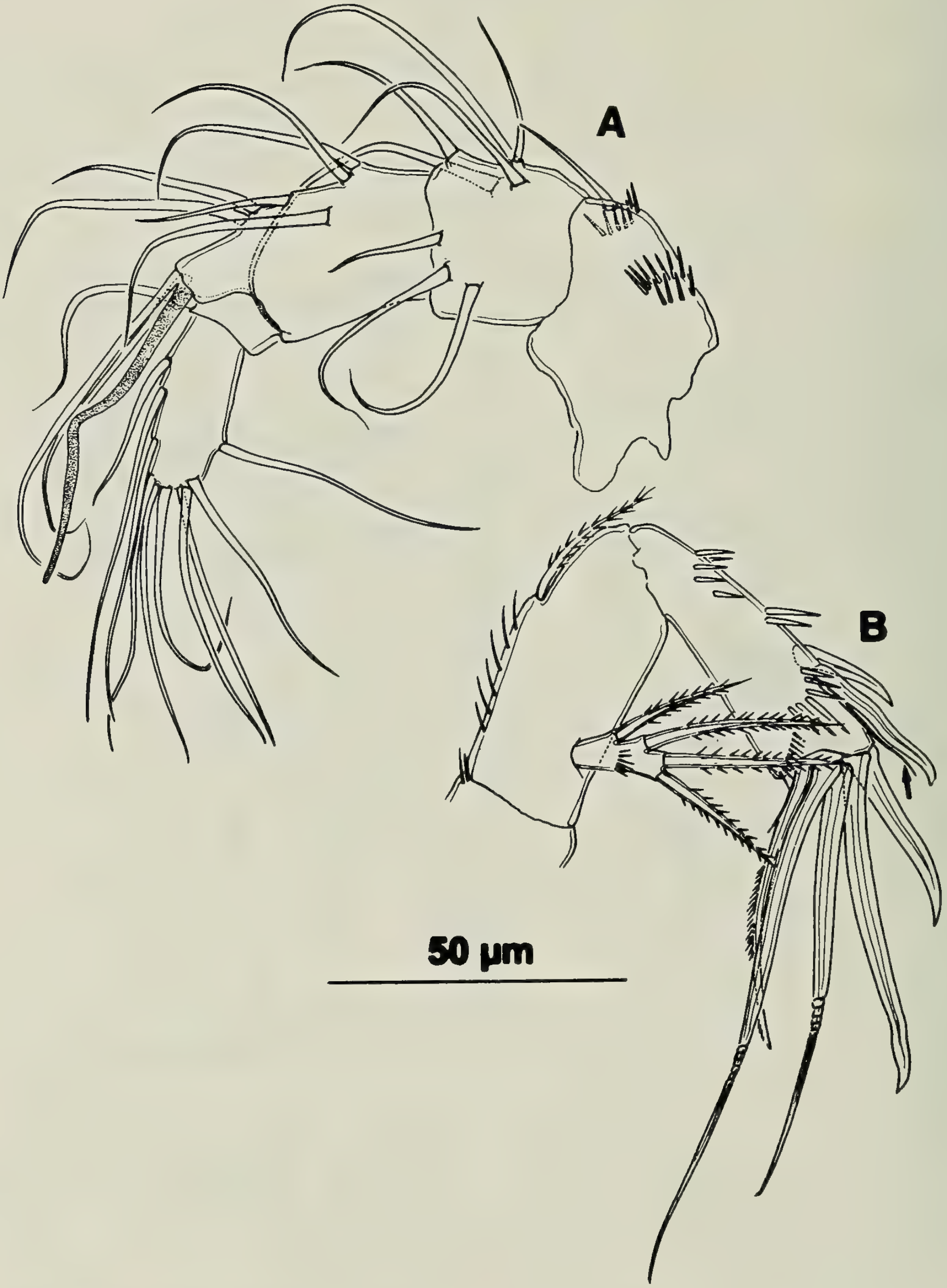

Fig. 7. *Onychocamptus krusensterni* Schizas & Shirley, 1994. Paratype, female, USNM 259322. A, antennule; B, antenna.

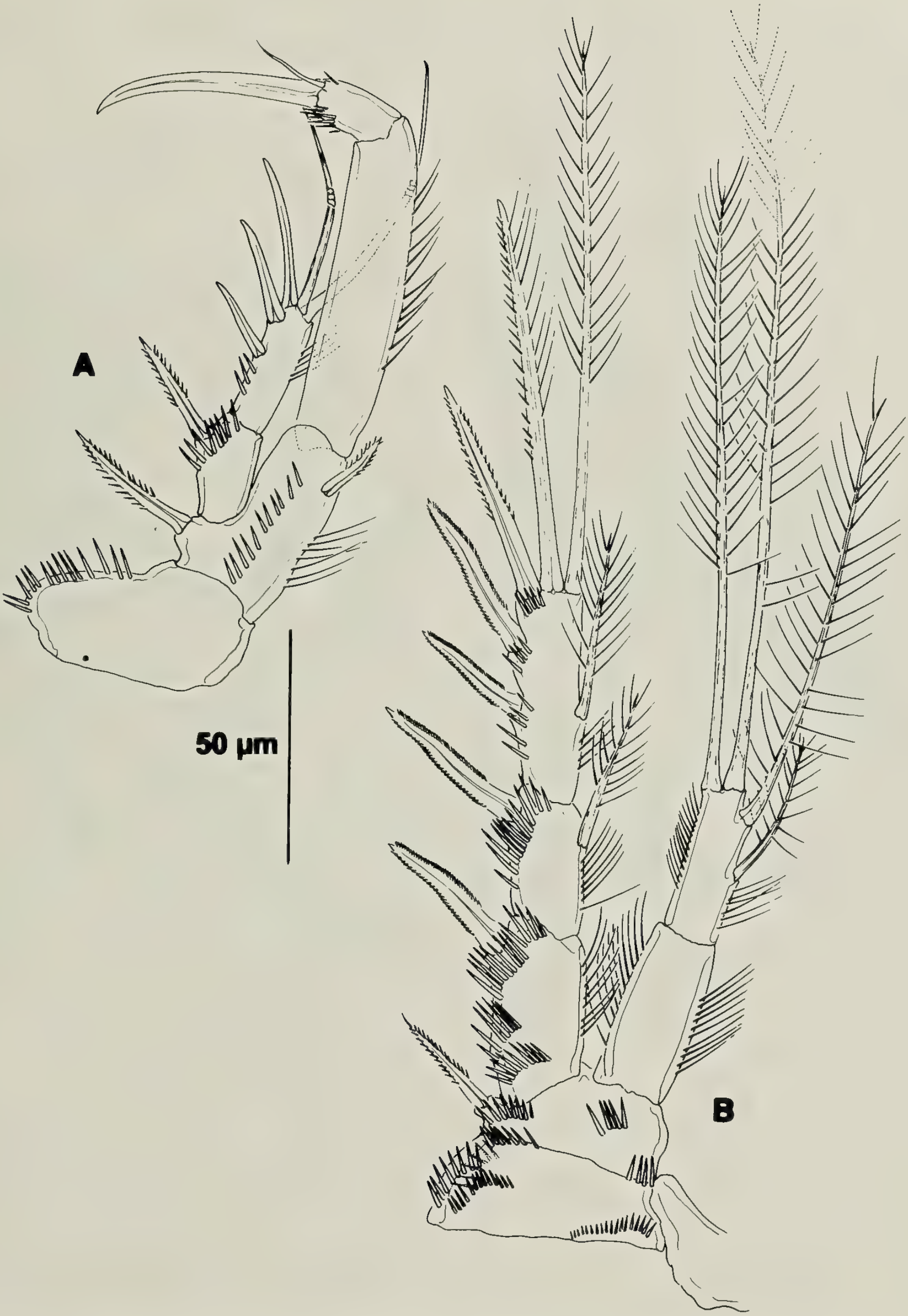

Fig. 8. *Onychocamptus krusensterni* Schizas & Shirley, 1994. Paratype, female, USNM 259322. A, P1; B, P2.

Fig. 9. *Onychocamptus krusensterni* Schizas & Shirley, 1994. Paratype, female, USNM 259322. A, P3; B, P4; C, P5.

Table 1.—Armature formula of *Onychocamptus fratrisaustralis.*

	EXP	ENP
P1	I-0; III, 2, 0	0-0; 0, I, 1
P2	I-0; I-1; III, I1, 1	0-0; 2, 2, 2
P3	I-0; I-1, III, I1, 1	0-0; I, 2, 3
P4	I-0; I-1; II, I1, 1	0-0; 1, 1, 1

O. krusensterni (Paratype USNM 259322) several subtle differences became evident.

Although *O. fratrisaustralis* proved closely related to *O. krusensterni* by the unusual formula of the P4 exopod, these species can be separated by the follow states. The caudal rami of *O. krusensterni* is about 2.8 times longer than wide (Fig. 6), while the caudal rami of *O. fratrisaustralis* is about 2 times longer than wide (Fig. 2). The genital double-somite and fourth urosomite of *O. fratrisaustralis* lacks the minute spinules along the posterior margin (Fig. 2A); such ornamentation is present in *O. krusensterni* (Fig. 6A). *Onychocamptus krusensterni* possesses a spinular row on the genital field, close to P6 (Fig. 6B); *O. fratrisaustralis* lacks such a spinular row (Fig. 2B). The sixth leg represented by a single, naked seta appears to be directed laterally in *O. fratrisaustralis* (Fig. 2B), but posteriorly in *O. krusensterni* (Fig. 6B). The outermost lateral seta on the last segment of the antennule is as long as the segment itself in *O. fratrisaustralis* (Fig. 3A), but clearly longer in *O. krusensterni* (Fig. 7A). The two lateral setae of the exopod of the antenna are comparatively stronger and longer in *O. krusensterni* (Fig. 7B) than in *O. fratrisaustralis* (Fig. 3B). The first swimming leg of *O. krusensterni* possesses a longitudinal spinular row on the basis (Fig. 8A), which is absent in *O. fratrisaustralis* (Fig. 4A). The spinules near the outer spine of basis and first exopodal segment of the first swimming leg are much smaller in *O. krusensterni* (Fig. 8A) than in *O. fratrisaustralis* (Fig. 4A). The spinules along the margin of the inner spine of the basis of P1 are longer in *O. fratrisaustralis*. The second swimming leg of both species differ in the relative length of the inner setae of the second and third exopodal segments (comparatively longer in *O. fratrisaustralis*), innermost apical seta of the second endopodal segment (almost two times longer than innermost seta in *O. krusensterni,* and barely longer in *O. fratrisaustralis*), and armature of the most apical outer spine and outermost apical element of the third exopodal segment (larger and thicker in *O. fratrisaustralis*) (Figs. 4B, 8B). The relative length of the second endopodal segment of the third swimming leg is about 1.3 times longer than the first endopodal segment in *O. fratrisaustralis* (Fig. 5A), but 1.7 times longer in *O. krusensterni* (Fig. 9A). The outermost setae on the second endopodal segment of the fourth swimming leg of *O. fratrisaustralis* is ornamented with setules, but the same seta is ornamented with spinules in *O. krusensterni.* The relative size of the two inner setae of the endopodal lobe of P5 is nearly or slightly longer than exopod in *O. fratrisaustralis* (Fig. 5C), but clearly longer in *O. krusensterni* (Fig. 9C). The site of insertion of the apical seta of the endopodal lobe reaches the tip of the exopod in *O. fratrisaustralis,* but hardly reaches the middle of exopod in *O. krusensterni.*

Onychocamptus anomalus (Ranga Reddy, 1984) shares the same formula of the P4 exopod, but differs from *O. fratrisaustralis* and *O. krusensterni* in the A2 exopod (with 4 setae in *O. krusensterni* and *O. fratrisautralis*; with 1 seta in *O. anomalus*) and the female P5 exopod (with 4 setae in *O. anomalus*; with 3 setae in *O. krusensterni* and *O. fratrisautralis*). *Onychocamptus besnardi* Jakobi, 1954, also possesses a P4 exopod with 2 outer spines, but lacks the inner seta of the same segment.

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Fridericia nanningensis, a new terrestrial enchytraeid species (Oligochaeta) from southwestern China

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Abstract.—*Fridericia nanningensis,* a new species from wetland soil of Nanhu Park, Nanning city, the capital of Guangxi Zhuang Autonomous Region in southwest China, is described. It is characterized by 2–4 chaetae per bundle, poorly-developed clitellar glands, slender, unbranched peptonephridia, and spermathecae with 2 ampullar diverticula, a deep constriction in the middle of the ampulla and one large ectal gland. It is closely related to the European species, *F. alata* Nielsen & Christensen, 1959 and the East European species, *F. tubulosa* Dózsa-Farkas, 1972 by the shape of peptonephridia and the undeveloped clitellar glands. It differs from *F. alata* by its shorter body length and fewer chaetae per bundle, its type of coelomocytes (type "c"), its deep constriction in the middle of the spermathecae ampulla and a larger ectal gland, and it differs from *F. tubulosa* by its pale epidermal glands, its more anterior origin of the dorsal vessel, a deep constriction in the middle of the spermathecae ampulla, shorter ectal duct, and only one ectal gland at the spermathecal orifice.

Since *Henlea ventriculosa* (d'Udekem, 1854) was first reported from Tibet by Stephenson (cited in Cernosvitov 1941), nearly 40 terrestrial enchytraeid species from China have been recorded (Chen 1959; Liang 1979; Xu 1989; Liang & Xie 1992; Wang 1999; Xie 1999a, 1999b; Xie 2000a; 2000b, 2000c, 2000d; Xie & Rota in press). In spite of these works, the terrestrial enchytraeids in the country are still poorly studied, and the investigated regions are mainly covered in the Changjiang (Yangtze) Basin and some localities of the northeastern regions. Concerning the southwestern region of China, however, no species have been reported. In 1992, a preliminary faunistic survey of terrestrial microdriles in Guangxi Zhuang Autonomous Region in China was carried out. Among the specimens collected, one species of *Fridericia* was recognized as a new species. Its description is given herein.

Methods

Enchytraeids were sampled from wetland soil of Nanhu Park (22°50′N, 108°15′E), Nanning city, the capital of Guangxi Zhuang Autonomous Region in southwest China and extracted by the wet-funnel method (O'Connor 1962). After observation in vivo, worms were fixed in 10% formalin. Whole worms were stained in borax carmine or paracarmine, dehydrated in an alcohol series and mounted in Canada balsam. Figures were drawn with a camera lucida. The types are deposited in the Specimen Room of Invertebrates, Institute of Hydrobiology, the Chinese Academy of Sciences, China.

Unless otherwise specified in the description, measurements of body dimensions and internal organs refer to whole-mounted specimens. The type of oesophageal appendages ("peptonephridia", see Rüdiger & Westheide 2000) and nucleated coelomocytes are defined according to Nielsen & Christensen (1959) and Möller (1971).

Fridericia nanningensis new species

Fig. 1A–E

Holotype.—Fully mature, whole-mounted specimen.

Type locality.—Nanhu Park (22°50′N, 108°15′E), Nanning city, wetland brown soil under grass roots, with little humus, pH 6.5, 15 Sep 1992, coll. Z. Xie and H. Wang.

Paratypes.—7 whole-mounted specimens, from type locality.

Other material examined.—Ca. 20 additional specimens were examined in vivo; they are preserved in 10% formalin, also from type locality, coll. Z. Xie and H. Wang.

Description.—Worms slender, somewhat sluggish. Live dimensions: length 7–9 mm, width of clitellum 230–250 μm. Preserved dimensions: length 3.5–6.5 mm (n = 8), width in IV 182–190 μm, 200–210 μm at clitellum, 160–170 μm in posterior segments. Segments 28–40 (n = 8). Epidermal gland cells pale in vivo, arranged transversely, 3–4 rows per segment. Chaetae straight, with distinct ental hook, 4 (usually 2–3 in II or III) per bundle anteriorly (ca. until XIV–XVI) and 2–3 posteriorly. The largest chaetae (outer pair) occurring in caudal segments, 48–54 μm long and ca. 5 μm thick. Head pore at 0/1, longitudinally elongate. Dorsal pores from VII onwards. Clitellum over XII-1/2XIII, clitellar glands poorly-developed, forming ca. 20–23 transverse rows.

Brain round posteriorly, 30–36 μm long and 22–26 μm wide. Three pairs of pharyngeal glands in IV–VI, all united dorsally and with distinct ventral lobes (Fig. 1A). Oesophageal appendages unbranched, slender, coiled (2–4 loops) in IV–V and ending in VI–VII in vivo and IV–V in fixed specimens (type "b", sensu Nielsen & Christensen 1959) (Fig. 1A). Chylus cells in XIII-XV. Chloragogen cells not dense from V onwards. A ridge of tall hyaline cells on intestinal floor of XIX–XXII (n = 4). Blood colourless. Dorsal vessel originating in XVII–XVIII. Nephridia from 6–7 onwards, 5 pairs before clitellum. Anteseptal part oval, 1.5–2 times as long as postseptale; postseptale oval, with efferent duct originating mid-ventrally (Fig. 1D). Nucleated coelomocytes oval, with regular outline, evenly granulated (type "c" sensu Möller 1971), 27–30 μm long in vivo and ca. 18–22 μm in fixed materials. Anucleate corpuscles discoid, 7–8 μm in size (Fig. 1B).

Seminal vesicles well-developed, dorsal, anterior distension extending to X, and posterior to XII. Sperm funnels cylindrical, ca. 160–180 μm long and 70–80 μm wide, with a narrower collar (Fig. 1C). Vasa deferentia confined to XII, irregularly coiled. Penial bulbs hemispherical in lateral view and nearly oblong in ventral view, with compact glandular mass, ca. 147 μm long, 42 μm wide, 38 μm high. No egg sac. Usually 2 mature eggs at one time.

Spermathecae in V, ental ducts short and communicating with oesophagus separately (Fig. 1E). Ampulla conical, with deep constriction in middle region, 100–105 μm long and 45–50 μm wide; carrying two sessile, oval diverticula (44–50 μm long and 25–30 μm wide). Spermatozoa scattered in lumen. Ectal ducts 154–160 μm long and 11–12 μm wide. One oval granular gland (ca. 18–20 μm) at each ectal opening.

Etymology.—Named "*nanningensis*" for the type locality.

Distribution and habitat.—Known only from Nanning City. At the type locality, it co-occurs with other enchytraeid taxa: *Achaeta brevivasa* Graefe, 1980, *Hemienchytraeus bifurcatus* Nielsen & Christensen, 1959, *Hemienchytraeus stephensoni* (Cognetti, 1927), *Enchytraeus athecatus* Wang, 1999, and *Marionina* sp. (immature).

Discussion

Among all known species of *Fridericia* with elongate and unbranched oesophageal appendages, the new species is most closely

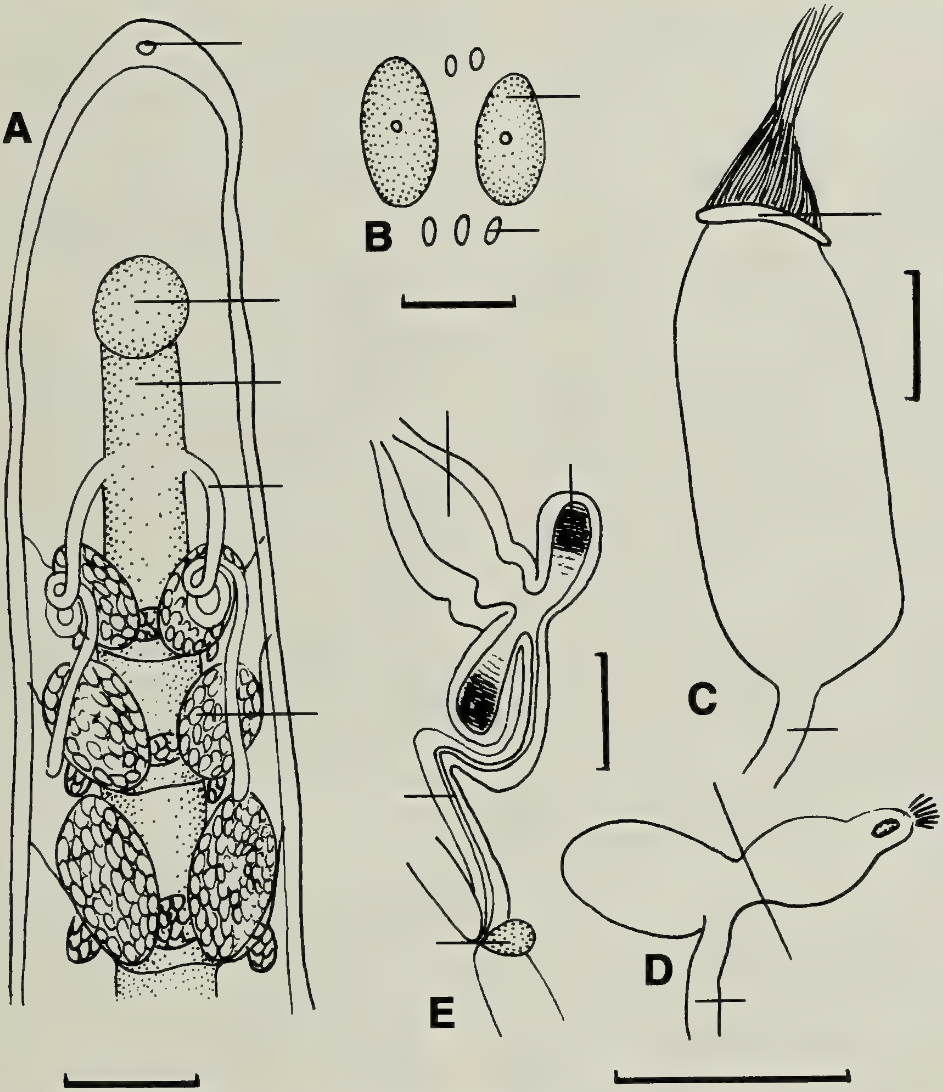

Fig. 1. *Fridericia nanningensis,* new species. A, Dorsal view of anterior segments; B, coelomocytes; C, sperm funnel; D, nephridium at 7/8; E, spermatheca; Scale: A, 100 μm; B, 20 μm; C, D, E, 50 μm. Abbreviations: ac, anucleate corpuscle; co, collar; di, diverticulum; ed, efferent duct; end, ental duct; eg, ectal gland; hp, head pore; nc, nucleated coelomocyte; oe, oesophagus; oea, oesophageal appendage; ph, pharynx; phg, pharyngeal gland; sa, spermathecal ampulla; vd, vasa deferentia.

related to the European species, *Fridericia alata* Nielsen & Christensen, 1959 and the East European species, *Fridericia tubulosa* Dózsa-Farkas, 1972. They all have a poorly developed clitellum and two spermathecal diverticula. However, *F. alata* differs from *F. nanningensis* by having a longer body size (12–20 mm, 54–64 segments), up to 6 chaetae per bundle, longer ental ducts (Nielsen & Christensen 1959, Fig. 80), the type of coelomocytes (type "a"; Möller 1971), and a smaller ectal gland. *Fridericia tubulosa* differs from *F. nanningensis* by having longer body size (12–18 mm, 40–50 segments), yellowish or brownish epidermal glands, a relatively more posterior

Table 1.—Comparison of *Fridericia nanningensis,* new species, with allied species.

	F. nanningensis, new species	*F. alata* Nielsen & Christensen, 1959	*F. tubulosa* Dózsa-Farkas, 1972
Length (mm)	7–9	12–20	12–18
Segments	28–40	54–64	40–50
Chaetae/bundle	2–4	4–6	2–4
Clitellum	weakly developed	weakly developed	weakly developed
Epidermal glands	pale	indistinct	yellowish or brownish
Oesophageal appendages	type "b"	type "b"	type "b"
Origin of dorsal vessel	XVII–XVIII	ca. XX	XIX–XXIII
Efferent duct of nephridia	mid-ventral	mid-ventral	ventral
Nucleated coelomocyte	type "c"	type "a"	?
Sperm funnel (length : width)	2:1	2.5–3:1	3:1
Seminal vesicle	well-developed	well-developed	well-developed
Ectal duct: ampulla	1.5–1.6:1	6–6.5:1	2–2.5:1
Ampulla	constriction	no constriction	no constriction
Number of ectal glands at each spermathecal opening	1	1	2
Distribution	China	Europe	East Europe

origin of the dorsal vessel (XIX–XXIII), a longer ectal duct, and 2 conspicuous ectal glands at each spermathecal opening. The differences between these species are summarized in Table 1.

With the addition of *F. nanningensis,* a total of 12 species of *Fridericia* are known from the country (Table 2).

Table 2.—Species of *Fridericia* previously recorded in China.

1. *Fridericia alba* Moore, 1895
2. *Fridericia bulboides* Nielsen & Christensen, 1959
3. *Fridericia bulbosa* (Rosa, 1887)
4. *Fridericia callosa* (Eisen, 1878)
5. *Fridericia carmichaeli* Stephenson, 1915
6. *Fridericia chongqingensis* Xie, 1999
7. *Fridericia maculata* Issel, 1904
8. *Fridericia multisegmentata* Wang, 1999
9. *Fridericia paraunisetosa* Xie, 2000
10. *Fridericia paroniana* Issel, 1904
11. *Fridericia unisetosa* Xie, 2000

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Description of a new species of *Parasphaerosyllis* (Polychaeta: Syllidae: Syllinae)

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Abstract.—During a study on the cryptofauna of coral reefs in Coiba National Park (Panama), specimens of an undescribed species of *Parasphaerosyllis* Monro, 1937 were collected. *Parasphaerosyllis malimalii,* n. sp. differs from all other species within the genus by its chaetal features. The new species has thick simple chaetae on median and posterior parapodia, produced by a loss of the blades and enlargement of the shafts. This type of chaeta is unique in this genus, but it has been observed in other genera of the Syllidae such as *Syllis* and *Sphaerosyllis.*

Between June 1996 and September 1998, four scientific cruises were carried out in the Coiba National Park, Panama for the study of marine invertebrates (San Martín et al. 1997). A provisional list of the polychaetes was presented in López et al. (1997), and a provisional list of syllids is included in Capa et al. (2000, 2001). In a sample of dead coral (*Pocillopora* sp.), two specimens of an undescribed species of the genus *Parasphaerosyllis* Monro, 1937 were collected.

Parasphaerosyllis is characterized by having bulbous, lemon-shaped dorsal cirri alternating with moniliform cirri on the middle-posterior part of the body. Monro (1937) originally included this genus in the subfamily Exogoninae; however, Fauvel (1939) transferred it to the subfamily Syllinae because its palps are fused only at their bases and, in addition to bulbous cirri, it bears long, moniliform dorsal cirri.

Parasphaerosyllis is a genus that comprises four described species: *P. indica* Monro, 1937, *P. uschacovi* (Chlebovitsch, 1959), *P. ezoensis* Imajima & Hartman, 1964 and *P. setoensis* Imajima, 1966. The characters used to distinguish these species are the chaetiger where the first bulbous cirri appear, the shape of the terminal papillae (articulated or simple) of the ovoid cirri, the presence or absence of a stalk at the base of these particular cirri, the degree of fusion of the palps, and the place of insertion of the lateral antennae.

Materials and Methods

The specimens were collected from a sample of a block of dead coral (*Pocillopora* sp.) in Arrecife Rosario (Northeast Coiba Island, Panama) on 16 Nov 1997. For further details, see Capa et al. (2000). Holotype and paratype are deposited at the Museo Nacional de Ciencias Naturales de Madrid (MNCNM), Spain.

Family Syllidae Grube, 1850

Subfamily Syllinae Grube, 1850
Genus *Parasphaerosyllis* Monro, 1937
Parasphaerosyllis malimalii, new species

Material examined.—Holotype MNCN 16.01/6107, paratype MNCN 16.01/6107. Substrata: *Pocillopora* sp. Arrecife Rosario 7°38′30″N and 81°45′20″W, 2.5 m depth, 16 Nov 1997.

Description.—Both specimens incomplete, posterior ends missing. Holotype 7.1 mm long, 0.4 mm wide, 59 chaetigers. Paratype 6.1 mm long, 0.3 mm wide, 55 chaetigers. Body without color markings, yellowish after fixation. Prostomium pentagonal, wider than long (Fig. 1A); two pairs of eyes in open trapezoidal arrangement, anterior eyes kidney-shaped, holotype with two small anterior eyespots. Three moniliform antennae; median antenna originating slightly in front of the posterior eyes (Fig. 1A, B), longer than prostomium and palps together, with about 26 articles; lateral antennae originating near anterior margin of prostomium, with about 21 articles (Fig. 1A). Palps oval, slightly longer than prostomium, fused at their bases (Fig. 1A). Tentacular segment somewhat shorter than following chaetigers, provided with two pairs of tentacular cirri; dorsal tentacular cirri with 32–35 articles and 600 μm long, ventral tentacular cirri with 18–20 articles and 200–260 μm long (Fig. 1A). Dorsal cirri longer than wide, difference more obvious in posterior region of specimens. Irregular alternation of length of dorsal cirri, 15–25 articles on anterior segments, 340–400 μm long, 14–18 articles in median-anterior region of the body, 140–200 μm long. From midbody posteriorly, long moniliform cirri alternating with other dorsal cirri, ovoid, bulbous, with an unarticulated terminal knob, apparently without stalk, some cases with fold between bulb and parapodia, having yellowish spiral fibrilar material inside (Fig. 1B–D). First bulbous cirri on holotype appear on chaetiger 20 (left side) and on chaetiger 24 (right side). On paratype bulbous cirri appear on chaetigers 25 and 27, respectively. Bulbous cirri alternate regularly with moniliform cirri to end of incomplete specimens. Anterior parapodia each with 6–7 compound chaetae with bidentate, falcigerous blades, distal tooth acute and proximal one short, small, with short spines along cutting edge; dorsoventral gradation in length of blades, 21 μm dorsally, 12 μm ventrally (Fig. 2A). Number of chaetae on each parapodium progressively decreasing, dorsal chaetae without blades and with enlarged shafts; remainder compound chaetae with shorter blades, with an indistinct proximal tooth and very short spines on cutting edge. Parapodia posterior to proventricular level each with 4–5 chaetae, dorsal-most simple and all others compound (Fig. 2B, E). Midbody and posterior segments only with simple, very thick chaetae, numbering three to five on each parapodium (Figs. 1C, D, 2F), sometimes ventral-most chaeta with very short, almost unidentate and smooth blade. Two aciculae in each anterior parapodium, one straight, with acute tip, other with curved tip (Fig. 2C). A single aciculum in median-posterior parapodia (Fig. 2D). Pharynx extending through 7–9 segments, 520 μm and 840 μm long in holotype and paratype, respectively; pharyngeal tooth located on anterior end. Proventriculus 520 μm long, extending through 6 chaetigers, with about 24 muscle cell rows (Fig. 1B).

Remarks.—*Parasphaerosyllis malimalii* mainly differs from all the other species described in the genus in having thick simple chaetae on midbody and posterior parapodia, produced by the loss of blades and enlargement of the shafts. This type of chaeta has been previously reported for other species in the family Syllinae, such as *Syllis amica* Quatrefages, 1865, *S. ferrani* Alós & San Martín, 1987 and *Sphaerosyllis bulbosa* Southern, 1914 (Fauvel 1923, San Martín 1984, Alós & San Martín 1987, Parapar et al. 1994). Furthermore, the blades of its compound chaetae are shorter and have a very small proximal tooth.

For comparison, we have examined the types of *Parasphaerosyllis indica* (Monro, 1937), a circumtropical species, one specimen from the Galapagos Islands (Westheide 1974) and several specimens from Cuba collected and reported by San Martín (1991); none of these specimens possesses this type of chaeta. According to Monro (1937) and Rioja (1958), the bulbous dorsal cirri first occur on chaetiger 16 on *P. indica,* whereas they first appear on chaetiger 20 on *P. malimalii,* n. sp. However, this character may not distinguish these

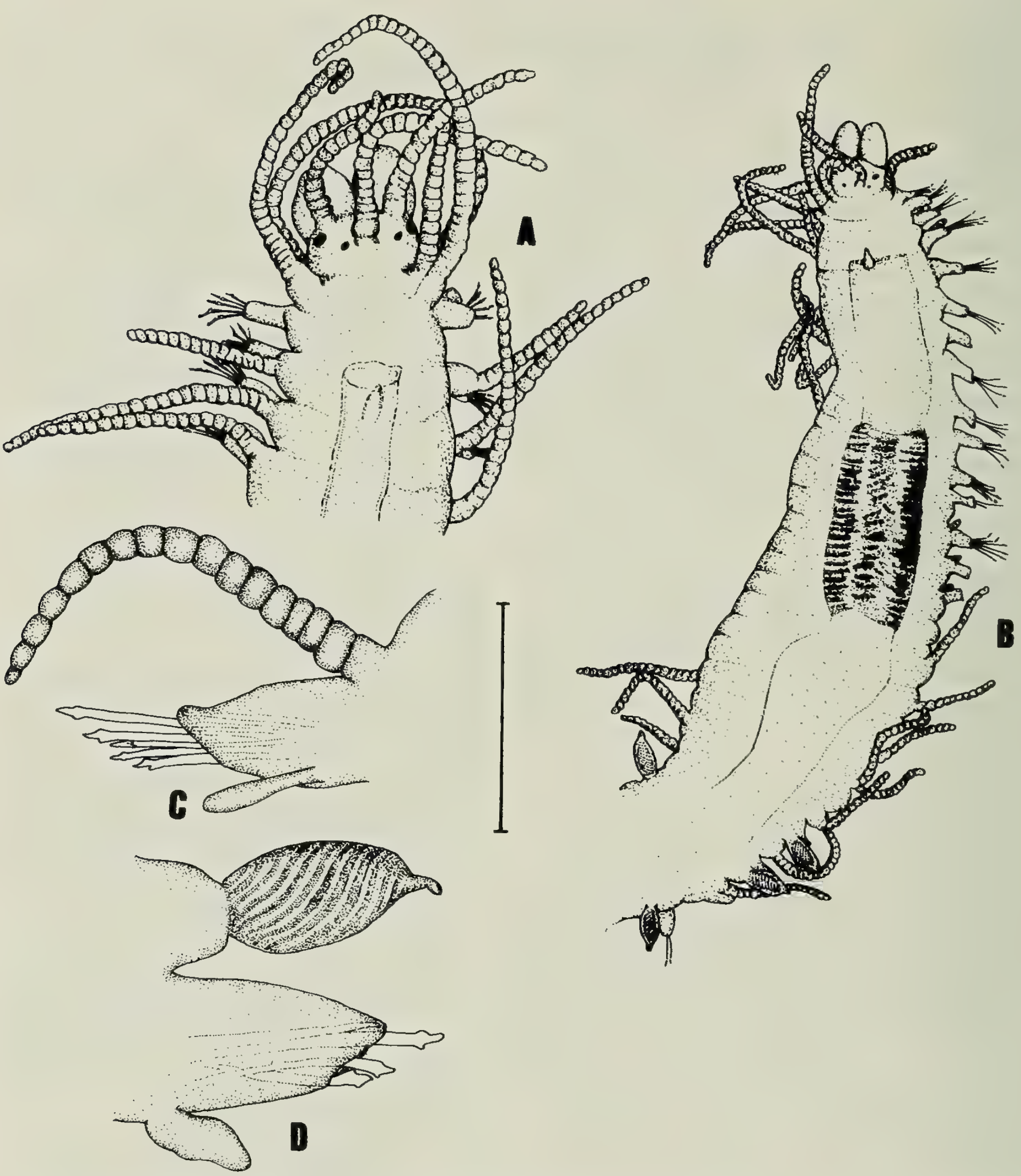

Fig. 1. *Parasphaerosyllis malimalii,* n. sp. A, holotype, anterior end, dorsal view; B, paratype, anterior end, dorsal view; C, midbody parapodium, with moniliform dorsal cirri; D, midbody parapodium, with bulbous dorsal cirri. Scale.—A, B: 225 μm. C, D: 55 μm.

species since all the specimens from Cuba recorded by San Martín (1991) from the same sample show a great degree of variation in the appearance of the first special cirri, from chaetiger 14 to 31.

Parasphaerosyllis setoensisis Imajima, 1966, a species with only one specimen recorded, could be synonymous with *P. indica.* The description and the drawings in Imajima (1966) seem to be made on the basis of a regenerating specimen. This can be concluded from the difference in width be-

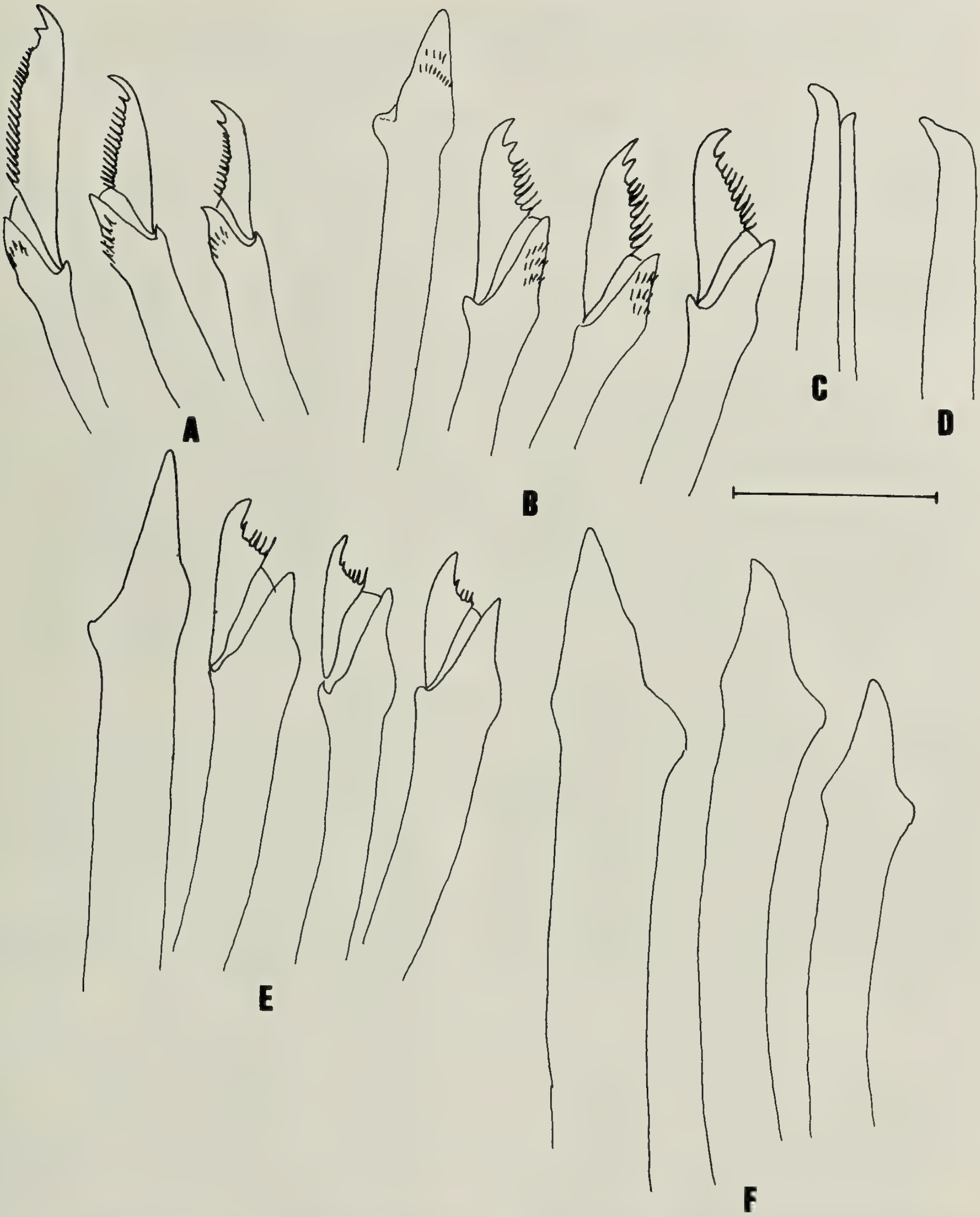

Fig. 2. *Parasphaerosyllis malimalii,* n. sp. Holotype. A, compound chaetae, anterior parapodia; B, compound and simple chaetae anterior-midbody; C, aciculae, anterior parapodia; D, acicula midbody parapodia; E, compound and simple chaetae, median-posterior region of the specimen; F, simple chaetae from posterior parapodia. Scale.—A–F: 20 μm.

tween the first four chaetigers and the remainder of the chaetigers and could explain the appearance of ovoid cirri in such an anterior position as chaetiger 4.

Parasphaerosyllis uschacovi, from Kurile islands and *P. ezoensis,* from Japan and Korea (Cheblovitsch 1959), differ from *P. malimalii* in having bulbous dorsal cirri with a terminal knob with an articulation. The only difference between these first two species is the origin of the median antenna, between the posterior eyes and anterior to them, respectively (Imajima & Hartman 1964, Lee & Rho 1994).

Etymology.—This species is dedicated to Narciso Bastida (Mali-Mali), a Kuna Indian, who was our guide during the expeditions to the Coiba National Park and who offered useful advice and friendship.

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New terebellids (Polychaeta: Terebellidae) living in colonies of a stony coral in the state of São Paulo, Brazil

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Abstract.—Two new species of Terebellidae, one of which also a new genus, were identified among the polychaetes associated with a stony coral in the state of São Paulo, southeastern Brazil. *Morgana bisetosa,* n. gen., n. sp. is an abranchiate Terebellinae with 18–25 pairs of notopodia, present from segment 4, all with two types of chaetae: bilimbate capillaries and serrated chaetae; neuropodia from segment 6, neurochaetal uncini, arranged initially in single rows, but in double rows from the sixth torus, continuing posteriorly. *Streblosoma oligobranchiatum,* n. sp. (subfamily Thelepodinae) has few branchial filaments inserted almost laterally on segments 2–4; 22–26 pairs of notopodia, with notochaetae as bilimbate capillaries and shorter spatulate chaetae with acuminate tips. A discussion of the relationships of these new species to closely related species is given.

The polychaete family Terebellidae Malmgren, 1867 comprises tubiculous and non-tubiculous species with numerous buccal tentacles, grooved, which are not retractile into the mouth. Although some species lack chaetae, notopodia generally possess capillary chaetae, with varied degrees of ornamentation, and neuropodia have uncini arranged in double rows for at least a few chaetigers; notopodia usually finish before the end of the body, and in several taxa the end of notopodia determines the transition between thorax and abdomen. Branchiae are completely absent in Polycirrinae and in some genera of Terebellinae, are present in Thelepodinae as unbranched filaments, and as large arborescent structures, or as single or branched filaments in most of the Terebellinae (Hutchings 1977, Hutchings & Murray 1984, Fauchald & Rouse 1997).

Terebellids are subdivided into three subfamilies: Terebellinae Linnaeus, 1767, Thelepodinae Hessle, 1917, and Polycirrinae Malmgren, 1866, depending on the presence or absence of branchiae, their structure, and on the arrangement of neuropodial uncini. A fourth family, Artacaminae Malmgren, 1866, has recently been synonymized with Terebellinae (McHugh 1995).

Brazilian terebellids have been studied by Nonato & Luna (1970), Rullier & Amoureux (1979), Nonato (1981), Blankensteyn (1988), and Morgado & Amaral (1989), among others. Prior to the present study, 28 species had been identified along the Brazilian coast, belonging to 15 genera.

Two new species of terebellids were identified among the material collected for a study of the polychaetes living in colonies of the stony coral *Mussismilia hispida* (Verrill, 1868) on islands off the coast of the state of São Paulo. These new species, herein described, are in a new genus of Terebellinae, and a new species in the Thelepodinae genus *Streblosoma* Sars, 1872.

Materials and Methods

Twelve colonies of *Mussismilia hispida* were collected at Laje de Santos (24°19′S, 46°11′W) and Ilha dos Alcatrazes (26°06′S, 45°42′W), on 17 Mar 1996 and 4 Dec 1996, respectively. Both locations are rocky shores with hemispherical colonies of *M. hispida* spread over the rocks, as well as large colonies of the cnidarians *Palythoa* and *Zoanthus,* and some algal tufts. Corals were fixed with formalin (4%) and subsequently de-calcified with formaline-formic acid solution; polychaetes were sorted from the resultant residue, washed, stored in 70% alcohol, and identified.

Observations and measurements were made using interference contrast optics (Nomarsky). Drawings were made with drawing tubes. Observations and micrographs by scanning electronic microscopy (SEM) were made at Laboratório de Microscopia Eletrônica do Instituto de Biociências da Universidade de São Paulo (IB-USP), except for Figs. 2B and 2C, which were taken at Laboratório de Microscopia Electrônica do Instituto de Biologia da Universidade Estadual de Campinas (IB-UNICAMP); these observations were made after critical point drying and coating with a 25 nm thickness of gold. Types are deposited at Museu de História Natural, Instituto de Biologia, Universidade Estadual de Campinas (MHN-BPO 80 and MHN-BPO 81) and at The Australian Museum (W 27132 and W 27133).

Family Terebellidae Malmgren, 1867

Subfamily Terebellinae Linnaeus, 1767

Terebellids with compact prostomium, notopodia present on a variable number of segments, bearing smooth or serrated chaetae, and neuropodia with avicular uncini, either short or long handled, or both types present; uncini pectinate in *Loimia* Malmgren, 1866. Uncini always arranged in double rows at least on some chaetigers. Branchiae, if present, as 1–3 pairs of arborescent or tufted filaments. Several genera with lateral lappets on anterior segments (Hutchings 1997).

According to Hutchings (1997), Hutchings & Glasby (1988, 1990), and Hutchings & Smith (1997), the most important characters for the identification of the terebellinean genera are the segment in which notopodia first appear, the number of pairs of notopodia, the structure of the blades of the notochaetae (serrated or smooth, when observed by light microscopy), the segment in which neuropodia first appear, the number of segments with uncini arranged in double rows, the dental formula of uncini, the presence and structure of branchiae, and the presence of lateral lappets on anterior segments.

Until recently, terebellineans have been called amphitritineans, but McHugh (1995), in a phyllogenetic analysis of the subfamily, pointed out that it contains *Terebella* Linnaeus, 1767, the type species of the family Terebellidae, and, therefore, the name Terebellinae Linnaeus, 1767 should have priority over Amphitritinae Malmgren, 1866.

McHugh (1995) studied 22 morphological characters for the phyllogenetic analysis of Terebellinae, using the type species of each known genus, except in cases in which the types were damaged. This study demonstrated that the group previously known as the subfamily Artacaminae should be considered as a clade within the Terebellinae, and the prominent peristomial "proboscis", as an autapomorphy for the genus *Artacama* Malmgren, 1866.

Genus *Morgana,* new genus

Type species.—*Morgana bisetosa,* new species.

Diagnosis.—Abranchiate terebellineans, without lateral lappets on anterior segments. Body slightly inflated on anterior chaetigers, with the 10 anteriormost chaetigers narrow and compacted; from posterior thorax onwards, segments larger, swollen, probably due to coelomic gametes; posteriormost segments much shorter, tapering to pygidium, with conspicuous external segmentation. Prostomium projecting ventrally, thickened and bilobed. Peristomium restricted to a narrow ring, present only ventrally. Segments 2 and 3 achaetous; ventral shields narrow, present on anterior segments.

Notopodia from segment 4, at least 18 pairs of notopodia present (some specimens have up to 25 pairs of notopodia), notopodial glandular patches absent. Two types of notochaetae alternating within the same fascicle in all notopodia: bilimbate capillaries, minutely denticulate (by highest magnification of light microscopy), and serrated chaetae, usually spiralled around the adjacent capillary chaetae.

Neuropodia from segment 6 (chaetiger 3), to the end of the body, as slightly elevated tori. Neurochaetal uncini avicular, short handled, with prow and dorsal button well developed; arranged in double rows, face to face position, interlocking from chaetiger 8 (segment 11) to posterior body, for more than half of body chaetigers.

Discussion.—*Morgana* is characterized by the large number of thoracic chaetigers, with two types of chaetae in all notopodia and by the neuropodia with uncini arranged in double rows on more than half of the body chaetigers. This genus is an abranchiate terebellinean, a group of poorly known species, some of which are known only from type material (Hutchings & Glasby 1988, McHugh 1995).

The general appearance of the body, the large numbers of notopodia and of neuropodia with uncini arranged in double rows make it very similar to *Baffinia* Wesenberg-Lund, 1950, according to the redescription by Fournier & Barrie (1984), but the latter differs from *Morgana* in that its anterior notopodia possess glandular patches and only bilimbate chaetae, posterior notopodia have only serrated chaetae, and neuropodia begin on segment 5 (Fournier & Barrie 1984, Hutchings & Glasby 1988, McHugh 1995), while *Morgana* lacks such glandular notopodial patches, has the two types of chaetae present in all notopodia, and neuropodia from segment 6.

The presence of neuropodia from segment 6 has been considered by McHugh (1995) as one of the autapomorphies of *Proclea* Saint-Joseph, 1894, but this genus differs from *Morgana* because it has 16 thoracic segments, compared to at least 18 in *Morgana,* lateral lappets on segments 2–4 that are absent in *Morgana,* and neuropodia with uncini arranged in double rows from segments 11–19, while in *Morgana* they are present in most of the body chaetigers (Fauvel 1927, Hutchings & Glasby 1988, Hutchings 1997).

Phyllogenetically, *Morgana* should be placed in a group in which the relationships between genera could not be resolved using the characters of McHugh (1995), and it appears as a polytomy in her analysis. This group is defined by the presence of notopodial glandular patches on anterior chaetigers, and includes *Amphitritides* Augener, 1922, *Baffinia, Pseudoproclea* Hutchings & Glasby, 1990, and *Terebella* Linnaeus, 1767; although *Morgana* lacks such glandular patches, its general body aspect, and the structure of the notochaetae and neurochaetae are very similar to these genera, and so it is possible that the loss of the white notopodial glandular tissues has occurred secondarily in the evolution of this genus.

Amphitritides and *Terebella* are branchiate and so they clearly differ from *Morgana*; *Pseudoproclea* shares some similarities with *Morgana,* such as the presence of uncini in double rows on a large number of neuropodia and the absence of branchiae, but the structure of notochaetae is different, and neuropodia first appear on segment 5, with uncini arranged in double rows from segment 10, while *Morgana* has neuropodia from segment 6 and double rows of uncini from segment 11.

Finally, another abranchiate genus similar to *Morgana* is *Phisidia* Saint-Joseph, 1894, which differs from the former by having only 14 pairs of notopodia, with notochaetae arranged in two tiers, and neuropodia from segment 5 (Hutchings & Glasby 1988, McHugh 1995). A more detailed comparison between the characteristics of *Baffinia, Morgana, Phisidia, Proclea,* and *Pseudoproclea* is provided in Table 1.

McHugh (1995) was unable to score the character "notopodial glandular patches" for *Phisidia* and *Proclea* and scored them as unknown. If it is later found that they are present, or that its loss has occured secondarily, they will probably belong to the same polytomic clade of *Amphitritides, Baffinia, Pseudoproclea,* and *Terebella.*

Etymology.—The generic name *Morgana* derives from Morgan Le Fay, from the Arthurian legend, as a homage to a friend of the first author, Maria Paula Martins Guerreiro, an admirer of King Arthur's novels.

Morgana bisetosa, new species
Figs. 1–2

Material examined.—20 specimens, all from Ilha dos Alcatrazes. Holotype and 4 paratypes, deposited at Museu de História Natural, Instituto de Biologia, Universidade Estadual de Campinas (holotype: MHN-BPO 80/0, paratypes: MHN-BPO 81/1–4); paratypes 5–7 deposited at The Australian Museum (W 27133). Holotype and three paratypes in 70% alcohol; four paratypes complete specimens, slide mounted; six specimens observed under SEM not preserved. Holotype and paratypes 1, 5–7 from Ilha dos Alcatrazes, paratypes 2–4 from Laje de Santos.

Description.—Small and slender animals, with 48–70 segments, preserved body usually curled, about 8–17 mm long, of which 2–3 mm are the buccal tentacles, and about 0.4–0.8 mm wide, at the level of chaetigers 4–6, the broadest part of the body (holotype with 62 segments, measuring 0.4 mm in width by 13.1 mm in length, of which the buccal tentacles extend through 2.2 mm). Preserved body whitish to pale orange, with long tentacles; tube mucous with debris. Body anteriorly inflated, with segments narrow, compacted and clearly distint, ventral shields present on anterior segments, as narrow glandular patches (Fig. 2C); posterior thorax with external segmentation indistinct; posterior segments well defined, tapering to pygidium. Prostomium ventrally projecting as two lobes (Figs. 1A, 2B, C). Peristomium restricted to a narrow ventral segment, with few lateral oceli (Figs. 1A, 2B, C). Lateral lappets and branchiae absent.

Notopodia from segment 4, as transversal ridges until chaetiger 11 (segment 13), progressively becoming short cylinders from chaetiger 7, continuing until chaetiger 18–25 (segment 21–28; holotype with 20 pairs of notopodia). Two types of notochaetae present in all chaetigers: bilimbate capillaries minutely denticulate by highest magnification of light microscope, and serrated chaetae, very thin and flat, usually curled (Figs. 1B, C, 2D, E).

Neurochaetae from chaetiger 3 (segment 6), as avicular uncini, short handled, with large main fang and 6–8 transverse rows of small teeth (Figs. 1D, 2B, F–H); prow and dorsal button developed, the last with a tuft of hairy bristles below the main fang, only visible by SEM (Fig. 2F–H); uncini similar throughout. Uncini arranged in double rows from chaetiger 8 (segment 11; except for one specimen which has them from segment 12), face to face, for more than half of the body (Figs. 2G, H; holotype with uncini in double rows for 46 chaetigers); 8–14 posterior chaetigers with uncini in single rows. Pygidium simple, rounded.

Variation.—The specimens examined differed considerably in length and probably most of the variation observed in other characters is size-dependent. Buccal tentacles regenerating in some specimens. The number of thoracic chaetigers varies from 18 to 25, but the structure of notochaetae does not change. Uncini arranged in double rows from segment 11 in most of the specimens, from segment 12 in one specimen; the first chaetiger with uncini in double rows has only a few uncini in the row with the main fangs directed posteriorly, and a complete row from the next chaetiger; there are 29 to 38 segments with uncini in double

Table 1.—Morphological features of *Baffinia* Wesenberg-Lund, 1950, *Phisidia* Saint-Joseph, 1894, *Morgana,* n. gen., *Proclea* Saint-Joseph, 1894, and *Pseudoproclea* Hutchings & Glasby, 1990 (sources: Fauvel 1927; Fournier & Barrie 1984; Hutchings & Glasby 1988, 1990; Hutchings 1997).

Characters	*Baffinia*	*Morgana*	*Phisidia*	*Proclea*	*Pseudoproclea*
Lateral lappets on segments 2–4	absent	absent	absent	present	absent
Notopodia (from segment 4 in all these genera)	until near posterior end	extending through 18–25 segments	extending through 14 segments	extending through 16 segments	extending through 16 segments
Notochaetae	in anterior chaetigers, bilimbate, with serrated tips; from chaetiger 10–12 geniculate, with strongly serrated tips	bilimbate capillaries (minutely denticulated by light microscopy) and serrated chaetae, in alternating positions in all notopodia	in two tiers: the longest tier with broad-bladed, narrowly limbed capillaries, with smooth tips; the shortest tier with the same chaetae together with alimbate serrated chaetae	in anterior chaetigers, short alimbate chaetae and long capillaries, with smooth limb; from chaetiger 9, short coarsely serrated chaetae together with long capillaries, with limb striated	in anterior chaetigers, long bilimbate smooth-tipped capillaries, and short serrated chaetae; from chaetiger 8, long capillaries distally serrated and with short limb, together with coarsely serrated chaetae
Neuropodia from segment	5	6	5	6	5
Neuropodia with uncini arranged in double rows	from segment 14 (in type species), for 20 or more chaetigers	from segment 11, for 29–38 chaetigers	from segment 11, for 10 chaetigers	from segment 11, for 9 chaetigers	from segment 10 until posterior end

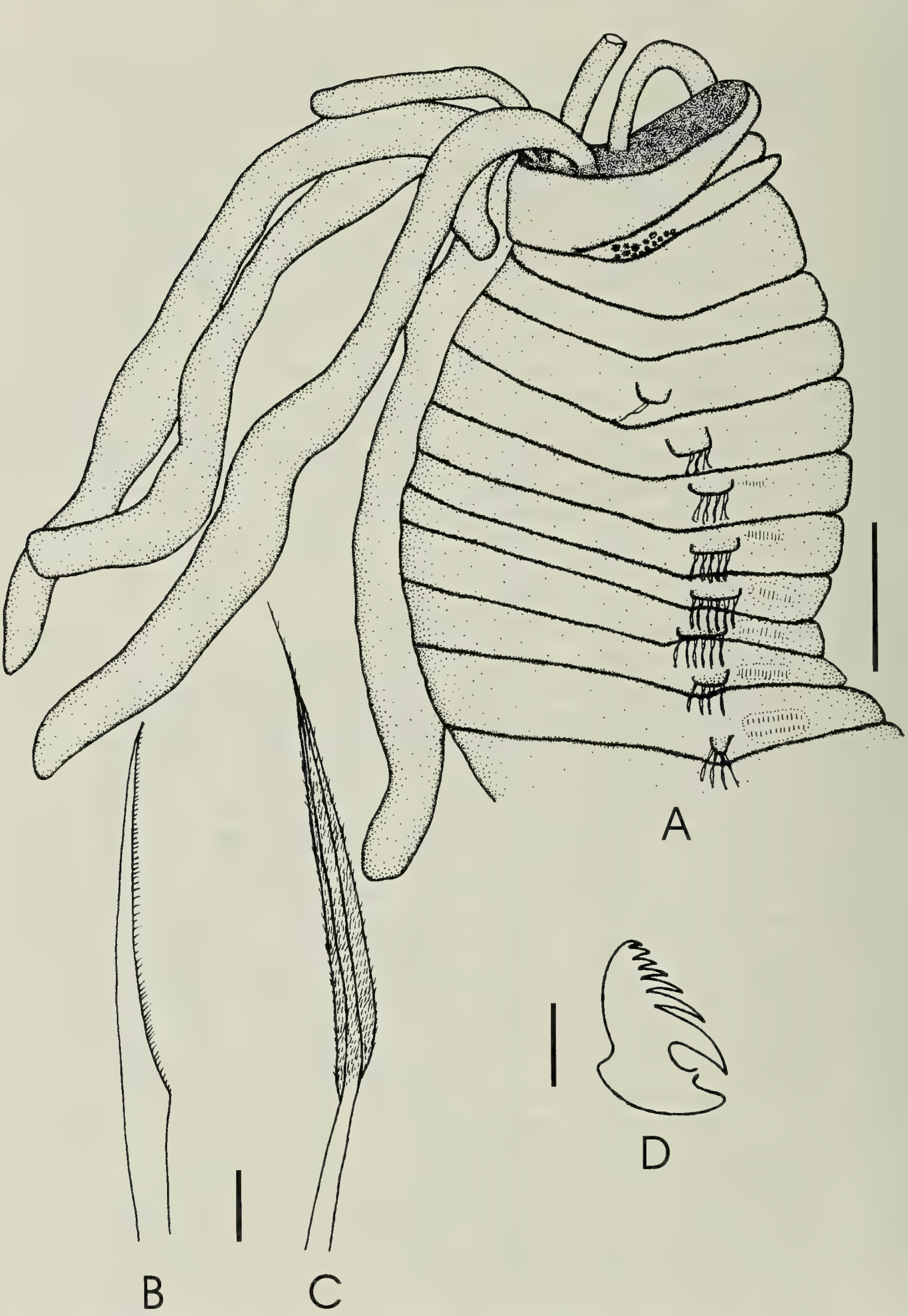

Fig. 1. *Morgana bisetosa* gen. n., sp. n. A—anterior end, lateral view; B—serrated notochaeta; C—bilimbate capillary notochaeta; D—uncinus, lateral view. Scale bars: A—200 μm; B, C—10 μm; D—5 μm.

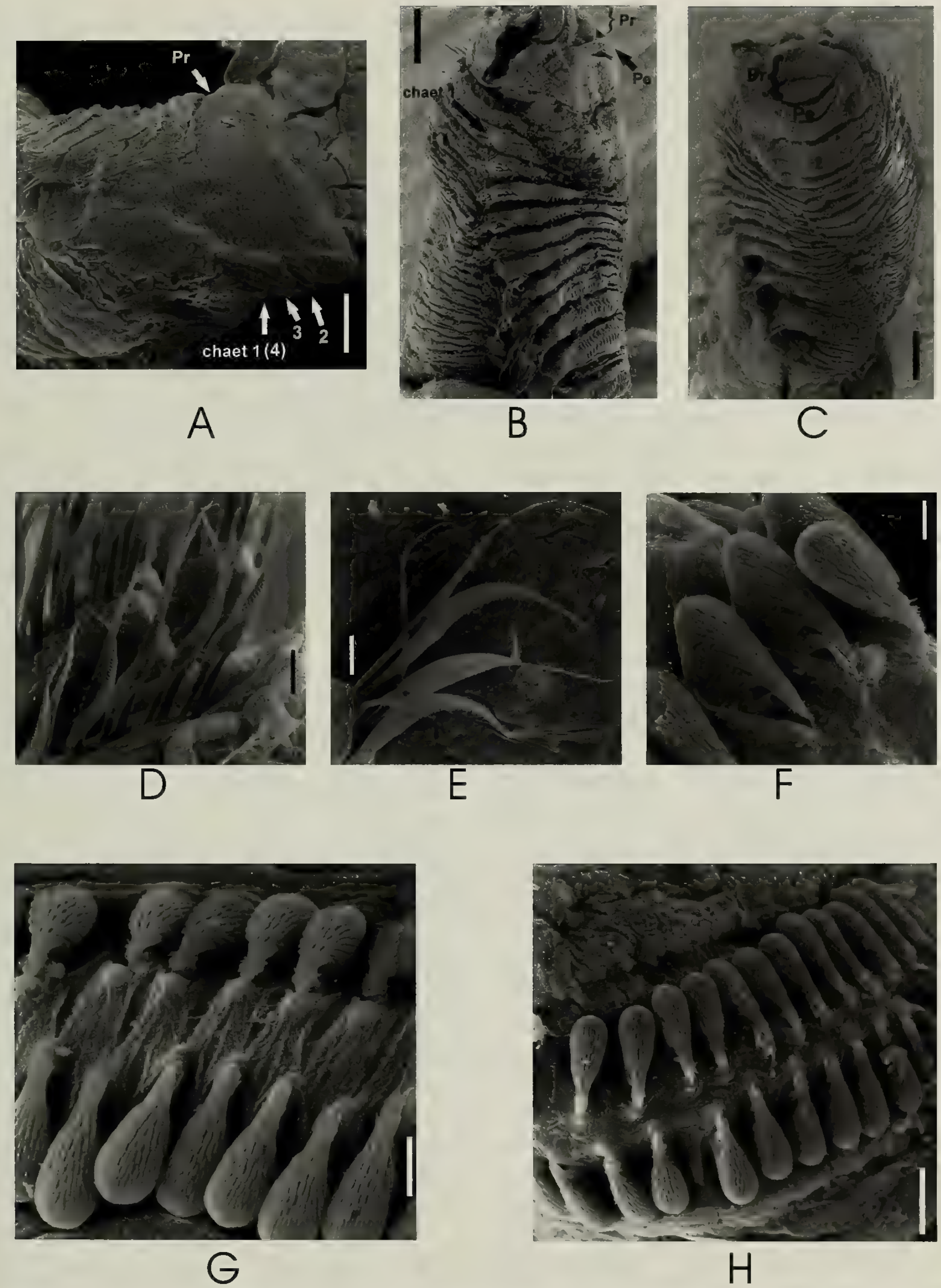

Fig. 2. *Morgana bisetosa* gen. n., sp. n. A—anterior end, dorsal view; B—same; lateral view; C—same, ventral view; D—notochaetae, chaetiger 3; E—notochaete, chaetiger. 23; F—antherior thoracic uncini; G—median thoracic uncini; H—abdominal uncini. Pe—peristomium; Pr—prostomium; chaet 1—chaetiger 1; the numbers reffer to the segments. Scale bars: A—150 μm; B, C—100 μm; D—20 μm; E—15 μm; F—5 μm; G—8 μm; H—15 μm.

rows; in spite of the variation in length, all specimens observed have uncini arranged in double rows on more than half of the body chaetigers.

Etymology.—The specific name *Morgana bisetosa* refers to the two types of notochaetae this species possesses in all notopodia; it derives from the latin prefix *bi-* = "two" + *setosus* = "bristly", from *seta* = "bristle".

Subfamily Thelepodinae Hessle, 1917

Telepodinaens are characterized by: branchiae, if present, as unbranched filaments, sometimes very numerous; neuropodia with uncini always in single rows, rows sometimes curved or forming a loop, but never in two rows as in Terebellinae; and body without clear distinction between thorax and abdomen (Hutchings & Glasby 1987). According to these authors, the most important features for the identification of genera and species are the morphology and the arrangement of branchiae, the segments on which notopodia and neuropodia first appear, and the shape and dental formulae of neuropodial uncini.

Genus *Streblosoma* Sars, 1872

Streblosoma.—Hutchings & Murray, 1984:93–95; Hutchings & Glasby, 1987: 222–226.

Type species.—*Grymaea bairdi* Malmgren, 1866, designated by Sars (1872).

Diagnosis.—Species with compact tentacular lobe, with notopodia from segment 2 and neuropodia from segment 5; notochaetae marginally smooth or minutely denticulate (by highest magnification of light microscope), for a variable number of segments; neuropodia with uncini arranged in single rows throughout. Branchiae usually present, as pairs of unbranched filaments on segments 2–4, very numerous in most species (Hutchings & Glasby 1987, Hutchings 1997).

Streblosoma oligobranchiatum, new species
Figs. 3–4

Material examined.—Nine specimens, all from Ilha dos Alcatrazes. Holotype and three paratypes deposited at Museu de História Natural, Instituto de Biologia, Universidade Estadual de Campinas (holotype: MHN-BPO 81/0, paratypes: MHN-BPO 81/1–3), two paratypes deposited at The Australian Museum (W 27132). Holotype and one paratype in 70% alcohol, other paratypes slide mounted; three specimens observed under SEM not preserved.

Description.—Small species, with 32–42 segments, measuring about 7.5–9.5 mm in length, of which 2–3 mm of buccal tentacles, and about 0.75–0.9 mm in width (holotype with 40 segments, measuring 9.5 by 0.8 mm). Preserved animal whitish to pale orange; anteriorly inflated, with segments clearly distinct; posterior thoracic and most of abdominal chaetigers swollen, with external segmentation indistinct, due to presence of coelomic gametes; posteriormost segments clearly defined, tapering to pygidium. Buccal tentacles with dark pigmented spots, spread along their length on two very narrow dark lines (Fig. 3A). Peristomium with numerous eyespots, irregularly placed in 1–2 rows, more concentrated laterally (Fig. 3A). Peristomium separated from segment 2 by a thickly ciliated sulcus dorsally (Fig. 4E). Branchiae as single filaments, inserted asymmetrically above notopodia in segments 2–4; left side: two filaments on segment 2 and one on segment 3; right side: one filament on segments 2–4; lateralmost filament on left segment 1 about half the length of the others (Figs. 3A, 4A–C).

Notopodia from segment 2, continuing until segment 23–27 (until segment 23 in holotype), as short elongate podia. Notochaetae as bilimbate capillaries, with long, gently tapering tips, on anterior chaetigers (Fig. 4F); two types of notochaetae from segment 5 (chaetiger 4), arranged in two fascicles: superior chaetae as those on pre-

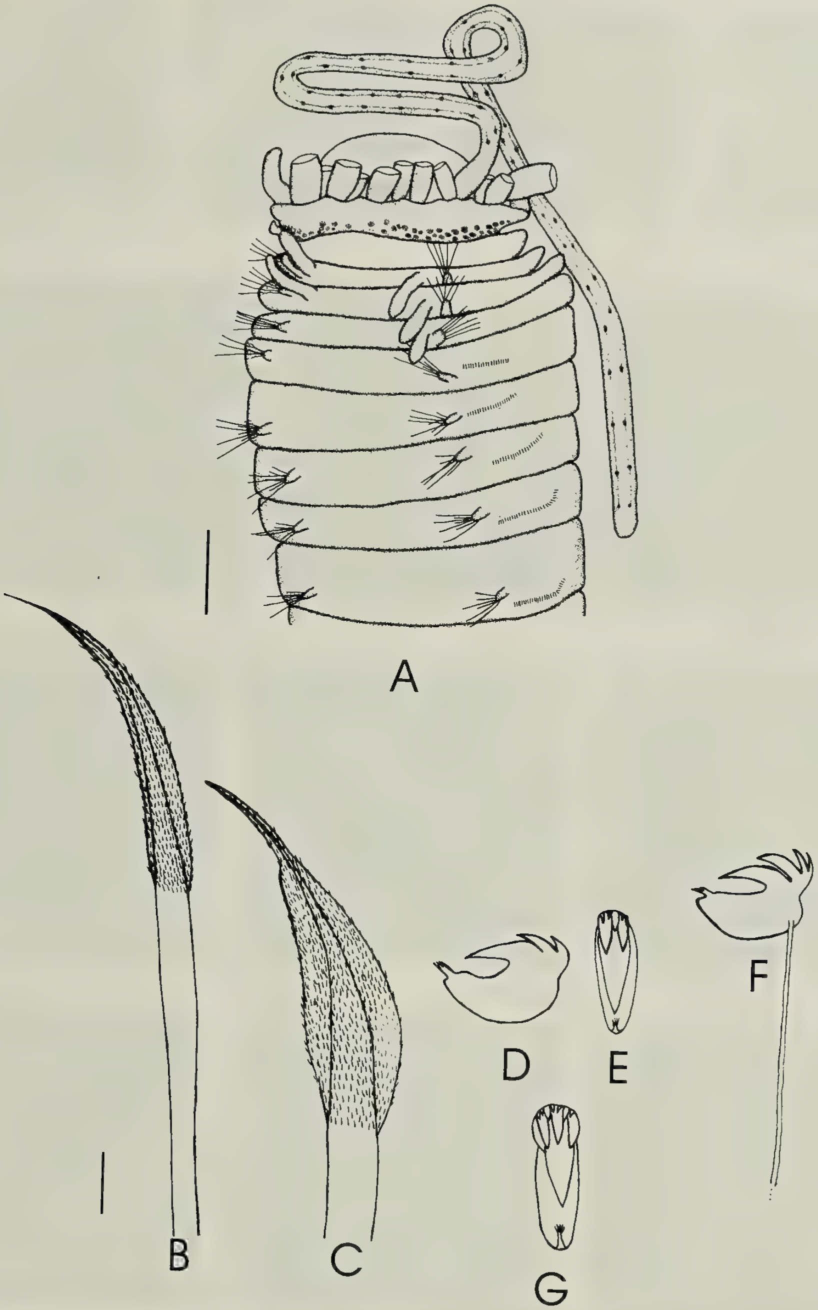

Fig. 3. *Streblosoma oligobranchiata* sp. n. A—anterior end, dorsolateral view; B—superior thoracic notochaeta; C—inferior thoracic notochaeta; D—uncinus, chaetiger 5, lateral view; E—same, frontal view; F—abdominal uncinus; G—uncinus, chaetiger 20. Scale bars: A—200 μm; B–G—10 μm.

vious chaetigers, inferior notochaetae also bilimbate with acuminate tip, but much shorter and with broader limb, nearly spatulate (Figs. 3B, C, 4 G–I); both types minutely denticulate by highest magnification of light microscopy.

Neuropodia from segment 5 (chaetiger 4), until posteriormost segments; in anterior

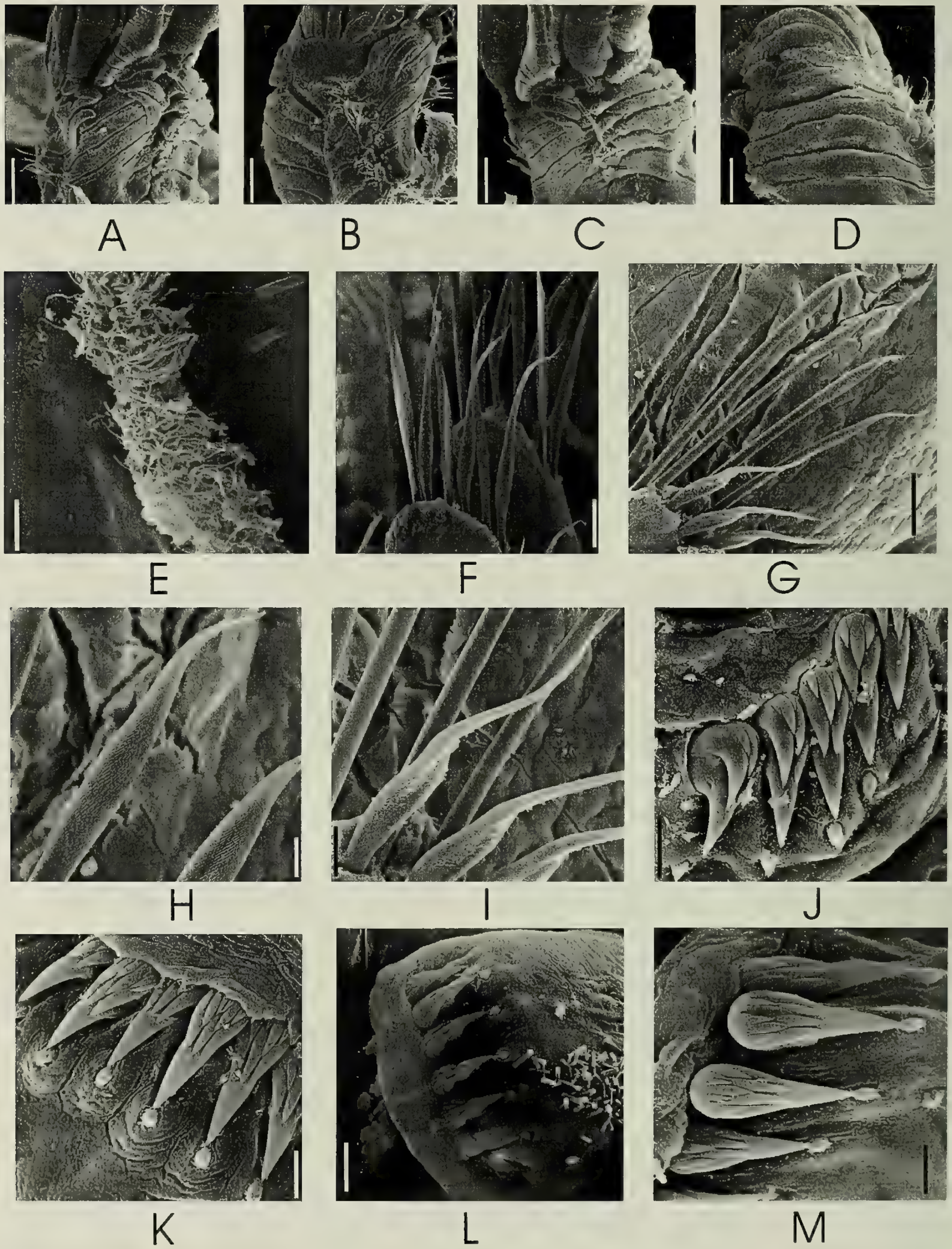

Fig. 4. *Streblosoma oligobranchiata* sp. n. A—anterior end, dorsal view; B—same, left lateral view; C—same, right lateral view; D—same, ventral view; E—dorsal separation between peristomium and segment 2; F—notochaetae, chaetiger 3; G—notochaetae, chaetiger 7; H—detail, superior notochaetae; I—detail, inferior notochaetae; J—uncinus, chaetiger 5; K—uncini, chaetiger 15; L—abdominal neuropodial papillae; M—abdominal uncini. Scale bars: A–D—200 μm; E—10 μm; F—30 μm; G—40 μm; H—10 μm; I—15 μm; J, K—10 μm; L—15 μm; M—8 μm.

chaetigers, as glandular tori, only slightly elevated; from posterior thorax, forming more erected pinnules (Fig. 4L). Neurochaetae as avicular uncini, always arranged in single rows; dorsal button developed, as a circular plate of short bristles in front of main fang (Figs. 3D–G, 4J–M); prow short; number of rows of secondary teeth increasing progressively towards pygidium; dental formula: anterior chaetigers: MF + 2 + 5 (last row with unequal teeth; Figs. 3D–E, 4 J); posterior thoracic uncini: MF + 3 + 7 + 2 (last two rows with unequal teeth; Figs. 3F, 4 K); abdominal uncini: MF + 4 + 9 + 2 (last two rows with unequal teeth; Figs. 3G, 4L, M). From posterior thorax, uncini with long and thin handles, along neuropodial pinnules (Fig. 3F).

Variation.—The number of segments with notopodia varies from 22–26; uncini may be present until last chaetiger before pygidium, or may be lacking on 1–6 posteriormost segments.

Discussion.—The genus *Streblosoma* Sars, 1872 is characterized by: branchiae, if present, as single unbranched filaments, inserted laterally on segments 2–4; notochaetae from segment 2; neurochaetae from segment 5.

Hutchings & Glasby (1987) pointed out that the structure of the tips of notochaetae, if marginally smooth or serrated, should not be regarded as an important character, as by SEM all notochaetae appear marginally serrated. We can add to the authors' statement that, as far as we have seen after examining chaetae of several polychaete families by SEM, limbate chaetae are always marginally serrated, and our capacity to see the denticles by light microscopy depends on the power of the apparatus and on the size of the denticles; in the case of *S. oligobranchiatum,* when notochaetae are magnified about 1000× by light microscopy, the limbs appear quadriculate, due to the denticles.

This genus includes many species, but, except for *S. minutum* Hutchings & Glasby, 1987, all the branchiate species have many more branchial filaments than *S. oligobranchiatum* (Kritzler 1971, Hutchings & Glasby 1987, Hutchings 1997). Even though all material examined was small, they were mature individuals, as several had abundant coelomic gametes. *Streblosoma oligobranchiatum* n. sp. is very close to *S. minutum,* differing from it by the arrangement of branchial filaments, the presence of bilimbate notochaetae, the dental formulae, and by having uncini with long and thin handles, from posterior thorax.

Etymology.—The specific name *Streblosoma oligobranchiatum* refers to the small number of branchial filaments present in this species; it derives from the prefix *oligo* = "few" + branchiae.

Acknowledgments

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First record for springsnails (Mollusca: Hydrobiidae: *Pyrgulopsis*) from the northern Rocky Mountains

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Abstract. *Pyrgulopsis bedfordensis,* new species, from southwest Montana, differs from other congeners having an enlarged penial lobe by its unique pattern of penial ornament, consisting of a transverse terminal gland and a raised gland on the inner edge of the lobe. This species is locally endemic in the headwater region of the Missouri River basin. Origin of this novelty is attributed to vicariance associated with Neogene migration of the continental divide.

Pyrgulopsis is the largest genus of inland aquatic mollusks in North America, with 123 described species in common usage. Although phylogenetic structure within *Pyrgulopsis* has not been well established, the genus is divisible into non-overlapping eastern and western subunits which are well differentiated morphologically (Hershler 1994). The large western fauna is restricted to the region extending from the southern Great Plains to the Pacific Coast, and from the Columbia Plateau to the Basin and Range of northern Mexico. The much smaller eastern fauna ranges from the Central Lowlands to the Atlantic Coast.

Snails conforming morphologically to the western group have been collected east of the continental divide only in the Pecos-Rio Grande drainage of the southern Great Plains (e.g., Taylor 1987). One of us (DLG), however, recently discovered a population of *Pyrgulopsis* living in a thermal spring in the upper Missouri River drainage just east of the continental divide which also conforms to the western group. Herein we describe this new species, which represents the first record of *Pyrgulopsis* in the Northern Rocky Mountains.

Specimens are deposited in the Florida Museum of Natural History (UF), and National Museum of Natural History, Smithsonian Institution (USNM). Terminology and methods of morphological analysis are of Hershler (1994, 1998) and Hershler & Ponder (1998). Measurements of shells of the holotype and a series of paratypes are in Table 1.

Pyrgulopsis bedfordensis, new species

Type material.—The holotype (UF 271731) is a dried shell (3.37 mm shell length, Fig. 1) from Warm Springs Creek (also known as Bedford Hot Spring), Townsend Valley, Broadwater County, Montana, T. 7N, R. 1E, sections 14, 23, elevation about 1,200 m (46.3537°N, 111.5641°W); collected by D. L. Gustafson and M. M. Hooten, 26 Jan 1991. The location of the type locality is shown in Fig. 2. Paratypes (USNM 854975, USNM 854976, USNM 892153, USNM 892154, UF 184057, UF 184058, UF 193049, UF 193050) consist of several series of dry shells and alcohol-preserved specimens collected from the type locality at the same time. Two additional series (USNM 892151, USNM 892152), which are not designated as paratypes, were collected at the type locality by D. L. Gustafson during 1995 and 1999.

Table 1.—Morphometric and meristic shell features of holotype and ranges of values for 10 paratypes of *Pyrgulopsis bedfordensis,* new species. Morphometric parameters are expressed in mm.

	Holotype	Paratypes
Shell height	3.37	2.94–3.69
Shell width	2.10	1.99–2.30
Body whorl height	2.42	2.22–2.70
Body whorl width	1.91	1.71–2.10
Aperture height	1.39	1.31–1.59
Aperture width	1.35	1.27–1.47
Shell width/shell height	0.62	0.58–0.70
Number of whorls	>5.0	>4.0–5.0

Diagnosis.—A medium-sized species of *Pyrgulopsis* with trochiform to ovate-conic shell having an eroded apex and well-developed columellar shelf. Penis large; filament medium length, lobe long. Penial ornament of a curved gland along the distal edge of the lobe (terminal gland) and a smaller unit (Dg3) borne on the distal edge of a well-developed swelling on the inner edge of the lobe.

Description.—Shell (Fig. 3A–E) clear-white, trochiform to ovate-conic, width/height, 58–70%; height (larger adults), about 2.9–3.7 mm; width, 1.9–2.3 mm; whorls about 5.0. Apex usually eroded in adult specimens. Protoconch valvatiform, whorls about 1.25, diameter about 260 μm, earliest 0.5 whorl slightly wrinkled, surface otherwise smooth (Fig. 3F, G). Teleoconch whorls of low to medium convexity, narrowly shouldered. Aperture ovate to pyriform, broadly adnate to slightly disjunct. Inner lip completed, slightly thickened, columellar lip strongly reflected in most adult specimens. Outer lip usually thin, orthocline or weakly prosocline, sometimes weakly sinuate. Umbilicus narrowly perforate, often obscured by columellar lip. Periostracum brown or tan. Shells of males forming distinctly smaller size class (about 2.5–2.6 mm) than those of females.

Operculum (Fig. 3H–K) medium thickness, light amber with darker red hue in nuclear region, ovate, paucispiral, nucleus ec-

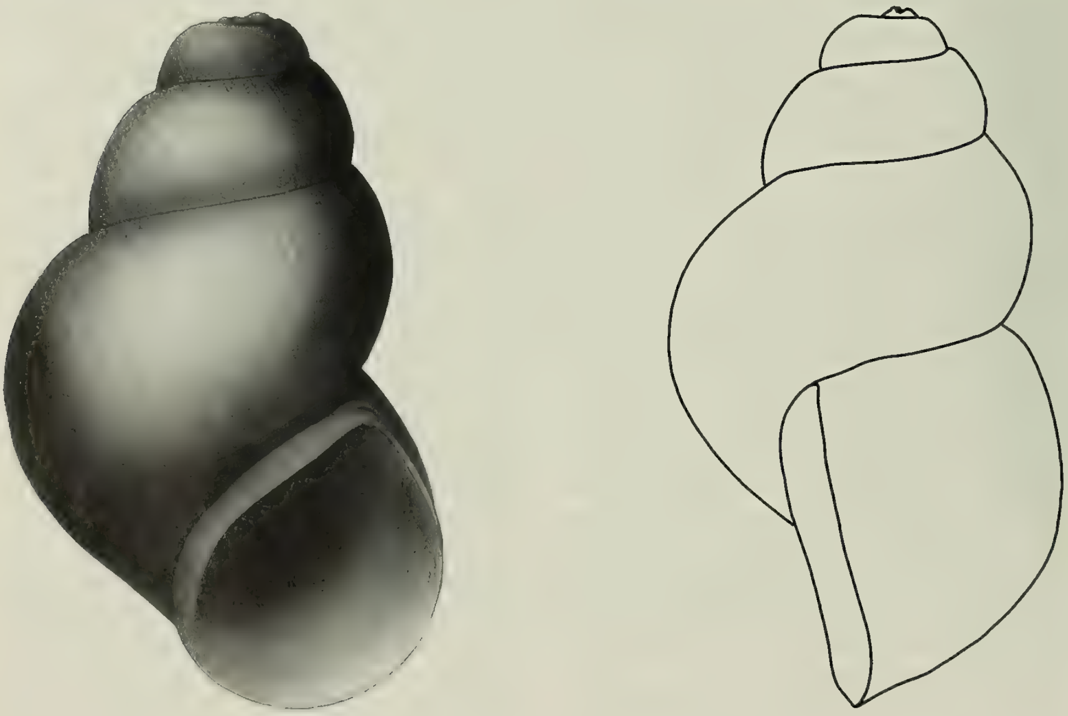

Fig 1. Holotype of *P. bedfordensis,* new species, from Warm Springs Creek, Broadwater County, Montana.

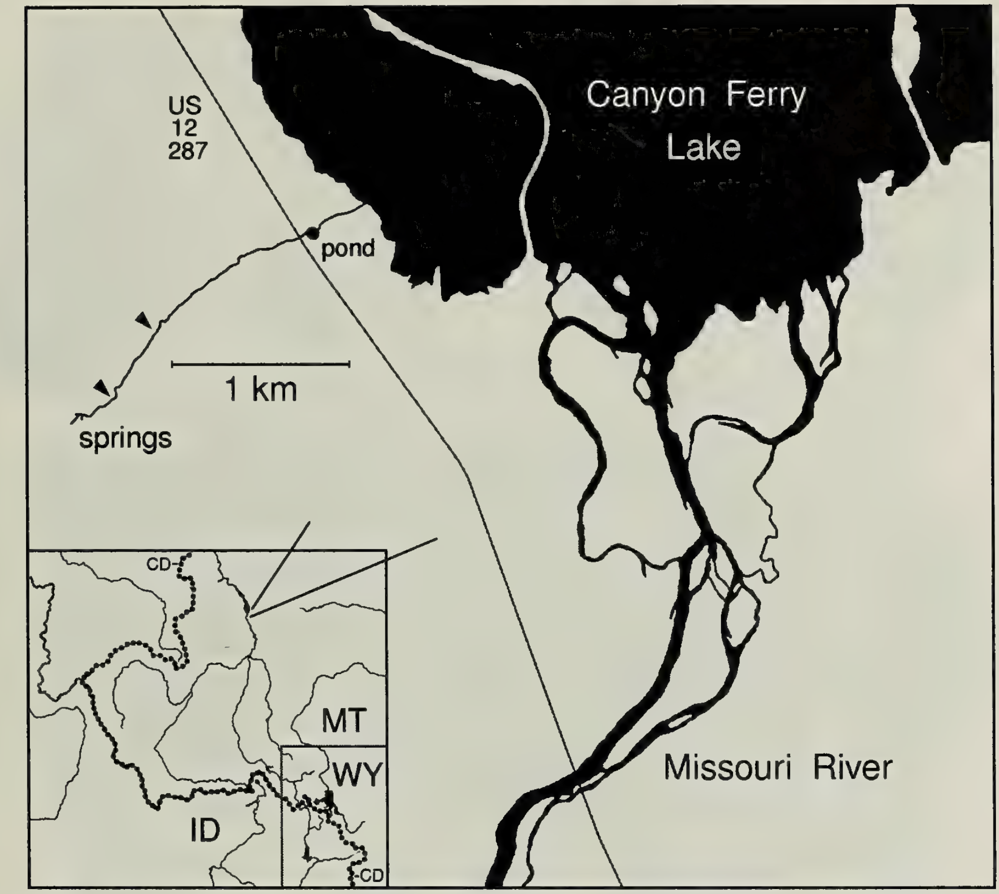

Fig. 2. Map showing location of Warm Springs Creek. Sampling sites are indicated by thick arrows. cd, continental divide.

centric. Edges of whorls without frills on outer surface (Fig. 3H); outer margin without rim. Attachment scar margin thickened between inner edge and nucleus (Fig. 3I–K).

Buccal mass large; radular sac extending behind buccal mass as small loop. Radula about 885 × 142 μm, with about 57 rows of teeth. Central teeth (Fig. 4A–C) trapezoidal, 33–39 μm wide, dorsal edge medium indented; lateral cusps 3–4; central cusp medium width, narrowly pointed, considerably longer than lateral cusps; basal cusp 1, large, arising from intersection of tooth face and lateral margin. Basal tongue of central teeth broad V-shaped or U-shaped, basal sockets medium depth. Lateral teeth (Fig. 4C, D) with 2–3 cusps on inner side and 2–4 cusps on outer side, central cusp large, spoon-shaped; neck weakly flexed; outer wing 135–145% width of tooth face. Inner marginal teeth (Fig. 4D–F) with 23–31 cusps, often bearing noticeably enlarged cusp proximally (Fig. 4F). Outer marginal teeth (Fig. 4D–F) with 34–38 cusps. Style sac about as long as remainder of stomach; stomach with very small posterior caecum.

Cephalic tentacles grey, dark brown, or black, pigmented lighter around eyespots. Snout usually dark brown (rarely lighter), distal lips often lightly pigmented. Foot medium to dark brown. Opercular lobe brown or black all around, central area pale. Neck with light to medium cover of grey gran-

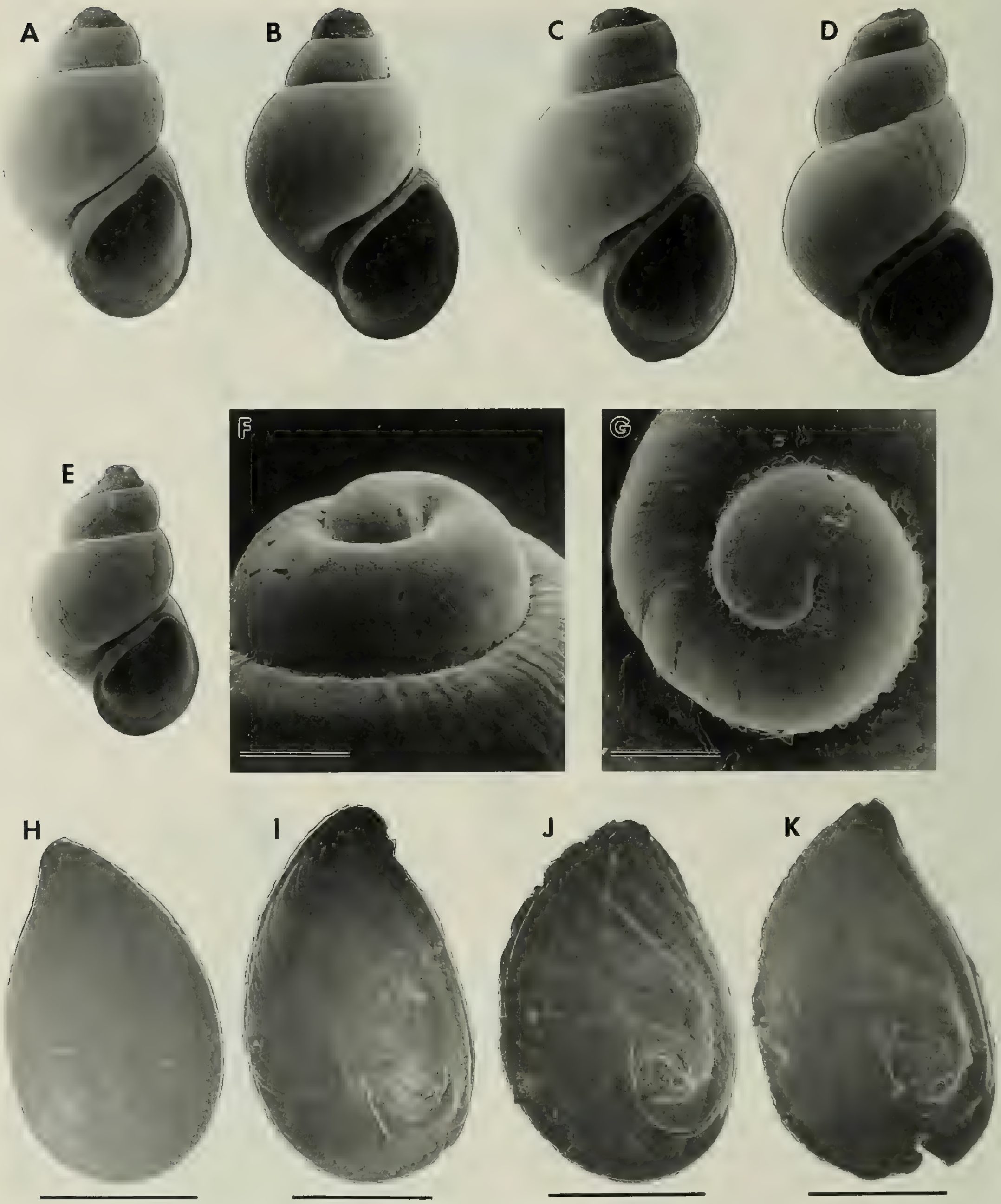

Fig. 3. Scanning electron micrographs of shell and opercula of *P. bedfordensis*, USNM 854976. A–E. Variation in shell shape (shell height, 2.86, 3.10, 3.26, 3.69, 2.66 mm, respectively). F. Shell apex, viewed from side (bar = 100 μm). G. Shell apex, viewed from above (bar = 100 μm). H. Outer surface of operculum (bar = 500 μm). I–K. Inner surface of operculum (bars = 500 μm).

Fig. 4. Scanning electron micrographs of radula of *P. bedfordensis,* USNM 854976. A, B. Central radular teeth (bars = 17.6 μm). C. Section of ribbon showing central and lateral radular teeth (bar = 38 μm). D, E. Sections of ribbons showing lateral and marginal radular teeth (bars = 43, 30 μm, respectively). F. Marginal radular teeth (bar = 27 μm).

ules. Pallial roof, visceral coil black on dorsal surfaces, lighter ventrally. Penial filament having dark melanin core.

Ctenidium with about 18 medium sized filaments (not extending to rectum); filaments with pleats, broadly triangular, apices centrally positioned; ctenidium abutting pericardium posteriorly. Osphradium small, intermediate width, centrally positioned. Renal gland slightly oblique; kidney with small pallial bulge and simple opening. Rectum straight, slightly overlapping capsule gland, abutting prostate gland.

Ovary a single yellow mass, weakly lobate dorsally, 0.5–0.75 whorl, filling slightly less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Albumen gland clear-white, having very short pallial component (Fig. 5A). Capsule gland yellow, about as long as but narrower than capsule gland, divided into two sub-equal tissue sections (anterior section smaller and lighter), ovate in section, right lobe thicker than left; rectal furrow absent. Ventral channel moderately overlapping capsule gland; longitudinal fold well-developed. Genital aperture a terminal slit positioned slightly posterior to anus. Coiled oviduct of a single anterior-oblique loop; gonopericardial duct not evident in dissection. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix small relative to albumen gland, narrow to ovate, longitudinal, extending slightly posterior to albumen gland, sometimes slightly overlapped by albumen gland dosrally (Fig. 5B). Bursal duct originating from anterior edge at mid-line, considerably longer than bursa copulatrix, medium to wide, usually broadening distally, surficial or slightly embedded in albumen gland proximally. Seminal receptacle small relative to bursa copulatrix, narrow or ovate, positioned near ventral edge of albumen gland slightly to well anterior to bursa copulatrix, duct slightly shorter than body (Fig. 5C).

Testis 1.25 whorls, composed of numerous compound lobes, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers anteriorly. Seminal vesicle a small mass of tight coils opening from and positioned alongside the anterior portion of testis. Prostate gland small, sub-globular, pallial portion very short or absent, ovate in section (Fig. 5D). Pallial vas deferens curving on columellar muscle. Penis large relative to head, base rectangular, smooth; filament about 67% length of base, tapering, distally pointed, narrow, longitudinal or oblique (Fig. 5E). Lobe about as long and wide as base, rectangular, longitudinal. Terminal gland transversely positioned along edge of lobe, narrow, curved, rarely split into two units. Dg3 borne on prominent stalk arising from inner edge of lobe, stalk often clearly demarcated from lobe; glandular unit shorter than terminal gland, slightly curved. Penial duct narrow, curved, coursing from close to inner edge proximally to near medial position distally.

Etymology.—An adjectival geographical name referring to location of the type locality near the historical site of Bedford, Montana. Gender female. We propose the vernacular name, "Bedford springsnail," for this species, also in reference to its single known locality.

Comparisons.—This novelty conforms morphologically to the western fauna of congeners, which share weak protoconch microstructure, surficial position of the female bursal duct relative to the albumen gland, and connection of the bursal duct and oviduct at the posterior pallial wall (Hershler 1994). *Pyrgulopsis bedfordensis* has an unique pattern of penial ornament, which consists of a transverse terminal gland and well-developed gland on the inner edge of the lobe (Dg3). Although not closely similar to any other member of the genus, this species uniquely shares with several other congeners living in western thermal springs an elongate-rectangular penial lobe that is much larger than the filament (e.g., *P. isolata, P. nana*; Hershler & Sada 1987, figs. 32, 38).

Habitat.—The type locality (Fig. 6A, B)

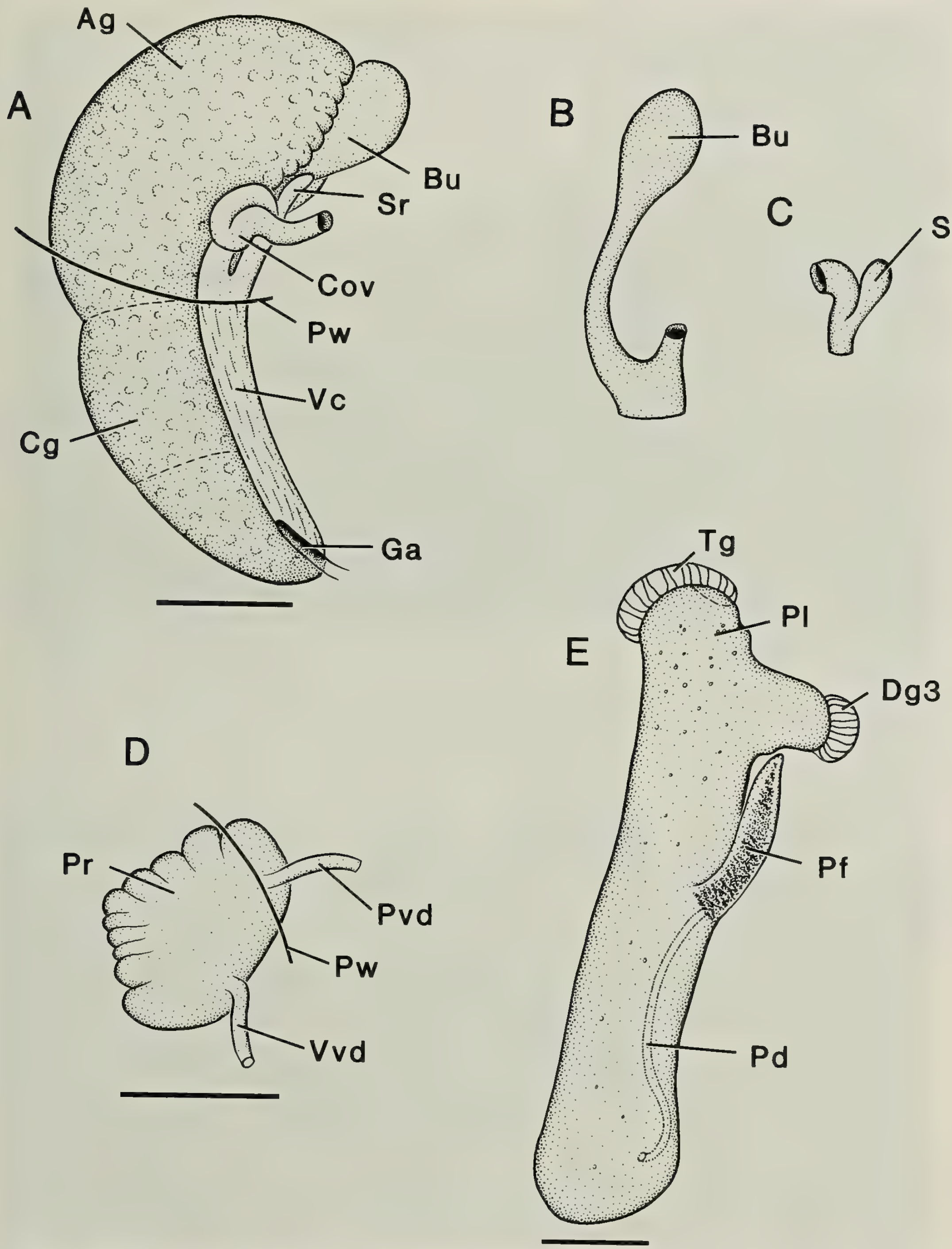

Fig. 5. Genitalia of *P. bedfordensis,* USNM 892152. A. Left side of female glandular oviduct and associated structures. B. Bursa copulatrix and its duct. Scale as in A. C. Seminal receptacle and its duct. Scale as in A. D. Left side of prostate gland, showing insertion of vas deferens. E. Penis. Bars—250 μm. Ag, albumen gland; Bu, bursa copulatrix; Cg, capsule gland; Cov, coiled oviduct; Dg3, gland along inner edge of penial lobe; Ga, genital aperture; Pd, penial duct; Pf, penial filament; Pl, penial lobe; Pvd, pallial vas deferens; Pw, posterior wall of pallial cavity; Sr, seminal receptacle; Vc, ventral channel of capsule gland; Tg, terminal gland; Vvd, visceral vas deferens.

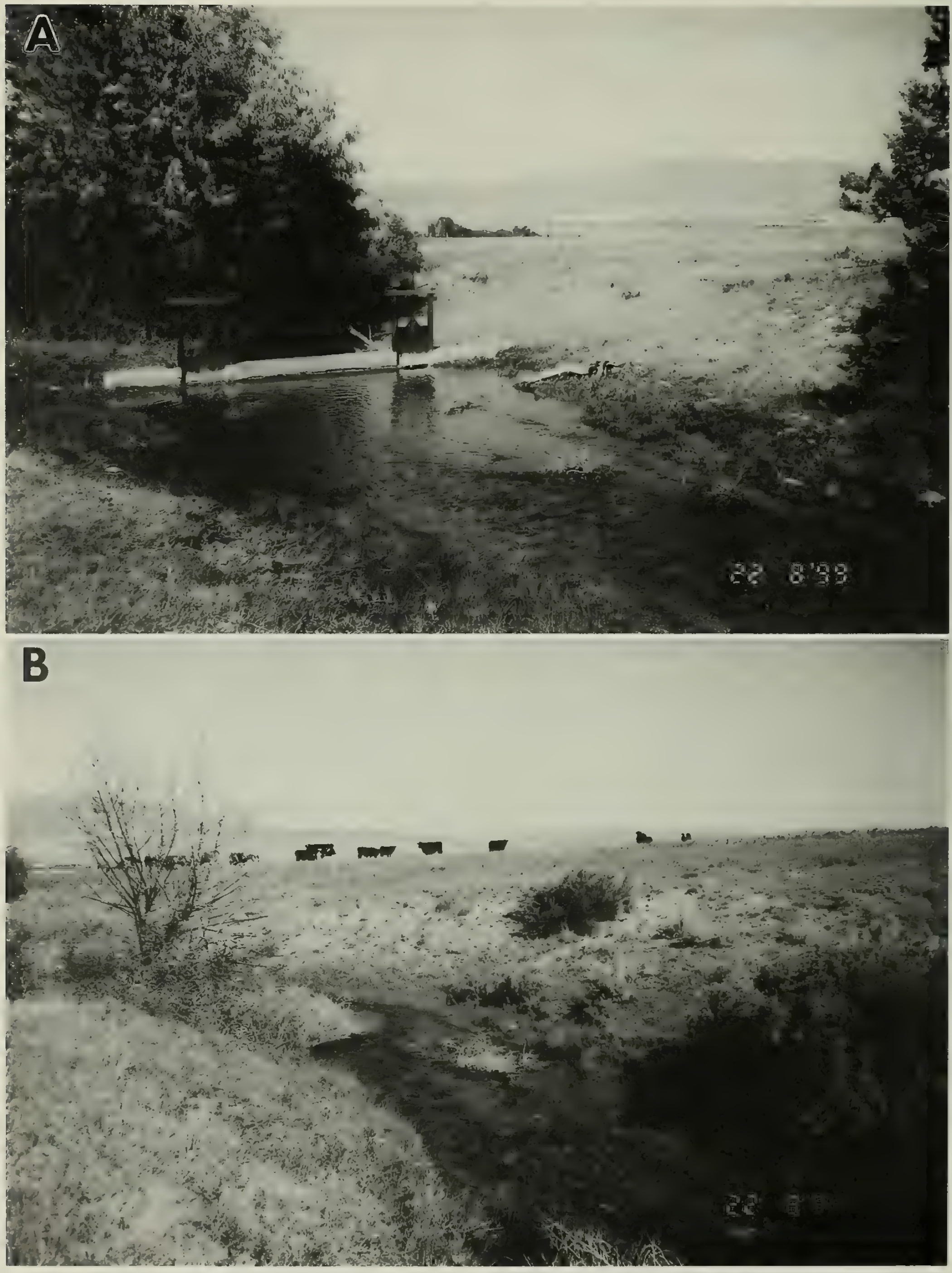

Fig. 6. Type locality of *P. bedfordensis.* A. Lower end of sampling area, with diversions structure used to irrigate nearby fields. Riparian area badly trampled by livestock. B. Typical reach of spring run (above diversion structure). Photographs, 22 August 1999.

is a large thermal spring which flows for about 2.0 km (dropping 56 m in elevation) before entering the western pond at the upper end of Canyon Ferry Reservoir just east of Bedford. (There are three more ponds to the east.) This creek drained directly to the Missouri River prior to construction of the original Canyon Ferry Dam in 1901. The water temperature was 21°C near the source on 26 January 1991 (when the air temperature was well below zero) and 23°C on 22 August 1999. (Mean annual air temperature at nearby Townsend is 6.74°C.) Sonderegger et al. (1981) indicated a temperature of 23.6°C for this spring, along with pH, 7.2; specific conductivity, 467 μmho/cm; and 350 mg/L TDS.

Pyrgulopsis bedfordensis was abundant throughout the sampled section of spring run and snail shells made up a large component of substrate in many areas. Snails were collected by sweeping a fine aerial insect net underneath riparian vegetation which lined the stream margins. (Snails released from the vegetation with the slightest disturbance.) Snails were also found on all other available substrates; mud, rocks, wood, mosses, aquatic and submerged vascular plants, and filamentous algae. This new species was collected along with another gastropod snail (*Fossaria* sp.) and 31 other invertebrates, most of which have broad geographic distributions. The other invertebrates include various species commonly found in thermal waters; e.g., *Libellula saturata* Uhler and *Argia vivida* Hagen (Odonata), *Ambrysus mormon* Montandon (Hemiptera), *Chimarra utahensis* Ross and *Protoptila erotica* (Trichoptera), and *Microcylloepus* sp. (Coleoptera). Three species of fishes were collected—*Rhinichthys cataractae* (Valenciennes), *Gambusia affinis* (Baird and Girard), and *Xiphophorus variatus* (Meek)—the latter two of which are introduced in Montana.

Distribution.—This species is thus far known only from the type locality. Local endemism is likely given that over the past 18 years one of us (DLG) has extensively sampled aquatic habitats throughout Montana and adjacent states (Fig. 7) without finding this snail elsewhere. This sampling included 30 of the Montana warm springs listed by Sonderreger et al. (1981), including all five of the springs in close proximity to Warm Springs Creek.

Discussion

Origin of *Pyrgulopsis bedfordensis* is conjectural given the poorly resolved phylogenetic relationships within the genus, and the incompletely known history of drainage in the northern Rocky Mountan region. An origin associated with upstream penetration of the Missouri River basin appears unlikely given the distinctiveness of the eastern and western faunas of *Pyrgulopsis* (see above). The well documented Pleistocene rerouting of the ancestral Missouri River, which coursed north to the Hudson Bay prior to blockage by the Laurentide ice sheet and assumption of the modern path to the Mississippi River (Howard 1958, Lemke et al. 1965), probably had no bearing on this issue as *P. bedfordensis* represents the northernmost record for the genus (living and fossil) in the West. We instead attribute origin to vicariance of an earlier paleodrainage implied by the close geographical proximity of this species of poorly dispersing snail to fauna living across the continental divide in the upper Snake River basin (e.g., *P. robusta*; Hershler 1994). Note that *Pyrgulopsis* has not been found in the upper Colorado River basin (Green River drainage), which also is in close proximity to the Missouri headwaters.

Extensional faulting responsible for development of the basin and range of southwest Montana began during the middle Miocene and profoundly disrupted an ancestral landscape that consisted of broader, shallower basins (Reynolds 1979, Fields et al. 1985, Boronsky et al. 1993, Sears & Fritz 1998). (The Townsend pull-apart graben, to which *P. bedfordensis* is endemic, lies along the boundary between this zone

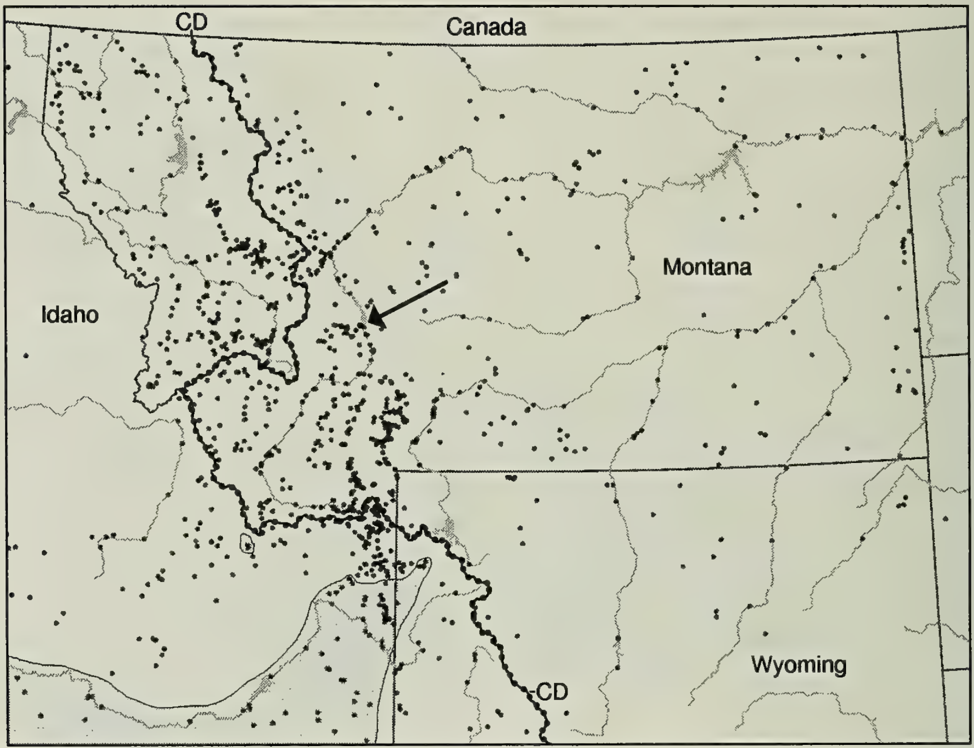

Fig. 7. Map showing location of sampling sites in Montana and adjacent states. The shaded area depicts the regional distribution of *Pyrgulopsis,* with the disjunct occurrence of *P. bedfordensis* indicated by the arrow. CD, continental divide.

of deformation and more stable crust to the north [Reynolds 1977].) The continental divide probably had a complex history in this region (Fields et al. 1985) and the modern north-trending Missouri headwater drainage may not have been assembled until the Quaternary (Robinson 1963, Fritz & Sears 1993). Anderson (1947) presented physical evidence that the continental divide shifted about 161 km to the east during the late Tertiary, with associated severence of a paleodrainage that integrated southwest Montana and southeast Idaho (also see Ruppel 1967). The development and migration of volcanic centers and a topographic swell in association with passage of the North American plate across the Yellowstone Hot Spot (beginning ca. 16 Ma) has provided a cogent explanation for such an eastward shift of the divide (Pierce & Morgan 1992, 1999; Smith & Braile 1994). Fritz & Sears (1989, 1993; also see Kreps et al. 1992) recently proposed that during the early middle Miocene, the portion of southwestern Montana now comprising the upper Missouri River basin drained south to the present site of the Snake River Plain, with tectonic break-up of this landscape and reversal of flow direction occurring about 6.5 Ma in association with local passage of the hotspot. While some of the stratigraphic interpretations of this proposal have been challenged, the hypothesized drainage reversal has been accepted (Cheney et al. 1994, Fritz & Sears 1994).

The western fossil record of *Pyrgulopsis* dating to the late Miocene (Hershler & Sada 2001) is congruent with the above time frame of physical events contributing to vicariance of a postulated Missouri-Snake paleodrainage. This hypothesis is also consistent with other organismal distributions suggesting prior connections across the Pacific divide in this region, including those of fishes (Miller 1959, Smith 1981, Behnke 1992, Smith 1999), mollusks (Taylor 1985), and a recently described oligocheate, *Rhynchelmis gustafsoni,* which is narrowly endemic to headwaters of the Missouri and Snake river basins and is the only member of its species group that ranges east of this divide (Fend & Brinkhurst 2000). Note, however, that for some of these cases (e.g., Cutthroat Trout) it has been argued that biotic pattern reflects montane headwater transfers effected by Pleistocene or younger faulting or landslides rather than an earlier disruption of through-going basinal drainage. The possibility that, in accordance with our hypothesis, this snail may have long persisted locally in southwest Montana and endured the harsh conditions of the Quaternary is supported by its endemism slightly south of the continental Wisconsin ice sheet and by the minimal record of alpine glaciation in the ranges enclosing Townsend Valley (Alden 1953). Furthermore, this valley was not inundated by glacial Lake Great Falls, which was ponded further downstream in the Missouri River Valley against the southern edge of the ice sheet (Calhoun 1906, Alden 1932). The large discharge (88.3 l/s; Waring 1965), high temperature, and long, high-gradient outflow of this spring also may have contributed to local persistence of *P. bedfordensis.*

Acknowledgments

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The mineral component of the axis and holdfast of some gorgonacean octocorals (Coelenterata: Anthozoa), with special reference to the family Gorgoniidae

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Abstract.—This is the first detailed investigation of the mineral component of axes and holdfasts of Gorgonacea, including 58 species belonging to 5 families and 21 genera of Holaxonia and 4 families and 13 genera of Calcaxonia. X-ray diffraction, electron probe, and scanning electron microscope analyses indicated that aragonite or Mg-calcite occurred in most axes and holdfasts of 6 families. In marked contrast, amorphous carbonate hydroxylapatite occurred solely in the family Gorgoniidae, which in some species also had Mg-calcite or aragonite in holdfasts. These skeletal minerals appear to be taxonomically controlled. The distinctive morphology of carbonate hydroxylapatite in Gorgoniidae is illustrated by scanning electron micrographs.

Early studies of gorgonian corals provide only a smattering of information on their chemical composition, all but ignoring their mineral content (Cook 1904; Clarke & Wheeler 1915, 1917). As far as known, sclerites of all octocorals are composed of Mg-calcite (Chave 1954, Lowenstam 1964, Milliman 1974). Lowenstam (1964:379) documented the co-occurrence of calcite and aragonite in Octocorallia and discussed the possible relationship of skeletal mineralogy to temperature of the environment. More recently, Kingsley & Watabe (1982: 325, 337, 338) reported "amorphous calcium material" in the axis of *Leptogorgia virgulata* but ruled out calcium phosphate owing to insufficient amounts of phosphorous; and Lewis et al. (1992:283) described amorphous carbonate in *Leptogorgia virgulata, Lophogorgia cardinalis, Gorgonia ventalina,* and *Plexaura flexuosa.* In addition, Jeyasuria & Lewis (1987:218) reported that some gorgonians contain as much as 85.36 mole% of $MgCO_3$.

To obtain a broader view of the mineral content of the axial skeleton of gorgonians, Macintyre et al. (2000) examined 51 samples of Gorgonacea belonging to 47 species in 28 genera and 6 families of the orders Holaxonia and Calcaxonia. Any mineral present in the axes and holdfasts of the holaxonian families Keroeididae, Acanthogorgiidae, Paramuriceidae and Plexauridae, and the calcaxonian families Ellisellidae, Chrysogorgiidae, Ifalukellidae, and Primnoidae was either Mg-calcite or aragonite; no phosphorous was detected by X-ray microprobe energy dispersive scans. The axes of Isididae and all families of Scleraxonia were not considered in that study as they are known to consist of Mg-calcite sclerites or crystalline calcite.

Macintyre et al. (2000) also observed mineralization in the axes and holdfasts of the genera *Eugorgia, Gorgonia, Leptogorgia, Pacifigorgia, Phycogorgia, Phyllogorgia,* and *Pseudopterogorgia.* In some cases it was extensive, in others weak, and was detected by X-ray diffraction only in *Leptogorgia setacea* and *L. stheno,* which yielded weak patterns consistent with dahllite as the authors reported for mammoth teeth.

Analysis by electron microprobe showed that this "amorphous" mineral is carbonate hydroxylapatite Ca_5 $(PO_4, CO_3)_3(OH)$ (Gaines et al. 1997), hereafter abbreviated CHAp; see Macintyre et al. (2000).

No CHAp was found in the axis and holdfast of the gorgoniid genera *Eunicella, Rumphella* and *Pterogorgia,* and a single species of *Leptogorgia* (*L. caryi*). The axis of *Olindagorgia marcgravii* and *Pseudopterogorgia bipinnata* contained CHAp, but the holdfast was strengthened with crystalline aragonite. No mineral was detected in the axis or holdfast of *Eunicella.* Although the axis of *Rumphella* and *Pterogorgia* yielded no mineral, the holdfast was strongly reinforced with crystalline $CaCO_3$.

This paper presents scanning electron micrographs of axis and holdfast morphology in representative species of Gorgoniidae to demonstrate the consistency of mineralization by CHAp in this widespread family of Gorgonacea.

Materials and Methods

All specimens examined during this investigation (Table 1) are preserved in the permanent research collections of the U.S. National Museum of Natural History, Smithsonian Institution. Some of the specimens were originally dried upon collection and have been maintained in that condition; others were preserved in alcohol and are stored in 70% ethanol.

Portions from terminal branches of the upright axis were stripped of all coenenchyme. Some pieces were split to expose the axial core, others subjected to prolonged (12–48 hours) maceration in 5.25% sodium hypochlorite solution (common household bleach). Any inorganic skeleton was thoroughly washed, affixed to 10-mm glass coverslips and mounted on aluminum stubs for examination by SEM.

Small samples were clipped from the edge of holdfasts or were peeled from the substrate to eliminate contamination. After maceration in sodium hypochlorite solution, the inorganic residue was repeatedly washed in distilled water to remove salt. A simple pipette was used to drop suspensions of residue either on clean 10-mm glass coverslips for attachment to standard SEM stubs, or on small Hitachi stubs covered with the adhesive film of "sticky tabs." Samples were then air dried.

Mineralogical analysis of samples was carried out by standard X-ray diffraction techniques (Goldsmith & Graf 1958, Milliman 1974) using a Scintag X-Ray Diffractometer with CuK_α radiation, a Peltier detector, and zero-background quartz mounting plates.

For electron probe analyses, samples were treated for removal of organic material, embedded in resin, sectioned, and carbon coated. The analyses of the amorphous carbonate hydroxylapatite, which generally was not recorded in X-ray diffractograms, were conducted with a 8900 JEOL electron microprobe (Macintyre et al. 2000).

In cases of heavily calcified holdfast that remained intact after prolonged maceration in sodium hypochlorite, some fragments were pulverized and subjected to analysis by X-ray diffraction as described above, while others were affixed with white glue to 10-mm glass coverslips for mounting on aluminum stubs for examination of fracture surfaces by SEM.

Preparations to be examined by SEM were pre-coated with carbon and sputter-coated with gold-palladium. Examination was done with a Hitachi Model S-570 scanning electron microscope at magnifications from 100× to 30,000× at 10kv accelerating voltage. Scatter preparations on glass coverslips were examined at working distances of 1–3 mm. Preparations on Hitachi stubs were viewed within the final lens of the microscope at working distances of -2 to -4 mm. Whole mounts of crystalline holdfast tissue were examined at working distances of about 15 mm. All images were recorded on Polaroid Type 52 positive film, in some

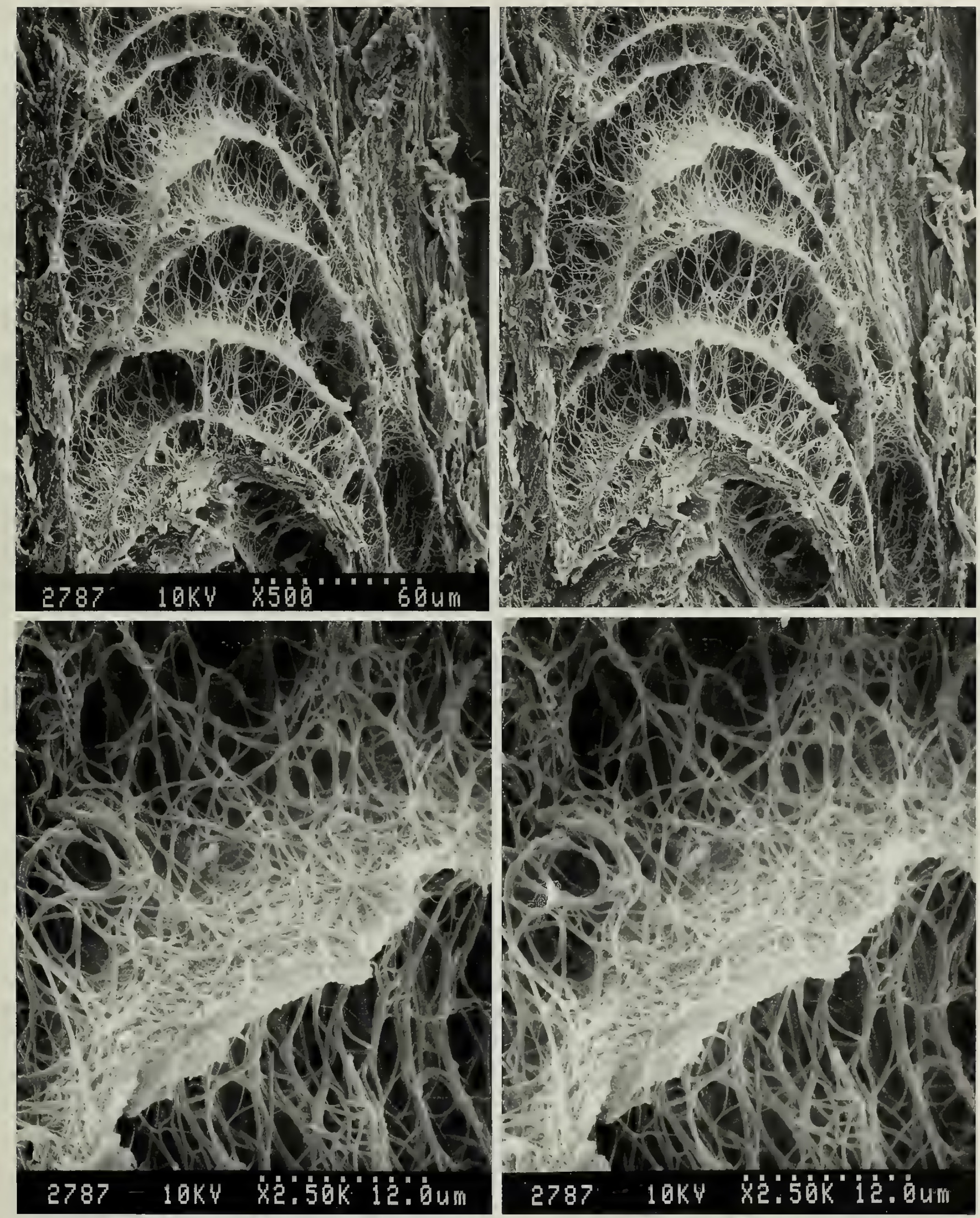

Fig. 1. Structure of non-mineralized gorgoniid axis. Top, longitudinal section of axial core of *Leptogorgia caryi* showing chambers; bottom, partition between chambers of core showing filamentous structure (SEM 2787–stereo pairs).

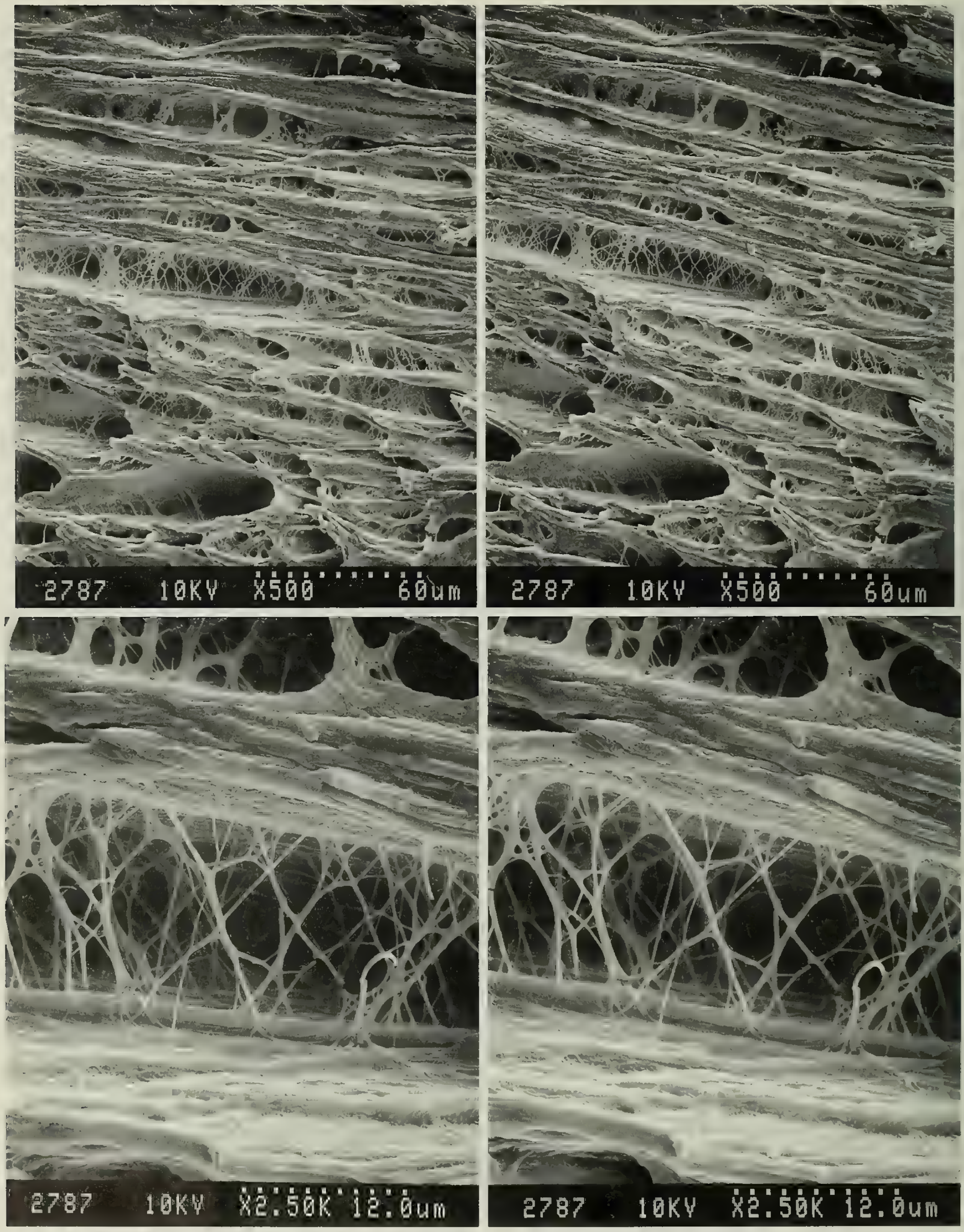

Fig. 2. Structure of non-mineralized gorgoniid holdfast: Top, section of holdfast of *Leptogorgia caryi* showing loculi between lamellae of gornonin; bottom, part of holdfast loculus and gorgonin filaments in lumen (SEM 2787–stereo pairs).

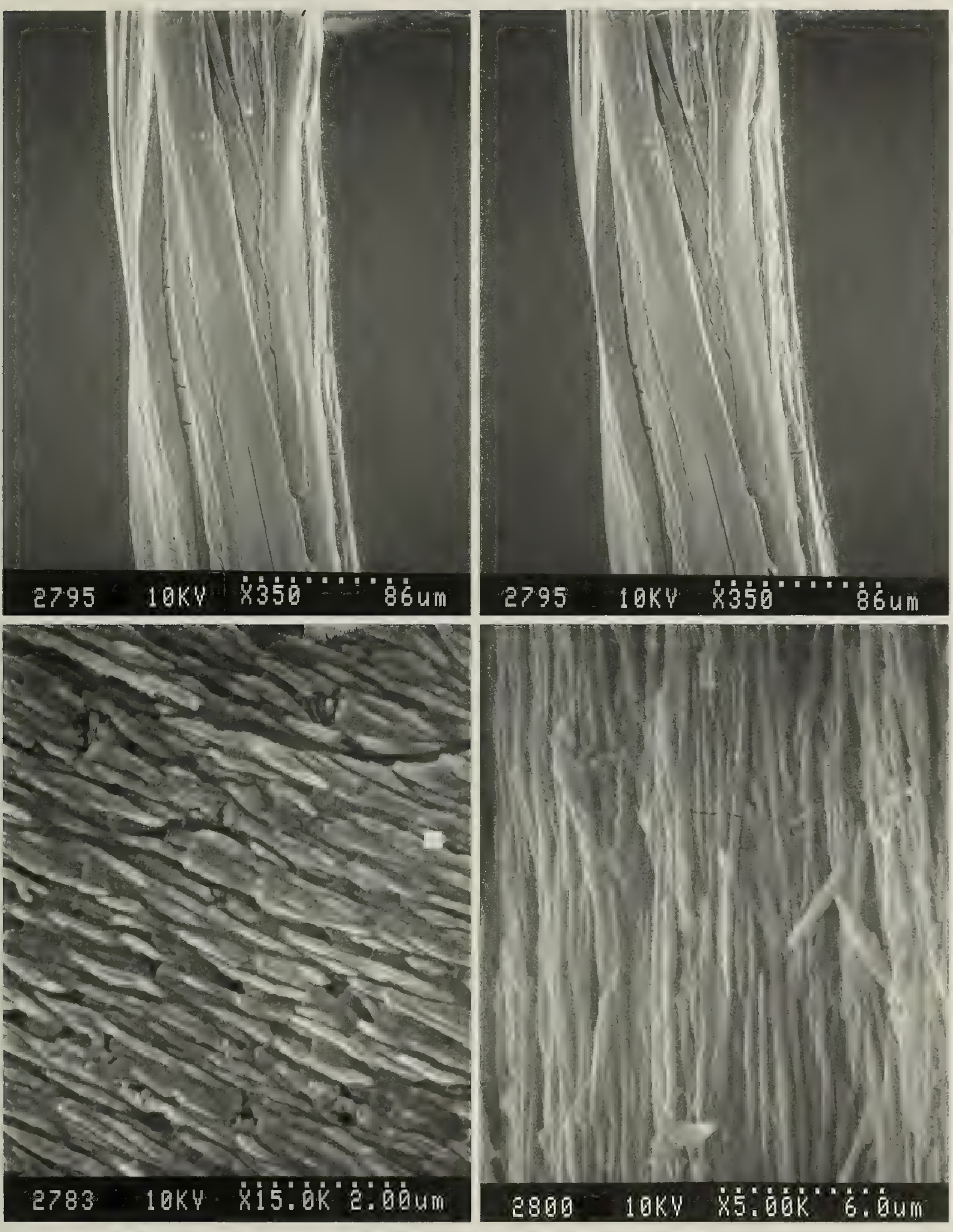

Fig. 3. Mineral component of gorgoniid axes. Top, axis of terminal branchlet of *Leptogorgia cardinalis* after removal of gorgonin by maceration in sodium hypochlorite, showing longitudinal strands of CHAp (SEM 2795–stereo pair); Bottom left, Surface of axis of *L. cardinalis* showing longitudinal fibers of CHAp (SEM 2783); Bottom right, Longitudinal break through axial cortex of *Leptogorgia stheno* showing longitudinal fibers of CHAp (SEM 2800).

cases accompanied by corresponding negatives on Kodak Tri X: film.

Axes and holdfasts of the following species in the family Gorgoniidae were examined in the present study:

Eugorgia ampla Verrill. USNM 8967 (SEM 2694, 2695, 2710, 2711, 2725, 2741, 2814). Taxonomic description: See Verrill 1869:407.

Eugorgia aurantiaca Verrill. Accession 166789 (SEM 2691, 2692); USNM 52317 (SEM 2696, 2697). Taxonomic description: See Verrill 1869:410.

Eugorgia rubens Verrill. USNM 50032 (SEM 2742–2747). Taxonomic description: See Verrill 1869:411.

Eunicella cavolini Koch. USNM 89285. Taxonomic description: Grasshoff 1992: 16. Axis not mineralized.

Eunicella filiformis Studer. USNM 82909. Taxonomic description: Grasshoff 1992: 43. Axis not mineralized; no holdfast, colonies recumbent, unattached.

Gorgonia flabellum Linnaeus. USNM 51766 (SEM 2843–2846, 2884). Taxonomic description: See Bayer 1961:259.

Gorgonia mariae Bayer. USNM 93965 (SEM 2698, 2699, 2748, 2749). Taxonomic description: See Bayer 1961:266.

Gorgonia ventalina Linnaeus. USNM 55027 (SEM 2828). See Bayer 1961:262. In establishing the two species of Caribbean sea fans, Linnaeus distinguished *G. ventalina* from *G. flabellum* because its branches are "a lateribus exterioribus compressis" rather than "versus ramulos compressis." Such distinctions can be seen among specimens of *Gorgonia,* but whether they are biological realities or merely the extremes of a morphological continuum remains to be determined.

Leptogorgia africana (Kükenthal). USNM 82884 (SEM 2840). Taxonomic description: See Grasshoff 1988:117.

Leptogorgia alba (Duchassaing & Michelotti), typical flabellate colony. USNM 49363 (SEM 2839, 2857, 2858). Taxonomic description: See Duchassaing & Michelotti 1864:19, pl. 4, fig. 2; Hickson 1928:400.

Leptogorgia cardinalis (Bayer). USNM 50052 (SEM 2781); USNM 49711 (SEM 2782–2784). Taxonomic description: See Bayer 1961:201.

Leptogorgia caryi Verrill. USNM 57157 (2787, 2790). Taxonomic description: See Kükenthal 1913:266. Verrill (1869: 404) established the species *Leptogorgia caryi* for specimens that he previously (Verrill 1864:35) had identified as *Plexaura fucosa* (Valenciennes). Material consistent with Verrill's description was described as *Psammogorgia spauldingi* by Nutting (1909:721). Two other new species assigned to *Psammogorgia* by Nutting (1909:720, 721), *P. simplex* and *P. torreyi,* are referable to *Swiftia,* but *P. spauldingi* has more the appearance of *Leptogorgia* than of *Swiftia.* Kükenthal (1913:266) further contributed to this complex history by describing specimens undoubtedly of this species as *Euplexaura marki,* although it has very little in common with *Euplexaura.* Morphologically, it resembles other species of *Leptogorgia* and many other gorgoniids in the form of its sclerites and the structure of its axis and holdfast. Unlike other species of *Leptogorgia,* the axis of *L. caryi* is not mineralized. The chambers of the axis core and the locular spaces in the lamellae of the holdfast are filled with a meshwork of fine filaments, but these lack the spherulitic mineral deposits present in other genera and species of Gorgoniidae. The gorgonin of both axis and holdfast are completely dissolved by sodium hypochlorite, leaving no mineral residue.

Leptogorgia gilchristi (Hickson). USNM 59824 (SEM 2830, 2831). Taxonomic description: See Williams & Lindo 1997: 507.

Leptogorgia lemasti (Hickson). USNM 52730 (SEM 2819). Taxonomic description: See Hickson 1928:349; Stiasny 1941:266.

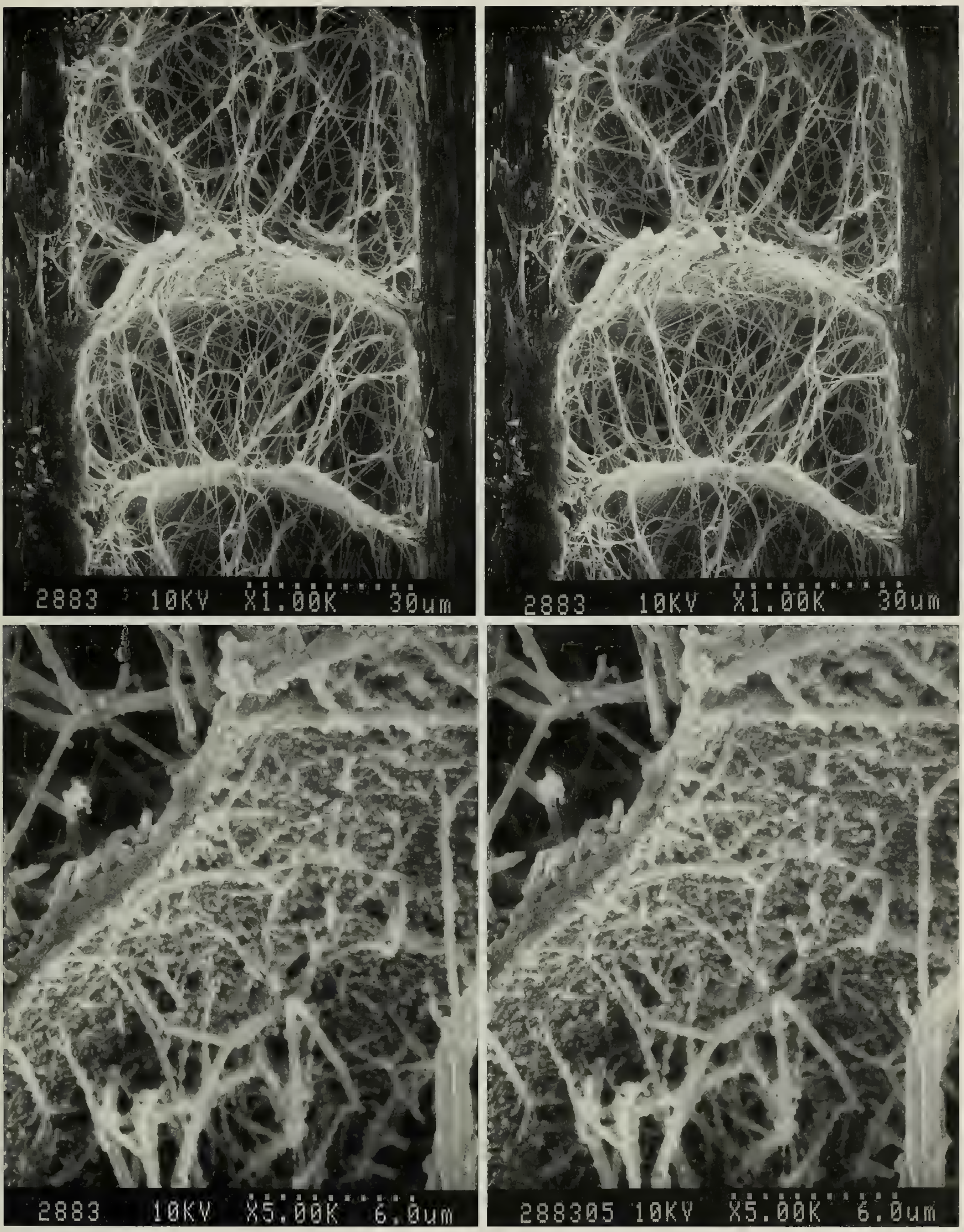

Fig. 4. Mineral component of gorgoniid axis. Longitudinal section of mineralized axis of *Leptogorgia viminalis* after removal of gorgonin showing chambers and filaments of core. Top, Chambers containing filaments mineralized with CHAp (SEM 2883, stereo pair); Bottom, Partition between chambers showing filaments mineralized with microspheres of CHAp and coalesced microspheres on chamber wall (SEM 2883, stereo pair).

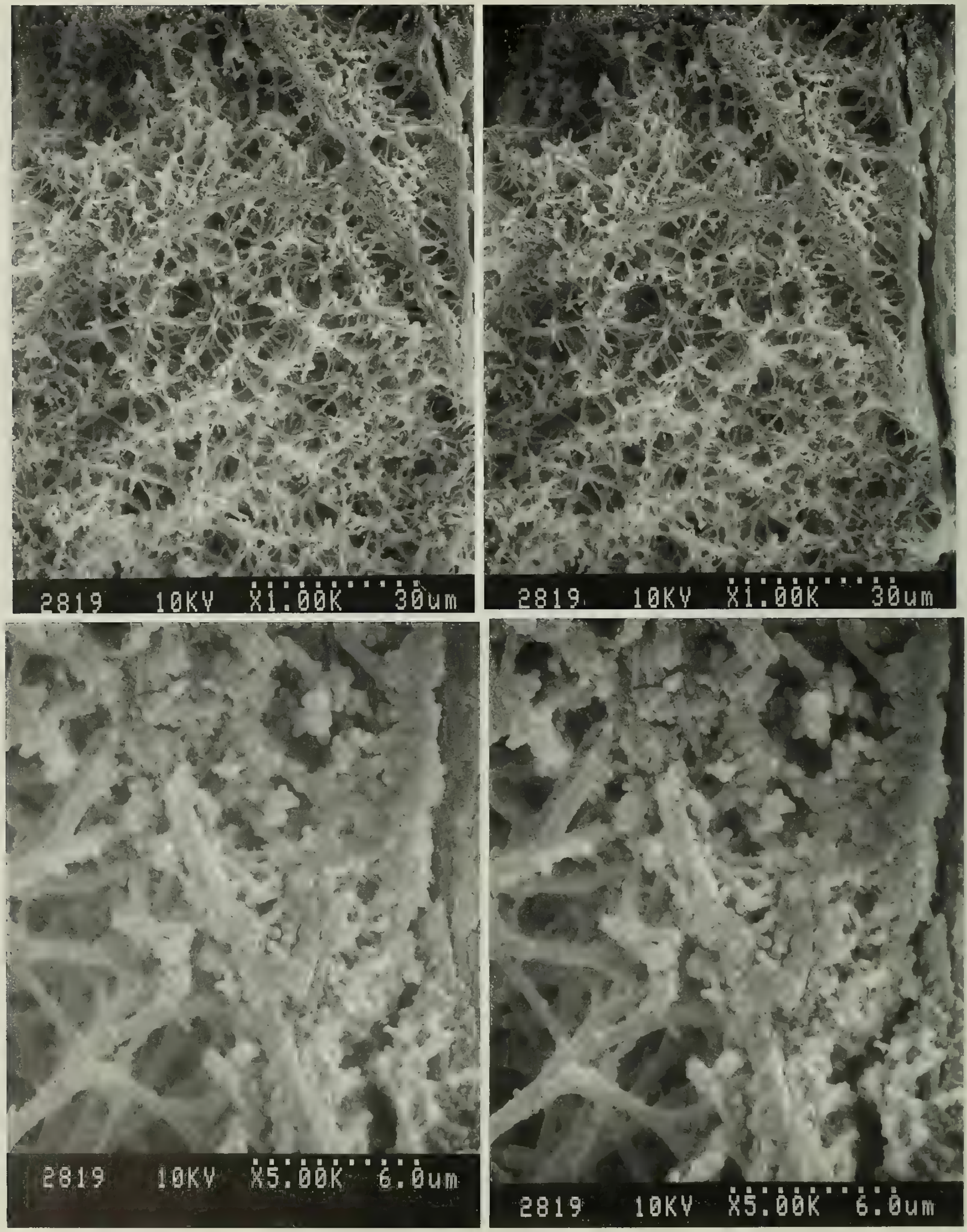

Fig. 5. Mineral component of gorgoniid axis. Longitudinal section of mineralized axis of *Leptogorgia lemasti* after removal of gorgonin. Top, Chambers of core containing filaments mineralized with CHAp (SEM 2819, stereo pair); Bottom, Chamber wall showing filaments mineralized with coalesced microspheres of CHAp (SEM 2819, stereo pair).

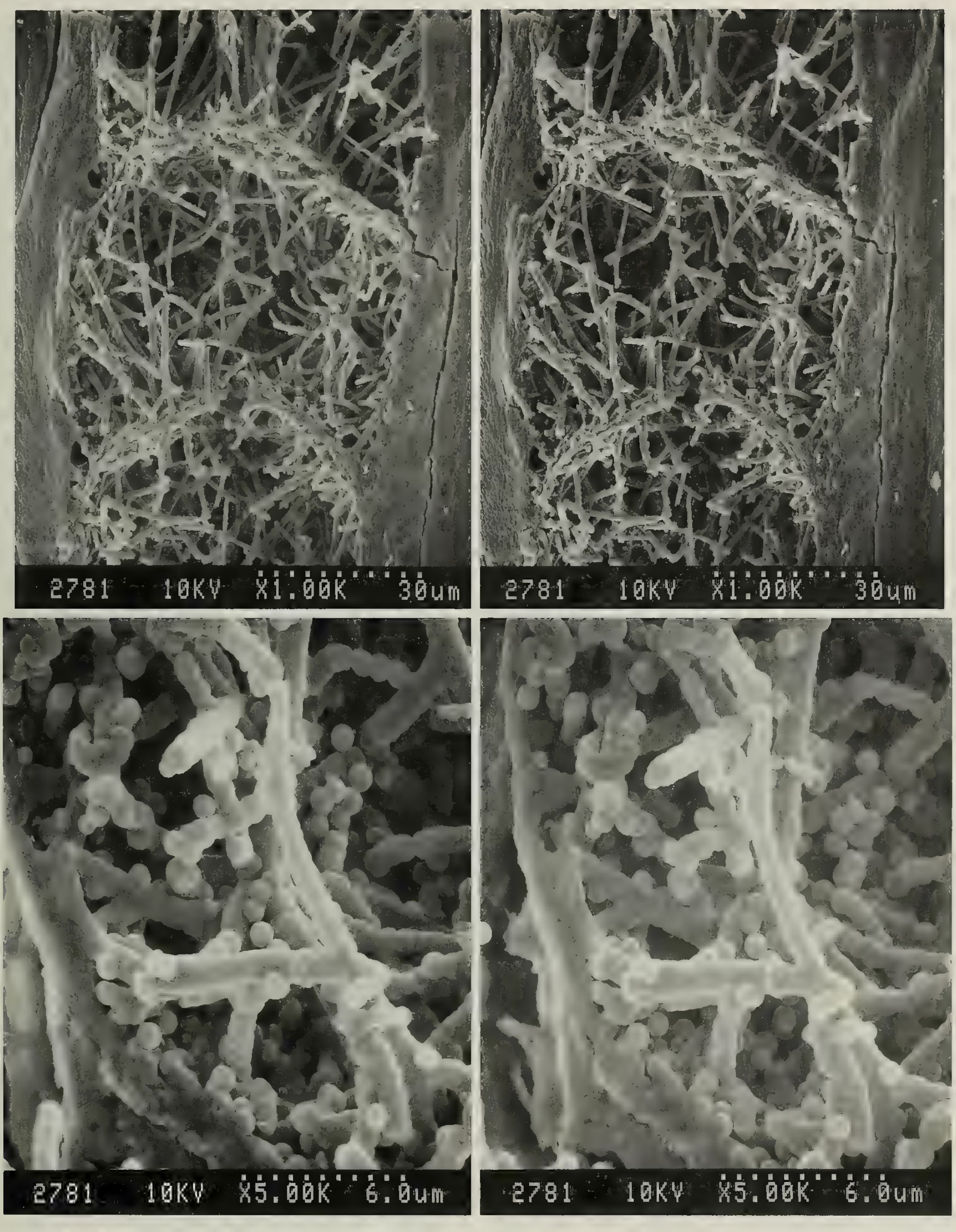

Fig. 6. Mineral component of gorgoniid axis. Longitudinal section of axis of *Leptogorgia cardinalis* after removal of gorgonin. Top, Chamber walls and filaments of core mineralized with CHAp; Bottom, Detail of chamber showing microspheres of CHAp coating filaments and chamber wall (SEM 2781–stereo pairs).

Leptogorgia riodouroi (Stiasny). USNM 82910 (SEM 2809). Taxonomic description: See Grasshoff 1988:116.

Leptogorgia sanguinolenta (Pallas). USNM 82904 (SEM 2793). Taxonomic description: See Grasshoff 1988:113.

Leptogorgia setacea (Pallas). USNM 43245 (SEM 2810–2812); USNM 43254 (SEM 2823); USNM 49777 (SEM 2822). Taxonomic description: See Bayer 1961:218.

Leptogorgia stheno (Bayer), pink colonies. USNM 49781 (SEM 2806–2807); USNM 50033 (SEM 2808); white colonies: USNM 49782 (SEM 2800, 2804). Taxonomic description: See Bayer 1961: 220.

Leptogorgia viminalis (Pallas). USNM 82905 (SEM 2818, 2864, 2883). Taxonomic description: See Grasshoff 1988: 102; 1992:60 (history, 97, 99, 102).

Leptogorgia virgulata (Lamarck). USNM 49690 (SEM 2753–2757, 2780, 2798). USNM 59331 (SEM 2796, 2798). Taxonomic description: See Bayer 1961:216.

Leptogorgia styx Bayer. USNM 98800 (SEM 2772–2775). Taxonomic description: See Bayer 2000:609.

Olindagorgia marcgravii (Bayer). USNM 73426 (SEM 2801–2803). Taxonomic description: See Bayer 1961:255.

Pacifigorgia cribrum (Valenciennes). USNM 49567 (fragment of holotype, MNHN Paris) (SEM 2870, 2871); USNM 49384 (SEM 2847–2849, 2851); USNM 1677 (SEM 2865, 2866); USNM 79433 (SEM 2867, 2868). Taxonomic description: Valenciennes 1846: pl. 13, figs. 1–3.—Verrill 1869:392, pl. 6, fig. 5 (*Leptogorgia rutila*); 391, pl. 5, fig. 5 (*L. adamsii* [part]).–Bielschowsky 1929:150. Although a detailed taxonomic evaluation has not been feasible in the present context, the specimens available suggest that most of the nominal species having fans consisting of fine, closely anastomosed networks may represent a single species.

Pacifigorgia irene Bayer. USNM 49365 (SEM 2855, 2856). Taxonomic description: See Bayer 1951:94, figs. 2, 3.

Pacifigorgia media (Verrill). USNM 57905 (SEM 2853, 2854, 2879). Taxonomic description: See Verrill 1864:33; 1869:389.

Pacifigorgia stenobrochis (Valenciennes). USNM 49366 (SEM 2767–2770). Taxonomic description: See Verrill 1869:393.

Phycogorgia fucata (Valenciennes). USNM 56886 (SEM 2776–2779). Taxonomic description: See Verrill 1869:413; Kükenthal 1919:921; Kükenthal 1924:360.

Phyllogorgia dilatata (Esper). USNM 5247 (SEM 2750–2752, 2758). Taxonomic description: See Verrill 1912:396, pl. 33, fig. 3; Bayer 1961:272, fig. 90, pl.10, fig. 6.

Pseudopterogorgia americana (Gmelin). USNM 53582 (SEM 2761, 2763, 2764, 2771). Taxonomic description: See Bayer 1961:242.

Pseudopterogorgia australiensis (Ridley). USNM 82139 (SEM 2765, 2766); USNM 80952 (SEM 2873–2875); USNM 80593 (SEM 2859, 2860, 2863). Taxonomic description: See Ridley 1884: 342, Kükenthal 1924:356.

Pseudopterogorgia bipinnata (Verrill). USNM 96216 (SEM 2826, 2876); USNM 50216 (SEM 2877, 2878, 2881, 2882). Taxonomic description: See Bayer 1961:229.

Pterogorgia anceps (Pallas). USNM 50057 (SEM 2655, 2656, 2676, 2732, 2857). Taxonomic description: See Bayer 1961: 275.

Pterogorgia guadalupensis Duchassaing & Michelin. Material: USNM 52029 (SEM 2861); 51311. Taxonomic description: See Bayer 1961:277, fig. 92, pl. 9, fig. 6.

Rumphella aggregata (Nutting). Material: USNM 50275 (SEM 2660); USNM 86004 (SEM 2788, 2789). Taxonomic description: See Nutting 1910:4.

Results and Discussion

The order Gorgonacea of the subclass Octocorallia traditionally has been divided into two suborders: (1) Scleraxonia, with a

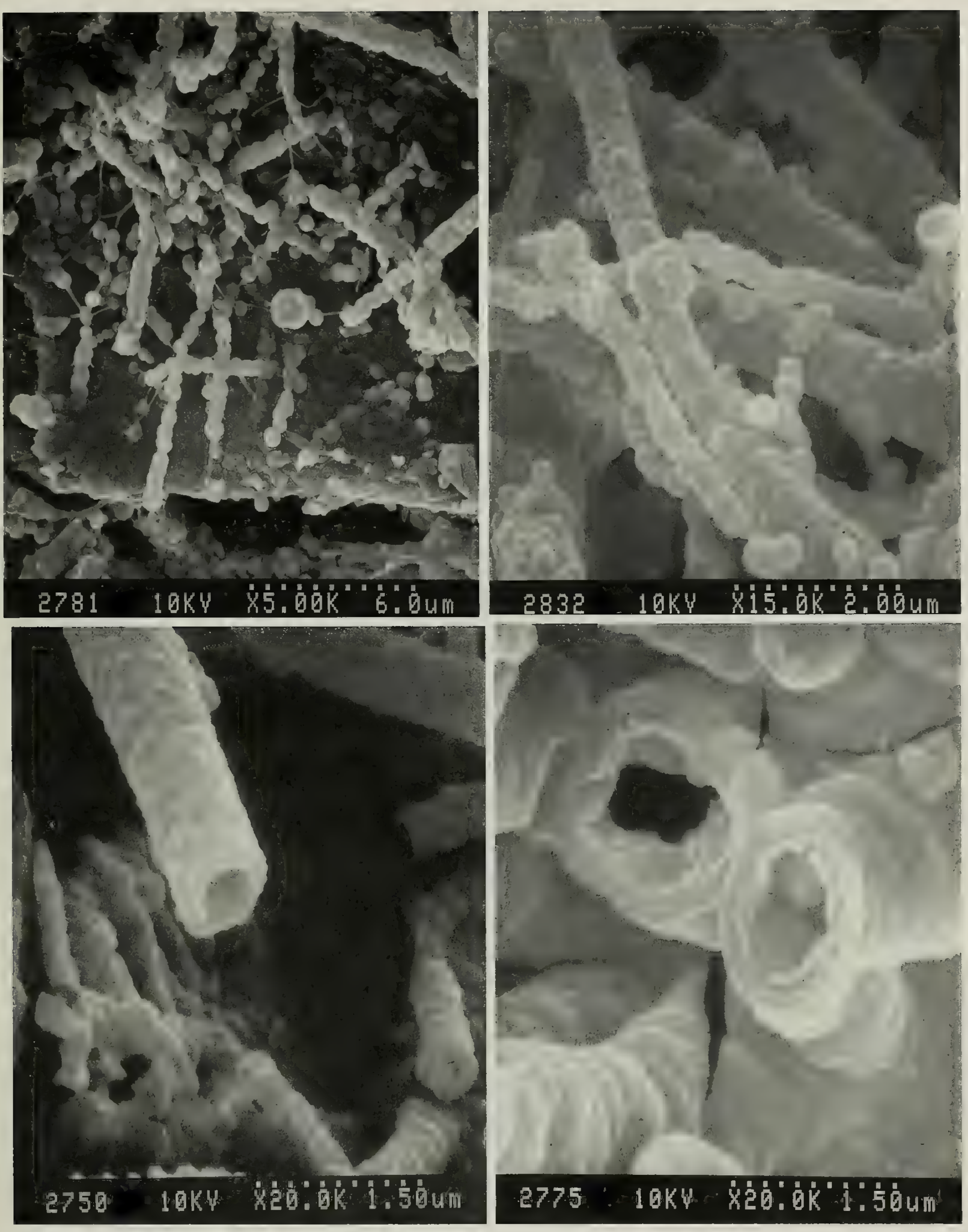

Fig. 7. Mineral component of gorgoniid supporting skeleton. Top left, Microspheres of CHAp in bead-like series covering organic filaments of *Leptogorgia cardinalis* holdfast (SEM 2781); Top right, Microspheres of CHAp fused to form rod-like coating on filaments of axial core of *Leptogorgia lemasti,* with some randomly located microspheres (SEM 2832); Bottom left, Mineral coating of filament of axial chamber of *Phyllogorgia quercifolia* consisting of CHAp microspheres fused to form rod-like structure with hollow core originally occupied by organic filament (SEM 2750); Bottom right, mineral coating of holdfast filaments of *Leptogorgia styx* showing deposition of CHAp in layers (SEM 2775).

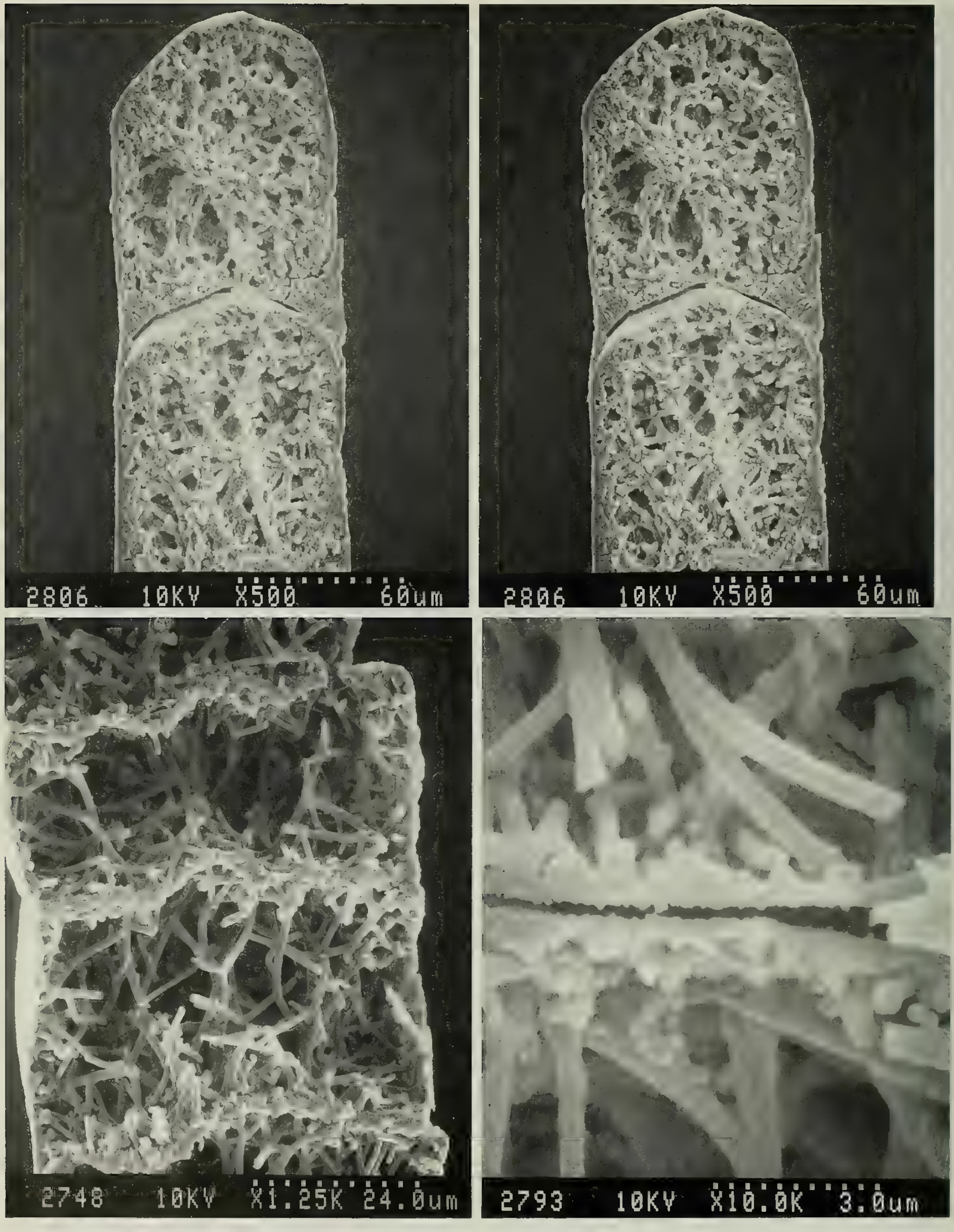

Fig. 8. Mineral component of gorgoniid axes. Top, Chambers of axial core of *Leptogorgia stheno* showing filaments coated with CHAp and space left after removal of organic partition by sodium hypochlorite (SEM 2806, stereo pair); Bottom left, Chambers of axial core of *Gorgonia mariae* showing filaments coated with CHAp (SEM 2748); Bottom right, Partition between chambers of axial core of *Leptogorgia sanguinolenta* showing space once occupied by organic lamella (SEM 2793).

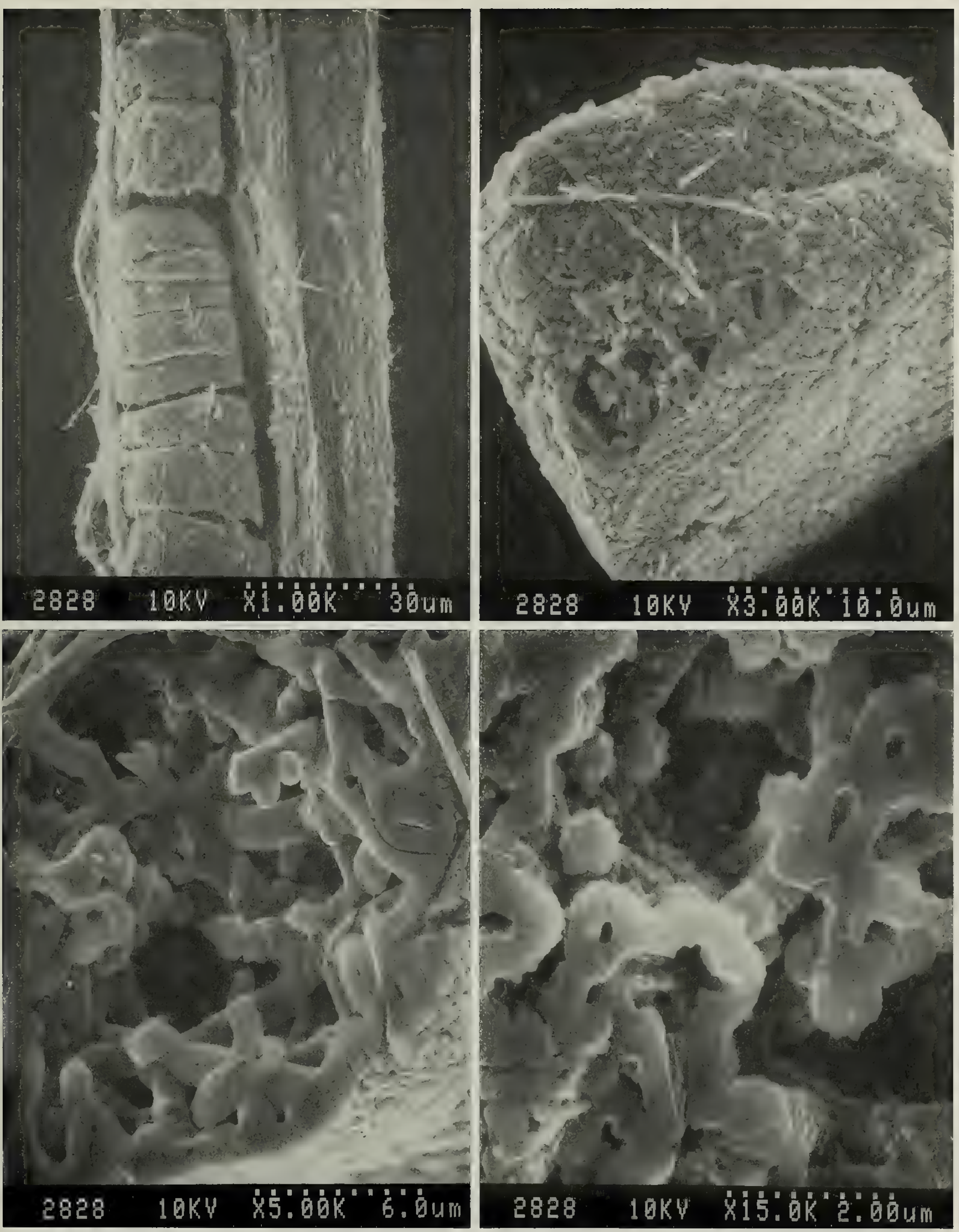

Fig. 9. Mineral component of gorgoniid axis. Top left, Heavily mineralized chambers of axial core of *Gorgonia ventalina* partially separated from axial cortex after maceration in sodium hypochlorite; Top right, Isolated chambers with break in wall showing internal structure; Bottom left, Filaments covered with CHAp in lumen of chamber; Bottom right, Filaments in lumen of chamber showing microspherulitic structure of mineral coating (SEM 2828).

supporting axis consisting of sclerites composed of magnesium calcite more or less completely bound together by gorgonin or crystalline calcite; and (2) Holaxonia, with a supporting axis consisting of gorgonin more or less heavily impregnated with $CaCO_3$ not in the form of sclerites. As mineralization of the axis has been considered of little practical taxonomic value, scant attention has been paid to its occurrence and distribution among holaxonian families. Recently, however, those families having a heavily calcified axis without a central core have been recognized as a separate suborder Calcaxonia (Grasshoff 1999:68), leaving those families with a chambered core in a flexible, poorly calcified or purely horny axis in the Holaxonia.

In the Holaxonia, the axis in the families Acanthogorgiidae, Paramuriceidae, and Gorgoniidae is reported as purely horny, that of the Plexauridae as containing some non-spicular calcareous matter, and that of the Keroeididae as containing smooth, fusiform calcareous sclerites (Aurivillius 1931, Bayer 1956).

When analyzed by X-ray diffraction, the mineral in the axis of all species of Calcaxonia proved to be $CaCO_3$ in the form of Mg-calcite or aragonite. In primnoids and chrysogorgiids, the holdfast may be a discoidal expansion firmly adherent to solid substrate or a branched, rootlike structure, either Mg-calcite or aragonite dependent upon species, embedded in soft substrate. The holdfast mineral of ellisellids was found to be Mg-calcite like that of the axis, and the holdfast mineral of ifalukellids proved to be aragonite like that of the axis, with possible contamination of Mg-calcite from the substrate.

In the chambered axial core in gorgoniids, CHAp is deposited in the form of ''submicron spheres'' (Macintyre et al. 2000) on the inner wall of the chambers and on the fine, organic fibrillar meshwork filling the chambers. In species having holdfasts containing CHAp, the mineral is similarly deposited as microspheres on the interior wall and the fibrillar network filling the loculi in the gorgonin forming the lamellae of the holdfast. In gorgoniids having holdfasts reinforced with Mg-calcite or aragonite, the mineral is deposited between thin lamellae of gorgonin.

We found that the amount of $MgCO_3$ in the calcite of the axis ranges from 7.9 mole% in *Primnoella scotiae* to 15.7 mole% in *Plexaurella grisea* and *P. nutans*; and in the holdfast from 6.4 mole% in *Ainigmaptilon edisto* to 13.8 mole% in *Junceella gemmacea* (Table 1).

In no case did we find calcite with magnesium in the 33–42 and 71–85 mole% ranges as reported by Jeyasuria & Lewis (1987:218). In fact, we found that axes having the very high mole percentages of $MgCO_3$ reported by them, e.g., the species *Plexaura flexuosa* (72.0 mole%), *Muriceopsis flavida* (79.20 mole%), and *Swiftia exserta* (76.3 mole%)—have no mineral whatever, although the holdfasts of the first two are strongly mineralized with crystalline aragonite. Jeyasuria & Lewis's observations were made by atomic absorption spectrography of axial substance dissolved in HNO_3. When samples of the axial substance of those same species are digested in 5.25% sodium hypochlorite, all organic components are dissolved, leaving no mineral framework for analysis by X-ray diffraction. Therefore, it can be concluded that the Ca and Mg concentrations found by Jeyasuria & Lewis (1987) were in ionic rather than mineral form. The amounts of $MgCO_3$ that they found in the calcite of *Plexaurella grisea* (18.1 mole%) and *Ellisella barbadensis* (14.6 mole%) are reasonably similar to our findings for *P. grisea* (15.7 mole%) and *Junceella gemmacea* (14.0 mole%).

We did not find crystals in the axis of *Muricea muricata, Plexaura flexuosa,* and *Eunicea tourneforti,* as reported by Lewis et al. (1992:281). However, after prolonged maceration (26–60 hours) in sodium hypochlorite, crystals similar to those they illustrated for *Plexaura flexuosa* (1992: fig. 1c)

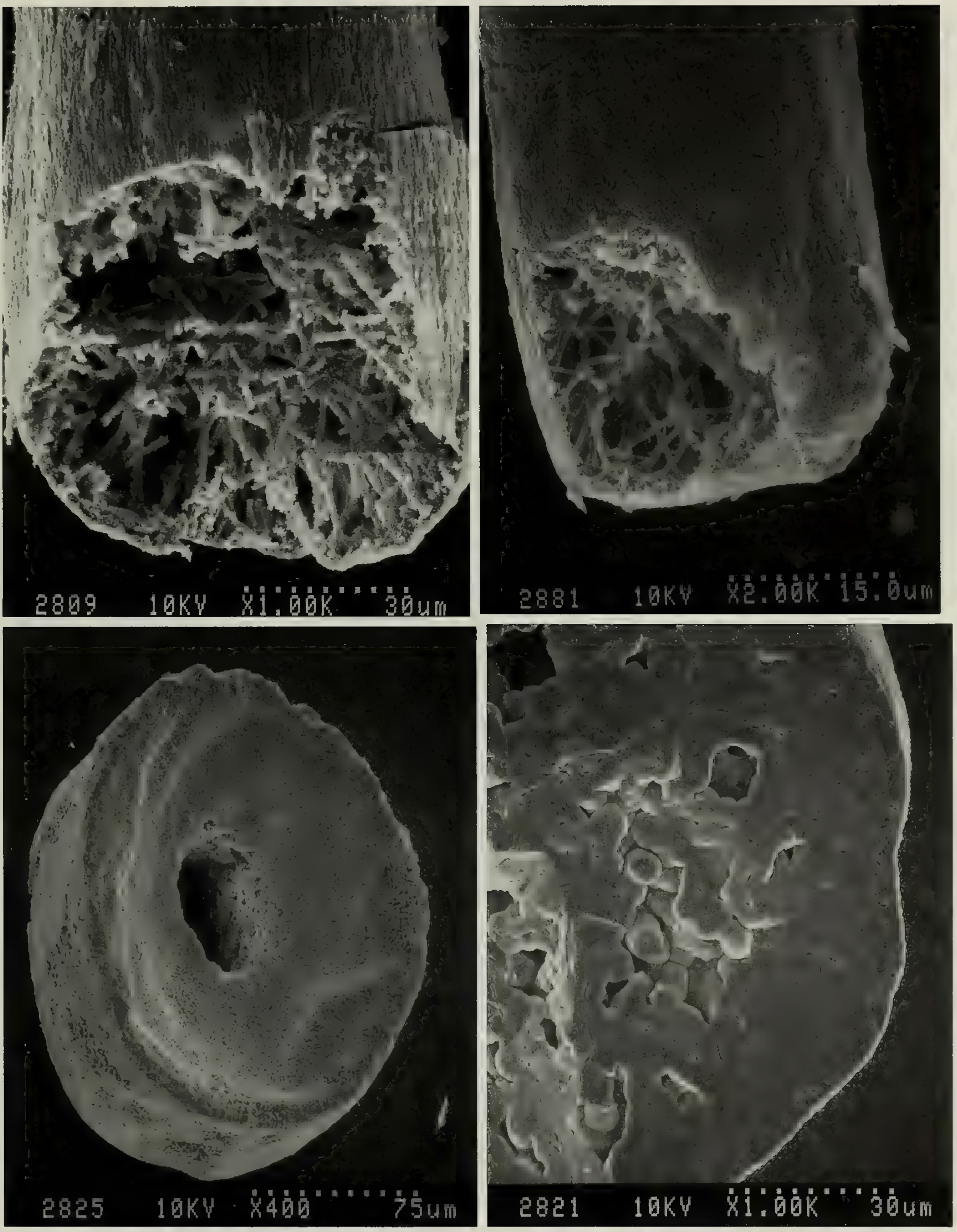

Fig. 10. Mineral component of gorgoniid axes. Top left, Core of axis of *Leptogorgia riodouroi* (SEM 2809); Top right, Core of axis of *Pseudopterogorgia bipinnata* (SEM 2881); Bottom left, Heavily mineralized contents of chamber of axial core of *Leptogorgia setacea,* (SEM 2825); Bottom right, Coalesced spherulitic structure of heavily mineralized chamber of axial core of *Leptogorgia setacea* (SEM 2821).

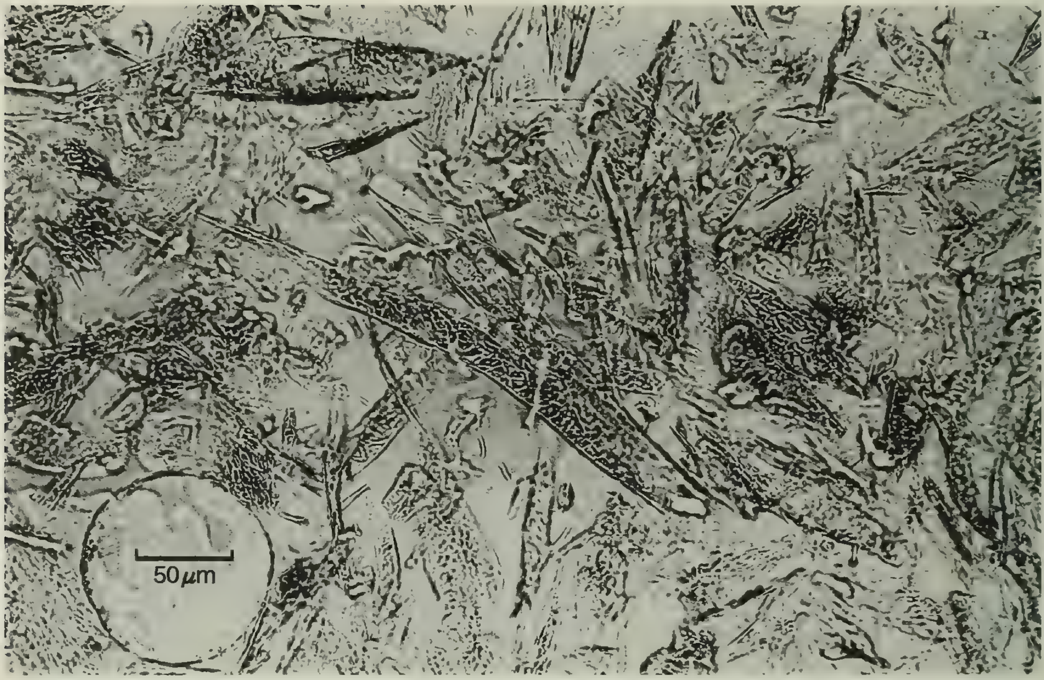

Fig. 11. Mineral residue from holdfast of *Eugorgia ampla* after removal of organic matrix by maceration in sodium hypochlorite. View of aqueous preparation in transmitted light showing one nearly complete loculus with mineralized internal filaments.

appeared on the lamellae of CHAp forming the axial cortex of *Leptogorgia virgulata* and *L. setacea,* but not on samples macerated for shorter periods (2–8 hours). X-ray diffraction showed those crystals to be calcium oxalate hydrate ($Ca_2CaO_4\cdot 2H_2O$).

The holdfast of a few gorgoniid species is strengthened by Mg-calcite or aragonite, but the only axial mineral in the family Gorgoniidae worldwide is carbonate hydroxylapatite (CHAp). The axis and holdfast in a few members of the family are not mineralized. Neither axis nor holdfast of those *Eunicella* species examined, including those listed in Table 1, revealed any mineral residue after complete maceration in 5.25% sodium hypochlorite; colonies of a few species of *Eunicella* form no holdfast, being unbranched or scantily branched and lying prone on the seafloor.

The following situations were observed in the present study:

1. Neither axis nor holdfast mineralized: *Eunicella, Swiftia, Leptogorgia caryi.*
2. Axis not mineralized, holdfast aragonite: *Pterogorgia, Eunicea, Muriceopsis, Plexaura* and *Pseudoplexaura.*
3. Axis not mineralized, holdfast Mg-calcite: *Rumphella.*
4. Axis and holdfast mineralized with CHAp: *Eugorgia, Gorgonia, Leptogorgia, Pacifigorgia, Pseudopterogorgia, Phycogorgia, Phyllogorgia.*
5. Axis mineralized with CHAp, holdfast with aragonite: *Olindagorgia, Pseudopterogorgia bipinnata.*
6. Axis with "loculi" filled with Mg-calcite, holdfast aragonite: *Plexaurella.*
7. Axis and holdfast Mg-calcite: *Junceella, Ellisella, Chrysogorgia, Radicipes, Ainigmaptilon, Fanellia, Fannyella, Primnoella.*
8. Axis and holdfast aragonite: *Narella, Candidella.*

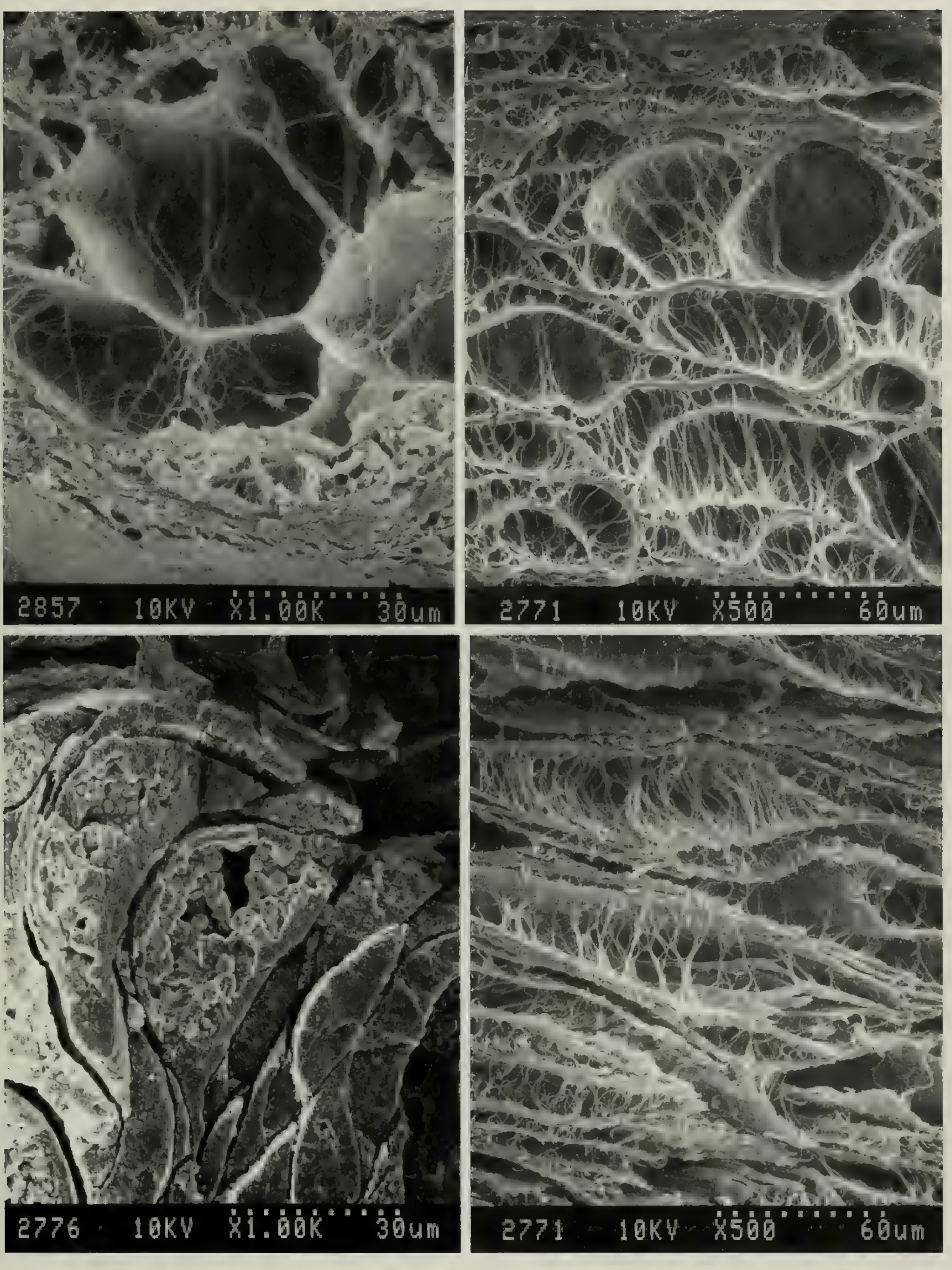

Fig. 12. Structure of gorgoniid holdfasts. Top left, *Leptogorgia alba:* Loculi polygonal in cross section (SEM 2857); Top right, *Pseudopterogorgia americana:* Loculi oval in cross section (SEM 2771); Bottom left, *Phycogorgia fucata:* Loculi crescentic in cross section (SEM 2776); Bottom right, *Pseudopterogorgia americana:* Loculi in longitudinal section (SEM 2771).

9. Axis aragonite, holdfast aragonite with Mg-calcite possibly as contamination from the substrate: *Plumigorgia, Ifalukella.*

Leptogorgia caryi and all species of *Eunicella* can be regarded as having the basic design of supporting skeletal structures of the Holaxonia (restricted sense) (Neumann 1911; Schimbke 1914; Schneider 1905). Unlike all other species of the genus *Leptogorgia* examined in this study, the axis and holdfast *L. caryi* yield no mineral component upon complete maceration in sodium hypochlorite.

Examination by SEM demonstrates that the chambers comprising the central core of the axis are filled with a meshwork of fine organic filaments (Fig. 1, top). The partitions between the chambers (Fig. 1, bottom) as well as the walls clearly consist of a close meshwork of fine organic filaments some of which extend between successive partitions to form the network filling the chambers. This microstructure of the partitions was not observed in paraffin sections of histological preparations, perhaps owing to the small diameter of the filaments: 0.3 μm and less.

The lamellae of the holdfast are likewise composed of fine filaments. Successive layers of holdfast are separated by approximately fusiform spaces (Fig. 2, top) corresponding to the loculi between concentric layers of gorgonin in the axial cortex of Paramuriceidae, Plexauridae and Acanthogorgiidae. These holdfast loculi contain filaments extending from wall to wall in a network more open than that in the chambers of the axial core (Fig. 2, bottom).

Mineral Morphology

Axis.—The gorgonin of the axis cortex of most gorgoniid species is permeated by CHAp. After removal of the organic matrix, it has the form of slender, tapered strands aligned in irregular spirals and arranged in concentric layers around the axis core (Fig. 3, top). These strands are the "crescentic calcareous loculi" described and illustrated by Lewis et al. (1992:291, fig. 6a, b) for *Lophogorgia cardinalis,* and comprise the "thin, crenulated layers or sheaths" mentioned by Macintyre et al. (2000).

The strands are in turn composed of fine mineral fibers ("crystals," Lewis et al. 1992:292, fig. 6d) longitudinally oriented and showing minute, irregular surface granulations (Fig. 3 bottom left). In many cases, the fractured surface of longitudinally fractured axial cortex consists of narrow mineral fibers closely packed in longitudinal orientation (Fig. 3 bottom right).

Among all genera and species in which it has been observed by SEM, CHAp has a strikingly consistent morphology in the chambered core of the axis and in the loculi of the hold-fast. The mineral is precipitated on the fibrillar structure of the walls and the meshwork of organic filaments in the form of microspheres that range in size from 0.15 μm (or smaller) up to 0.3 μm (Figs. 4–7), but sometimes as much as 6.5 μm (Fig. 21, top left).

The meshwork of filaments filling the chambers of the core varies greatly in complexity and extent of mineralization. In *Leptogorgia viminalis,* the filaments are very fine, only moderately anastomosed, and mineralized with very small microspheres (Fig. 4). In *L. lemasti,* the meshwork is dense and closely anastomosed, mineralized with small microspheres (Fig. 5), and in *L. cardinalis,* anastomosis is more open (Fig. 6) but the mineralization consists of larger microspheres.

Microspheres may be arranged uniserially, bead-like along the filaments, usually with isolated microspheres located at random. The microspheres commonly become fused around the filaments to produce branching, anastomosing rods with irregular surfaces retaining vestiges of the initially bead-like structure (Fig. 7). The hollow core visible in broken ends of filaments represents the space originally occupied by the organic filament removed by maceration in sodium hypochlorite (Fig. 7, bottom left).

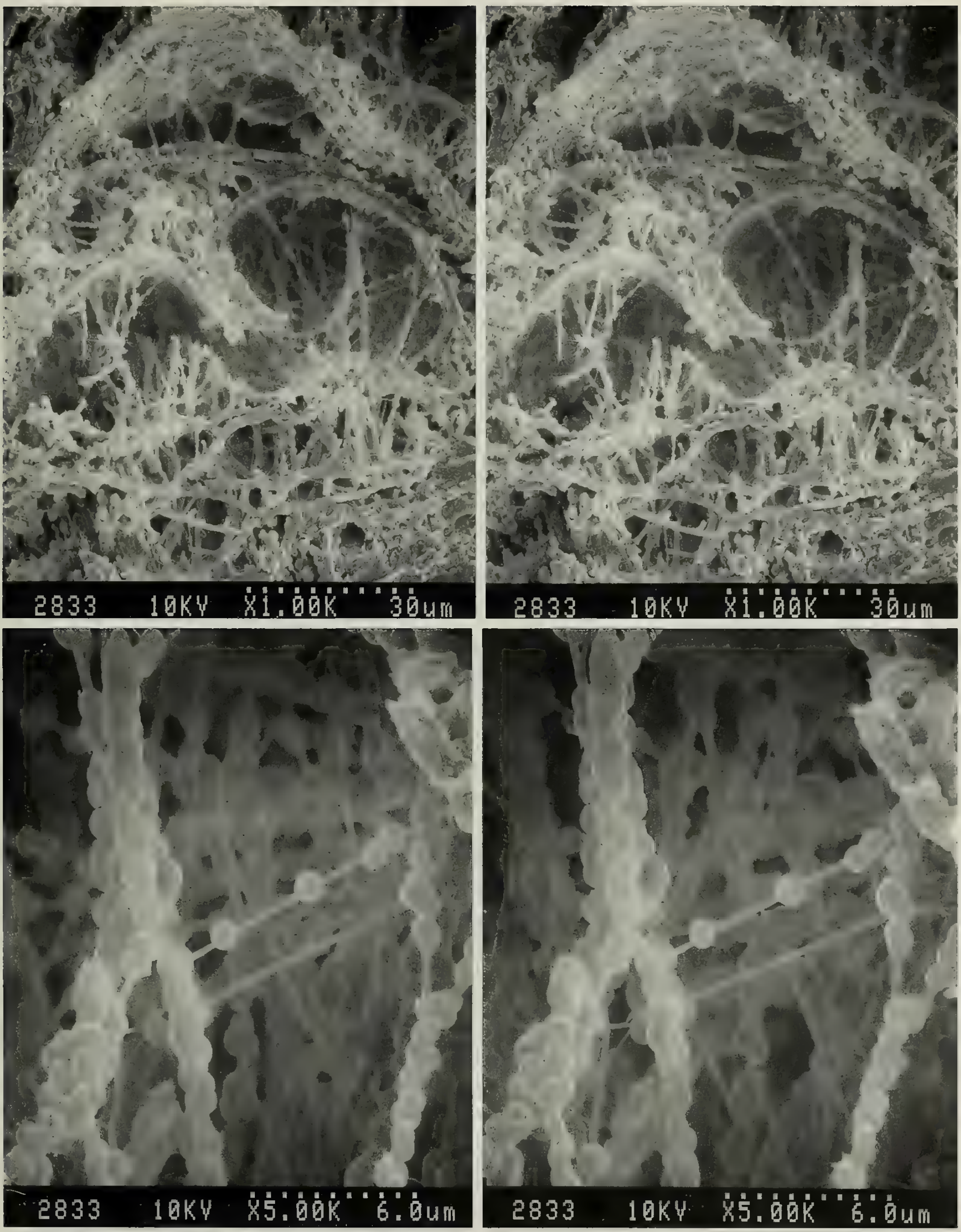

Fig. 13. Structure of gorgoniid holdfast. Cross section of loculi of *Leptogorgia lemasti* without maceration in sodium hypochlorite, leaving organic components in place, showing CHAp microspheres on organic filaments (SEM 2833, stereo pairs).

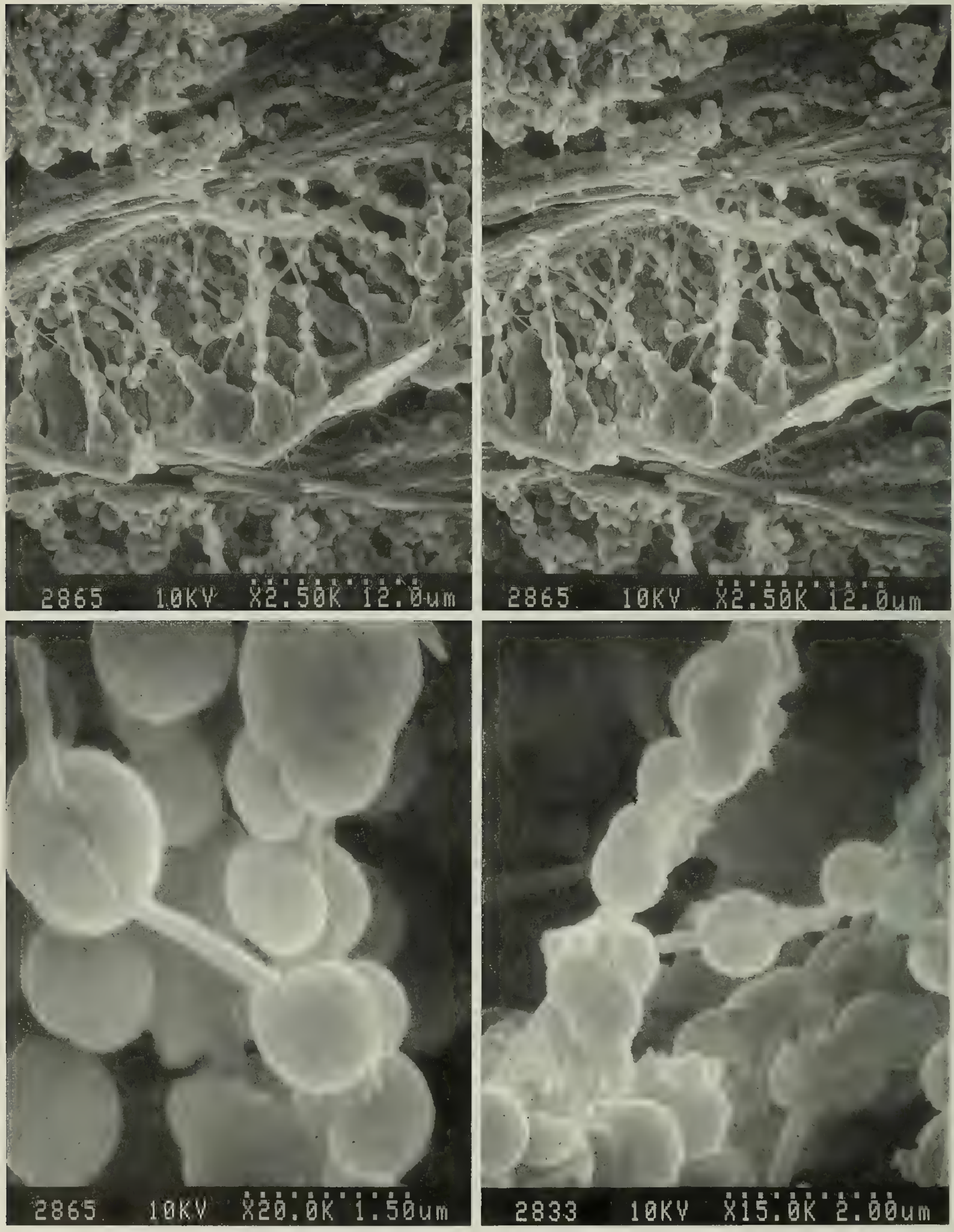

Fig. 14. Structure of gorgoniid holdfasts. Top, Longitudinal section of holdfast loculus of *Pacifigorgia cribrum* without maceration in sodium hypochlorite, leaving organic component intact (SEM 2865, stereo pair); Bottom left, Microspheres of CHAp on organic filaments of *Pacifigorgia cribrum* (SEM 2865); Bottom right, Microspheres of CHAp precipitated around filaments of holdfast loculi of *Leptogorgia alba* (SEM 2833).

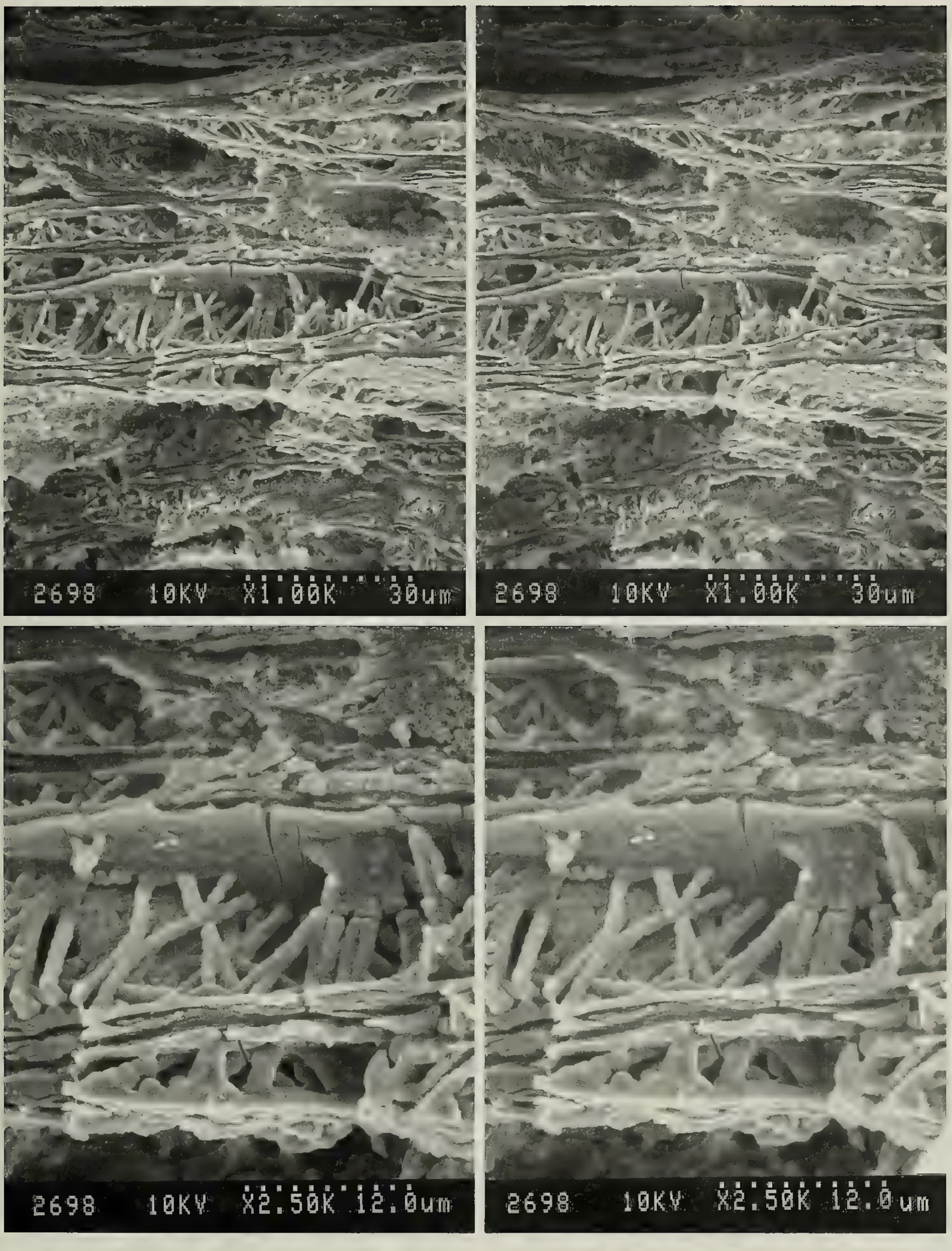

Fig. 15. Structure of gorgoniid holdfasts. Top, Longitudinal section of holdfast of *Gorgonia mariae* showing mineralized loculi; Bottom, Detail of above with filaments coated with microspheres of CHAp fused to form columns (SEM 2698, stereo pairs).

CHAp sometimes is deposited in distinct layers (Fig. 7, bottom right).

In weakly mineralized axes, the mineral component of the cortex separates from the core in delicate concentric sheets that break up into minute fragments during preparation. Depending upon the extent of mineralization, the core may remain more or less intact but in extremely fragile form, breaking up into longer and shorter fragments composed of a variable number of chambers that may expose the mineralized partitions and filaments within (Fig. 8 top). The partitions between chambers consist of two layers separated by a narrow space originally occupied by the organic lamella removed during maceration in sodium hypochlorite (Fig. 8 bottom).

The wall of the axial core may be so weakly mineralized that the contents of the chambers separate as individual disks, distally convex and basally concave (Fig. 9 top left). These disks are composed of the filamentous network so heavily mineralized that it is nearly solid CHAp (Fig. 9 top right), composed of the rodlike mineral coating of the organic filaments (Fig. 9 bottom left); greater magnification clearly shows the submicrospherulitic structure of the CHAp (Fig. 9 bottom right). When its wall is more strongly mineralized, the axial core may emerge from maceration as a cylinder of CHAp filled with a network of mineralized filaments (Fig. 10 top).

The greatest mineralization of the axial core was observed in the western Atlantic species *Leptogorgia setacea* and *L. stheno,* both of which form unbranched or weakly branched flagelliform colonies living prone on the seafloor. CHAp is precipitated more or less uniserially along the organic filaments in the form of microspheres that fuse together on the interior wall of the chambers, sometimes leaving a central lumen where incompletely fused microspheres were lost during preparation (Fig. 10 bottom left).

Holdfast.—At the base of the colony, the coenenchyme extends outward over the substrate and the basal axial epithelium secretes successive layers of gorgonin that form a spreading holdfast. The lamellae of the holdfast are partially separated by small open spaces of roughly fusiform shape, about 30 μm in diameter and undetermined length, analogous to the loculi between the layers of axial cortex present in the Paramuriceidae, Plexauridae and Acanthogorgiidae. These holdfast loculi contain fine organic filaments similar to those of the chambers of the axial core, secreted by the holdfast epithelium as it produces successive layers of gorgonin.

Maceration of holdfast tissue in sodium hypochlorite dissolves the gorgonin lamellae, leaving a finely divided residue consisting of the CHAp that lined the walls of the holdfast loculi. An aqueous preparation viewed under a petrographic microscope consists mostly of minute fragments of CHAp. Although the mineralized loculi are extremely fragile, a few may remain more or less intact, showing the fine, mineral-coated filaments filling the interior (Fig. 11).

Free-hand sections of untreated holdfast cut transversely and radially show the shape of the loculi. In cross section, loculi vary in shape from polygonal (Fig. 12 top left) to oval (Fig. 12 top right) and crescentic (Fig. 12 bottom left), often more or less irregular. In longitudinal section roughly along a radius of the holdfast, loculi are elongate, tapering, interdigitating with others at roughly the same level, separated vertically from those above and below by one or more layers of gorgonin (Fig. 12 bottom right). In the Gorgoniidae, CHAp is precipitated on the interior walls of the loculi and on the organic filaments, as is the case in the chambers of the axial core.

If not treated in sodium hypochlorite, the fine organic filaments remain essentially intact (Figs. 13, 14). Microspheres of CHAp are precipitated on the filaments apparently at random, as some filaments have none and others a few, while some are completely covered with mineral. The shape of the mi-

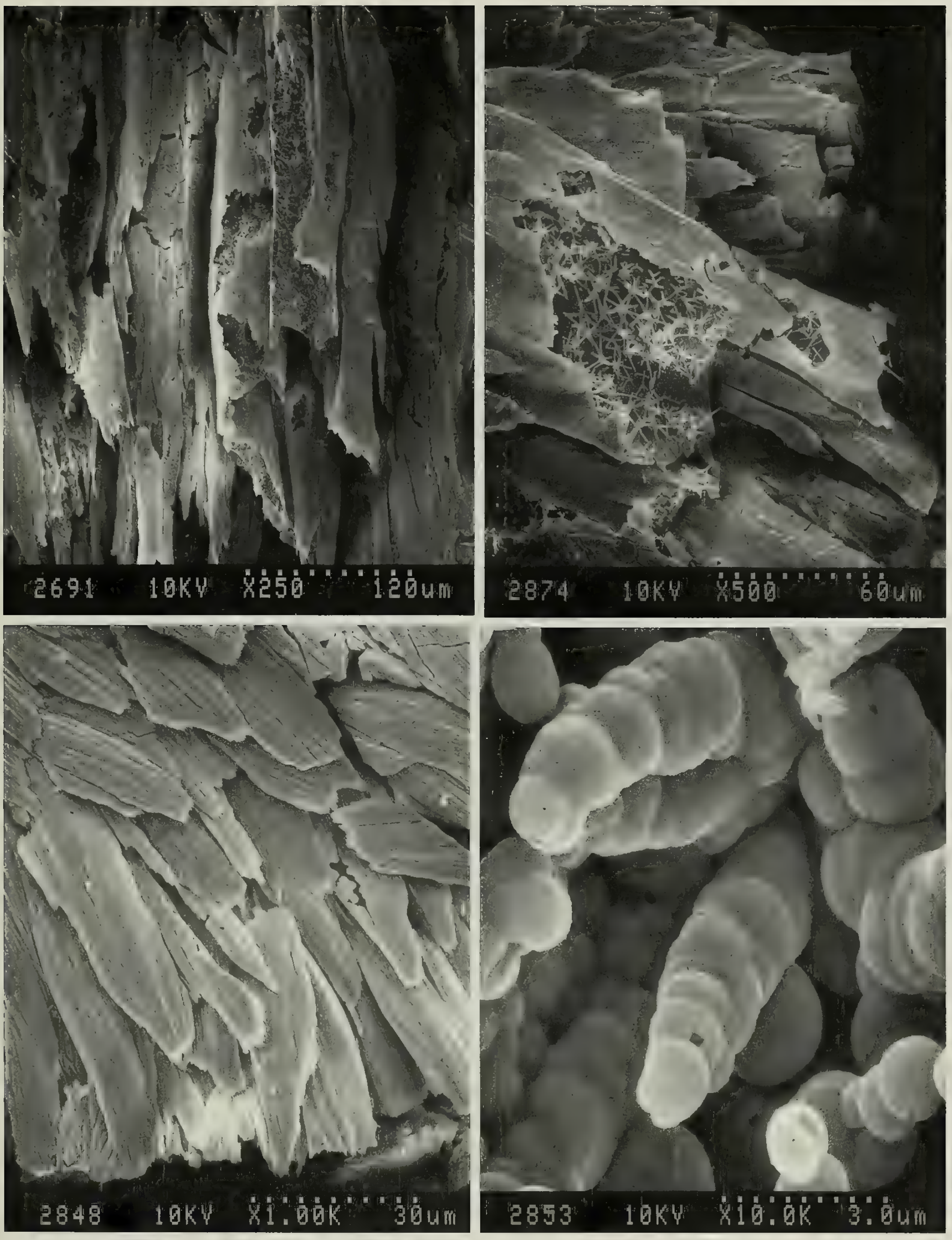

Fig. 16. Structure of gorgoniid holdfasts. Top left, *Eugorgia aurantiaca,* Mineralized loculi of holdfast partly etched from organic matrix (SEM 2691); Top right, *Pseudopterogorgia australiensis:* Mineralized loculi of holdfast partly etched from organic matrix (SEM 2874); Bottom left, *Pacifigorgia cribrum:* Mineralized loculi of holdfast partly etched from organic matrix (SEM 2848); Bottom right, *Pacifigorgia media,* Spherules of CHAp in lumen of holdfast loculus showing decrease in size along filament (SEM 2853).

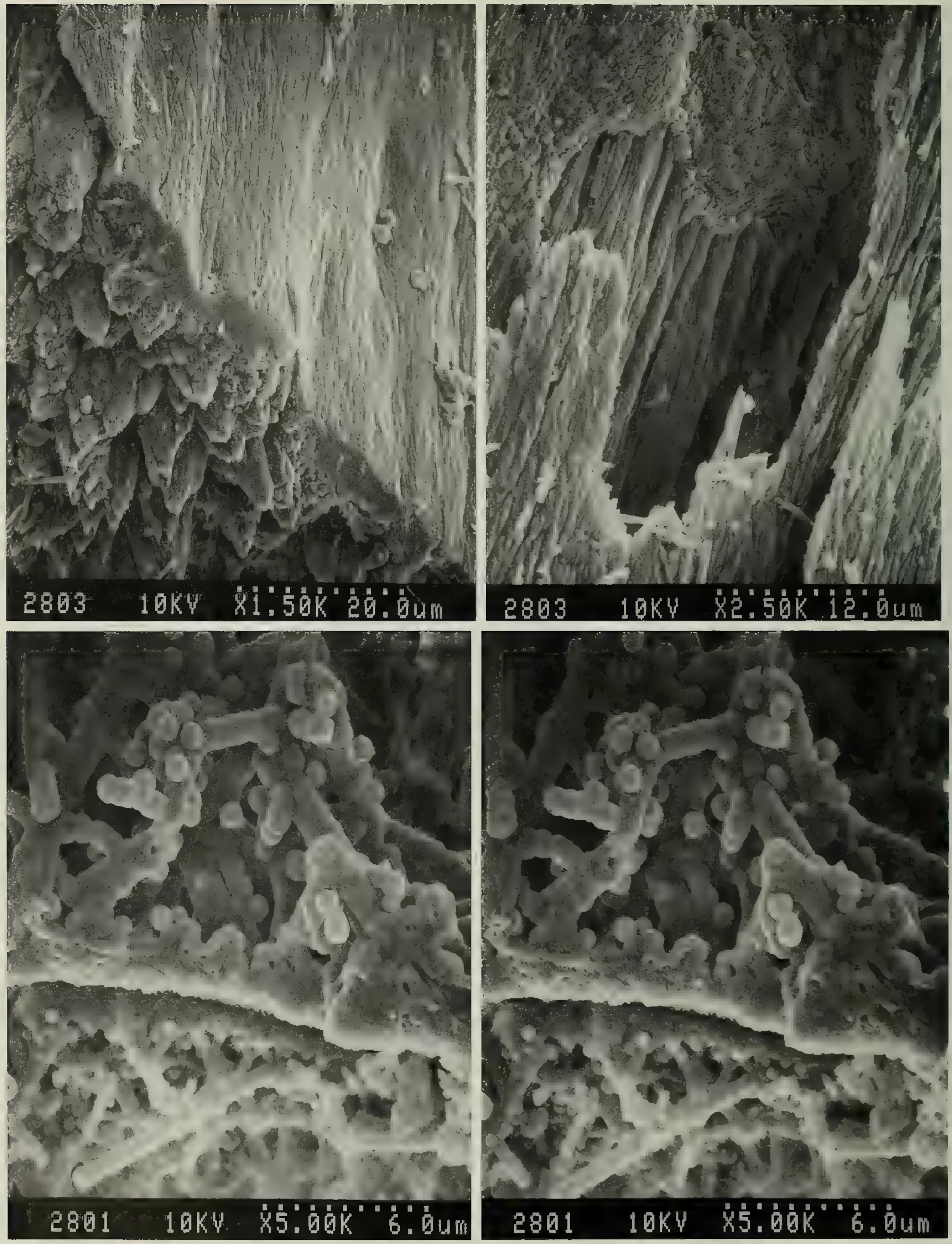

Fig. 17. Mineral components of gorgoniid supporting skeleton. Top, Crystalline aragonite of holdfast of *Olindagorgia marcgravii* (SEM 2803); Bottom, Coalesced microspheres of CHAp on filaments and partition between chambers of axial core of *Olindagorgia marcgravii* (stereo pair).

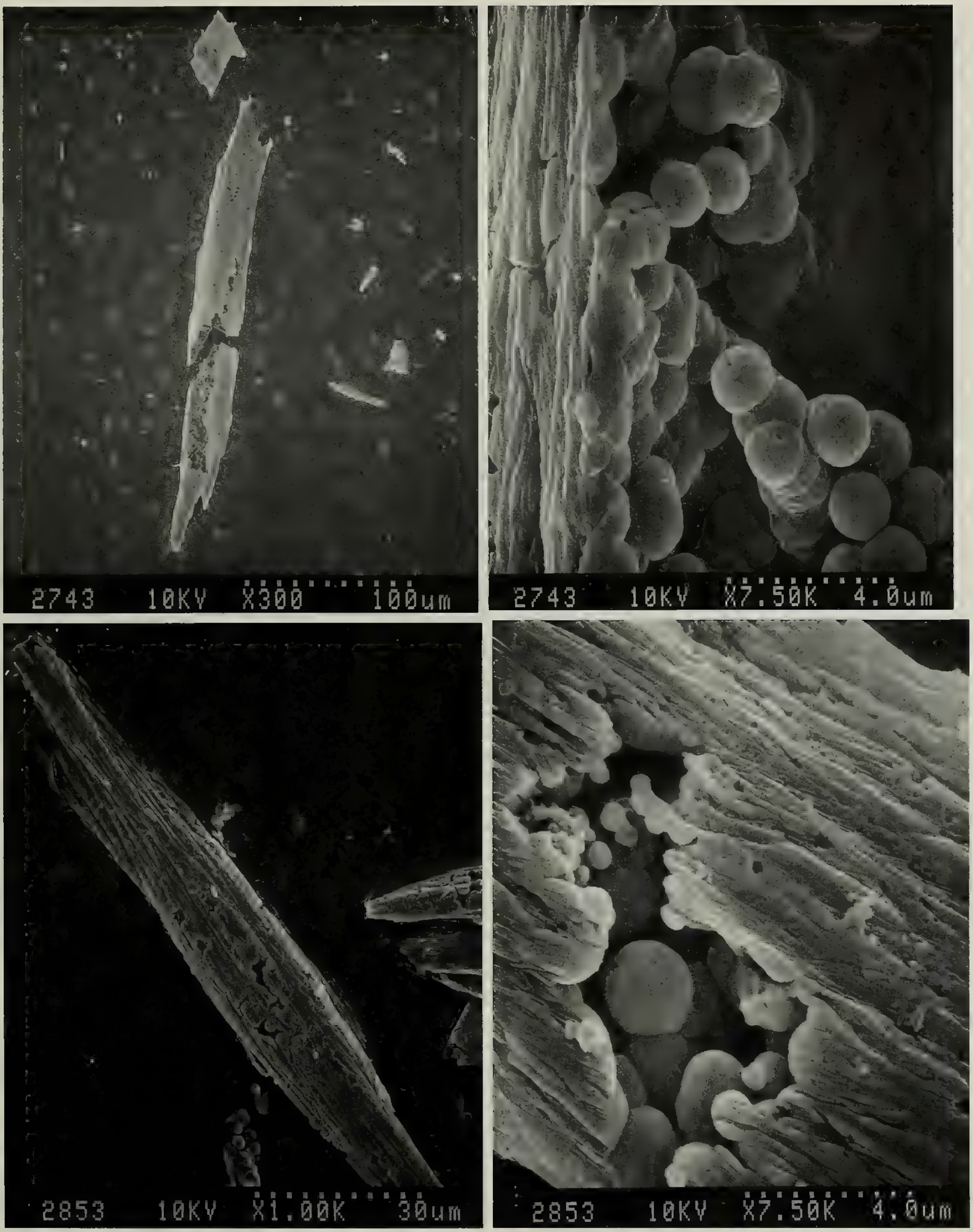

Fig. 18. Morphology of CHAp in Gorgoniidae. Top, *Eugorgia rubens:* Left, Single mineralized holdfast loculus isolated after maceration in sodium hypochlorite; Right, Microspheres of CHAp in lumen of loculus seen through break in wall (SEM 2743). Bottom, *Pacifigorgia media:* Left, Mineralized holdfast loculus isolated after maceration in sodium hypochlorite; Right, Microspheres of CHAp in lumen of loculus seen through break in wall (SEM 2853). The outer surfaces of the locular walls exhibit linear cast patterns of the gorgonin that surrounded them. These outer wall cast patterns can be seen also in Figs. 19 and 20.

crospheres indicates that precipitation of CHAp begins at a nucleation site on a filament and grows around it (Fig. 14, bottom).

The mineral component of the holdfast of *Gorgonia mariae* remains almost intact after brief treatment in sodium hypochlorite, as mineralization is stronger than in *L. lemasti*. The mineral lining of the loculi is strong, and uniserially arranged microspheres covering the filaments extend from wall to wall like columns (Fig. 15).

Partial removal of the organic surface of the holdfast reveals the surface of the underlying mineral. The mineralized loculi may be partially intact, fusiform as in *Eugorgia aurantiaca* (Fig. 16 top left), polygonal in cross section as in *Pseudopterogorgia australiensis* (Fig. 16 top right), or even scale-like as in *Pacifigorgia cribrum* (Fig. 16 bottom left). Transverse fractures and breaks in the locular walls provide a view of internal structure. The decreasing size of microspheres from the locular wall toward the interior (Fig. 16 bottom right) suggests a time element in formation of CHAp microspheres along the organic filaments during holdfast formation (also Fig. 13, top).

The holdfast loculi of *Phycogorgia fucata* are more strongly mineralized than in any other species examined in this study. Distinctly crescentic in cross section, they are filled more or less completely with partially fused microspheres (Fig. 12 bottom left).

Although the filaments and walls of the chambers of the axial core of *Olindagorgia marcgravii* are mineralized with microspherular CHAp of typical form (Fig. 17, top), the holdfast is mineralized with crystalline aragonite (Fig. 17, bottom), a combination unique so far in the family Gorgoniidae.

Complete removal of the gorgonin matrix frees the mineralized lining of the loculi, which retain more or less of their shape according to the degree of mineralization. Although fragile and extensively broken during preparation, the mineralized loculi in some cases may remain more or less intact, revealing their fusiform shape (Figs. 11, 18 top and bottom left). The microspheres of CHAp coating the wall and interior filaments can be seen through breaks in the wall (Fig. 18 top and bottom right). In species having a less extensively mineralized wall, the loculi and their interior microspheres break down into a fine white sediment composed of minute fragments, some of which retain traces of their original structure.

The outer surface of the locular wall is a cast of the surface of the gorgonin matrix upon which it was precipitated. In many cases the spheroidal form of the CHAp is distinctly retained (Figs. 19 top, and 20 bottom left), but in others it may be more or less completely obliterated owing to the small size of the component microspheres (Fig. 19 bottom left), and the wall may be composed of microspheres 0.6 μm in diameter fused to form a solid sheet (Fig. 19 bottom right). Typically, the microspheres comprising the locular wall are 1.1–1.4 μm in diameter, often but not always with a distinct central opening indicating the location of the organic filament that extended from the organic surface into the interior of the loculus (Fig. 19 top right) upon which it was deposited and which formed one of the "strings" for the bead-like microspheres filling the interior.

The surface of the microspheres of CHAp varies from smooth, even at high magnification (Fig. 20 top left, 21 top left) to sharply prickly (Fig. 21 top right and lower left) and coarsely thorny (Fig. 21 bottom right). In many species the surface is nearly smooth at moderate magnification (Fig. 21 top left), appearing finely granular or more coarsely granular at higher magnifications (Fig. 20 top right and bottom right).

The axes of *Pterogorgia anceps*, *P. citrina*, and *P. guadalupensis* reveal no mineral component upon maceration in sodium hypochlorite, but holdfasts are reinforced with dense crystalline aragonite (Table 1)

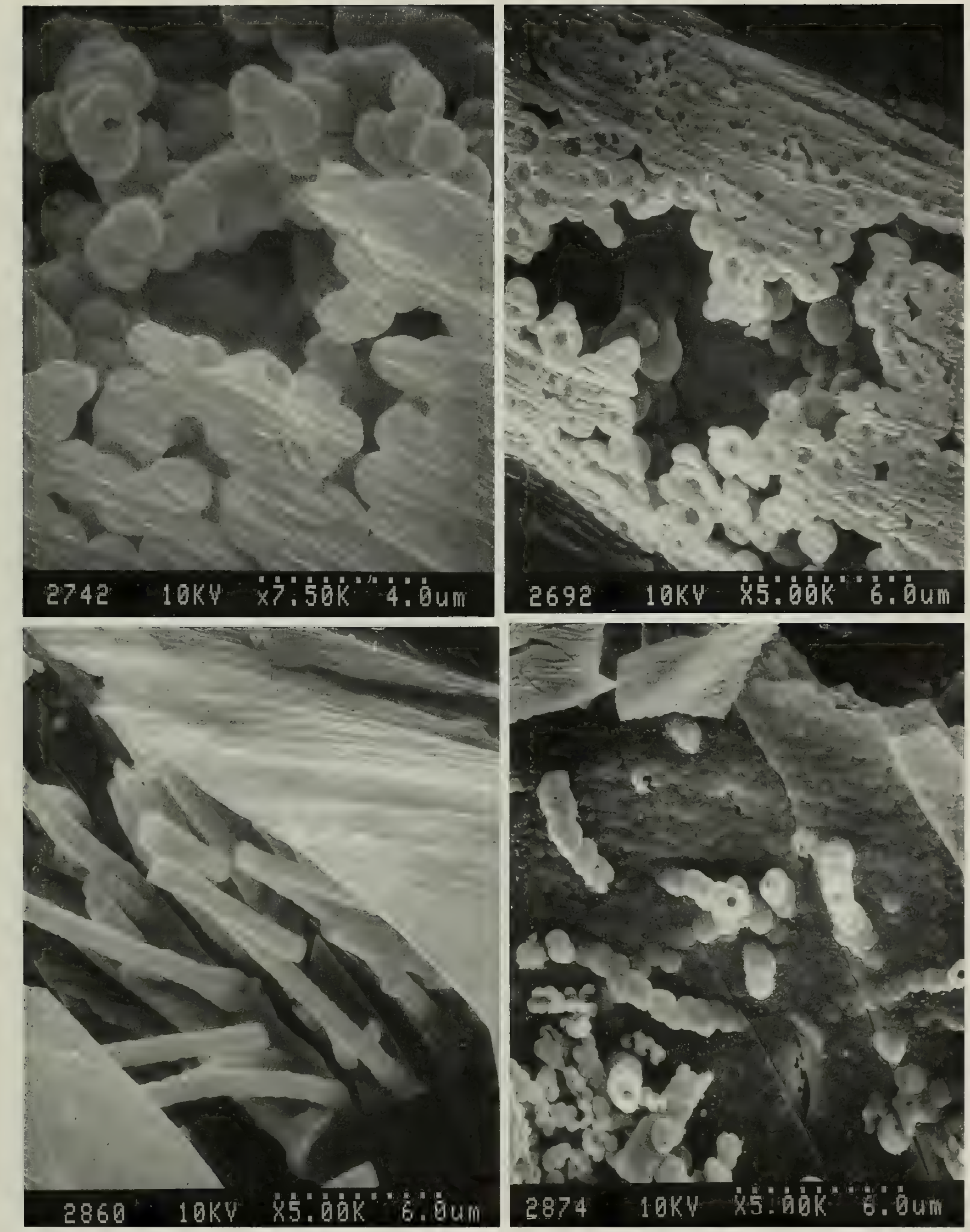

Fig. 19. Morphology of CHAp in Gorgoniidae. Top left, Surface of wall of holdfast loculus of *Eugorgia rubens* showing component hemispheres near gap in incompletely mineralized wall and microspheres of interior filaments (SEM 2742); Top right, Surface of wall of holdfast loculus of *Eugorgia aurantiaca* showing component hemispheres near gap in incompletely mineralized wall and microspheres of interior filaments (SEM 2692); Bottom left, Break in wall of mineralized holdfast loculus of *Pseudopterogorgia australiensis* showing filaments coated with fused microspheres of CHAp forming rod-like structures (SEM 2860); Bottom right, Interior of broken holdfast loculus of *Pseudopterogorgia australiensis* showing small microspheres of CHAp forming wall, and strands of uniserial microspheres extending from wall surface (SEM 2874).

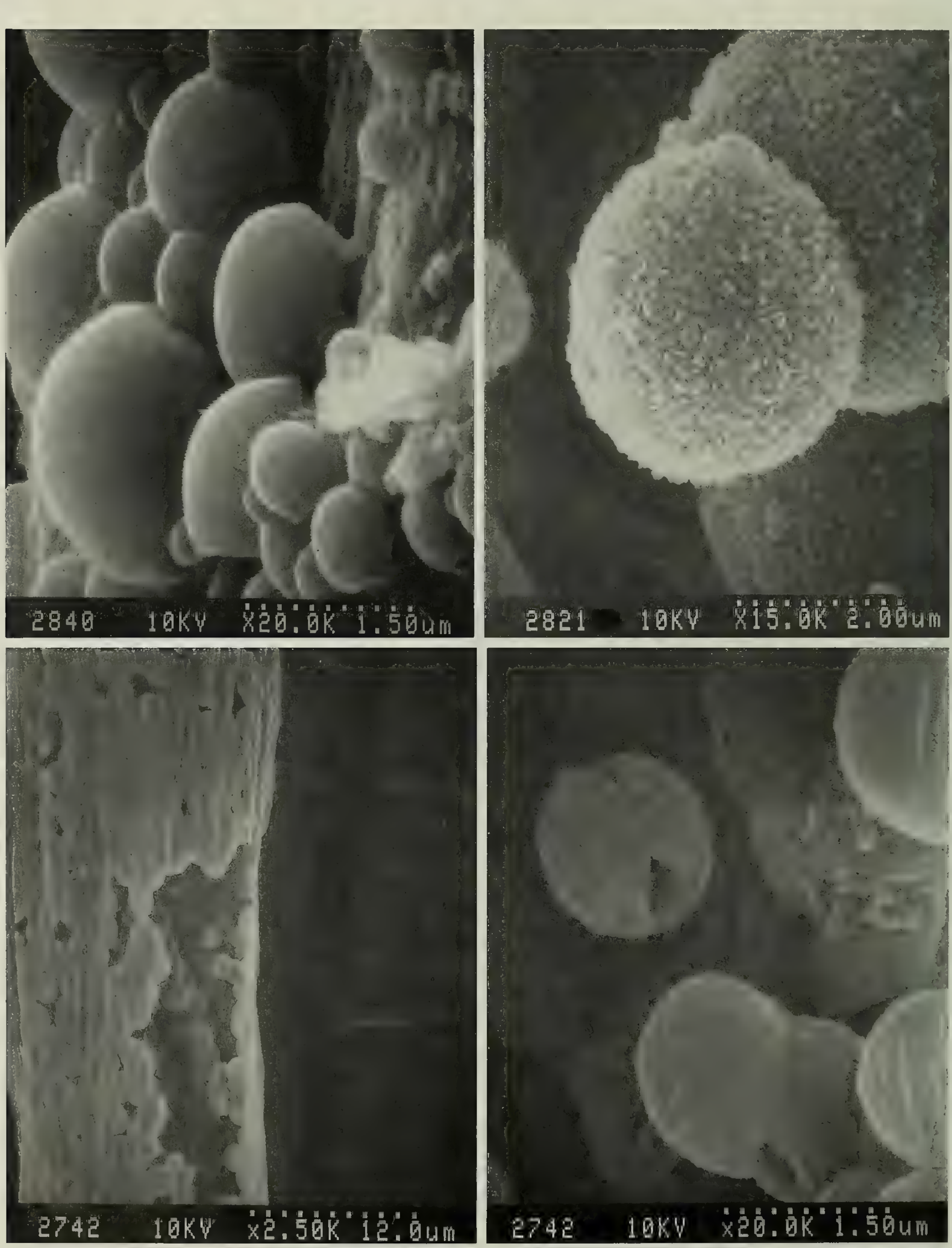

Fig. 20. Morphology of CHAp in Gorgoniidae. Top left, Microspheres of CHAp on wall of axial chamber of *Leptogorgia africana* (SEM 2840); Top right, Microsphere in axial chamber of *Leptogorgia setacea* (SEM 2821); Bottom left, Mineralized loculus of holdfast of *Eugorgia rubens* with incomplete wall consisting of hemispherical microspheres (SEM 2742); Bottom right, Microspheres of *Eugorgia rubens* at higher magnification to show surface texture and spaces formerly occupied by organic filament (SEM 2742).

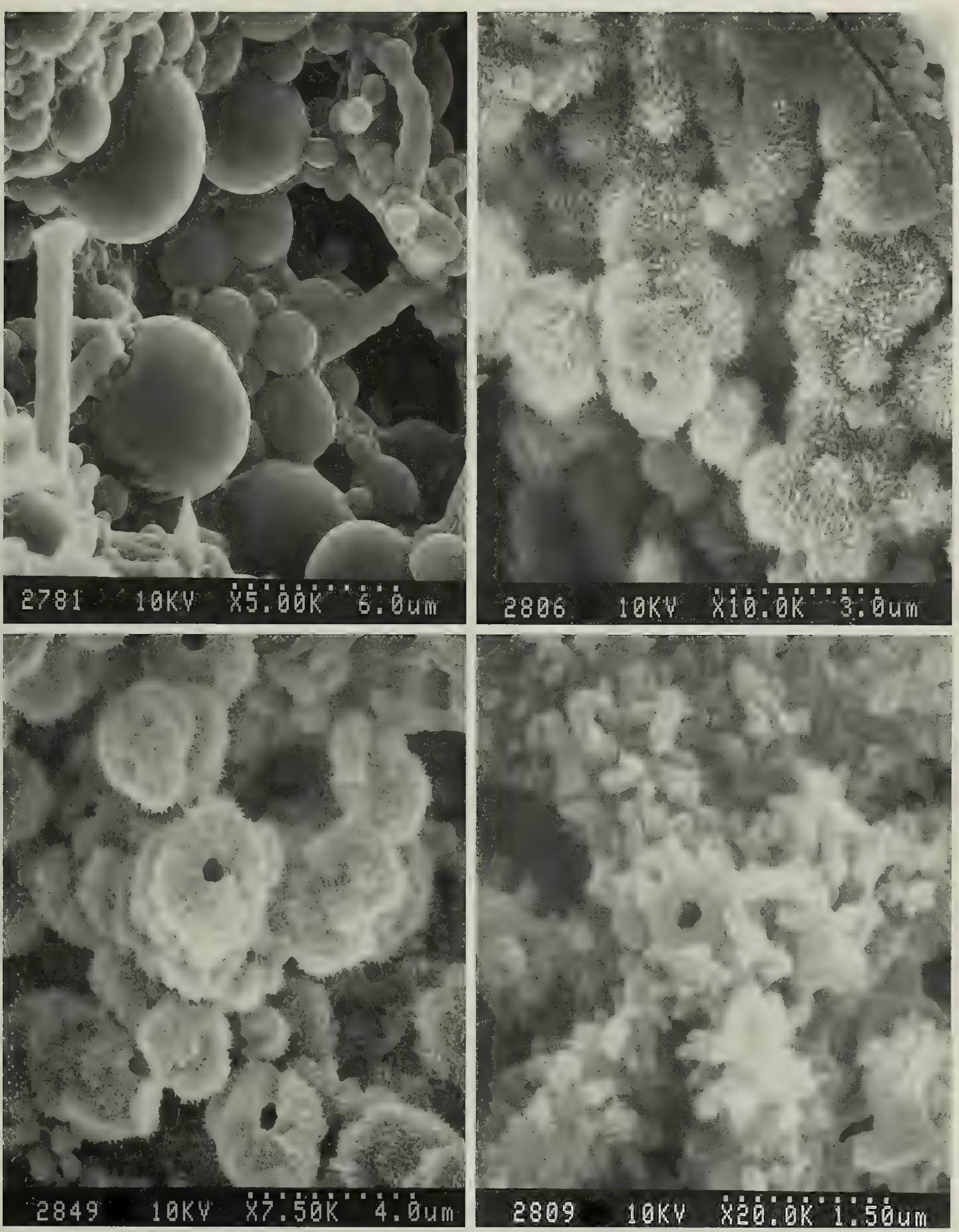

Fig. 21. Surface texture of CHAp in Gorgoniidae: Top left, Smooth microspheres in axial core of *Leptogorgia cardinalis*; Top right, Prickly microspheres in axial core of *Leptogorgia stheno*; Bottom left, prickly microspheres in axial core of *Pacifigorgia cribrum*; Bottom right, Thorny surface of CHAp coating filaments of axial core of *Leptogorgia riodouroi* (SEM 2809).

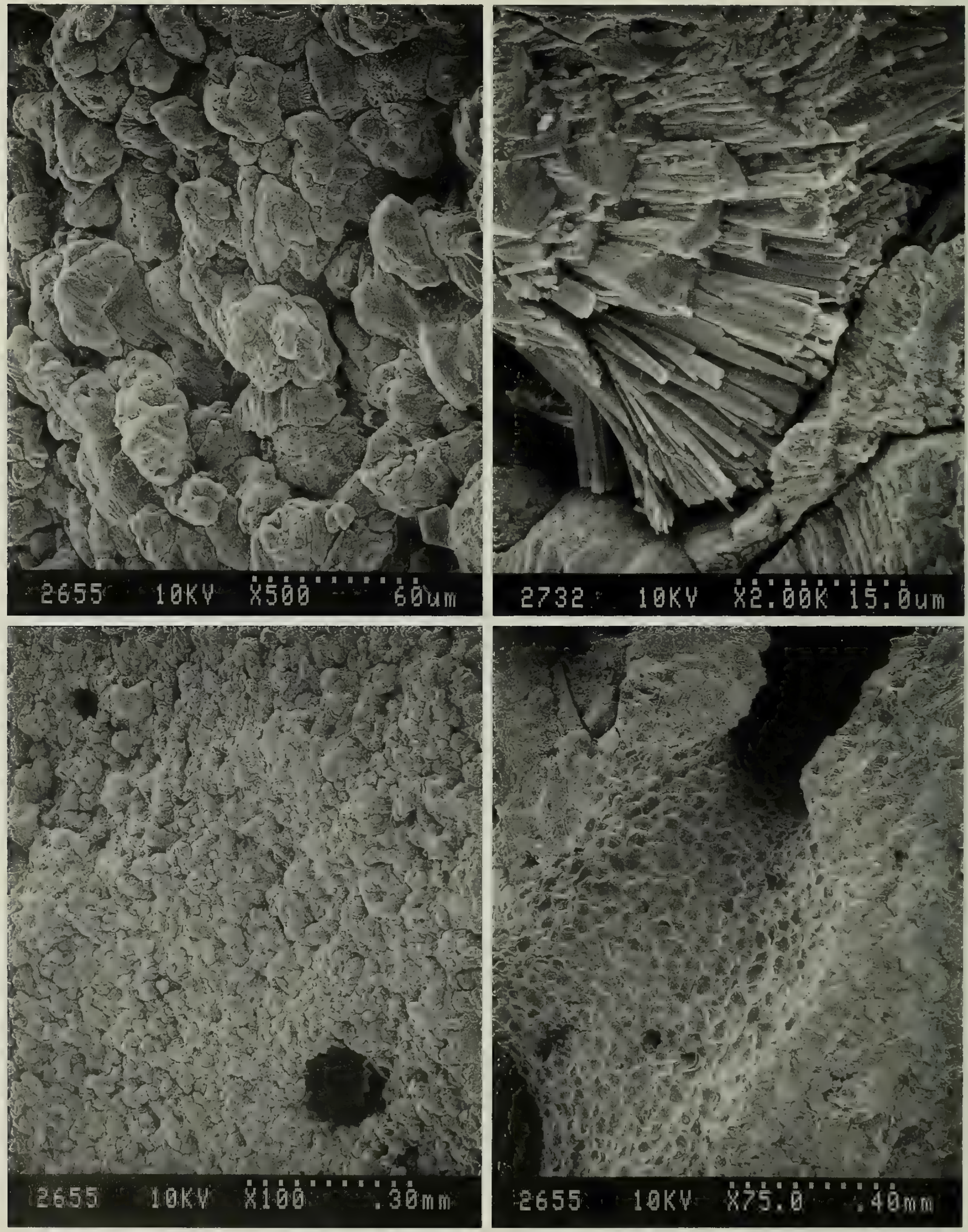

Fig. 22. Mineral of holdfast of *Pterogorgia anceps:* Top left, Surface of holdfast (SEM 2655); Top right, Fracture surface showing aragonite crystals (SEM 2732); Bottom left, Surface of holdfast showing entrance to sponge gallery (SEM 2655); Bottom right, fracture surface showing inner surface of sponge gallery (SEM 2655).

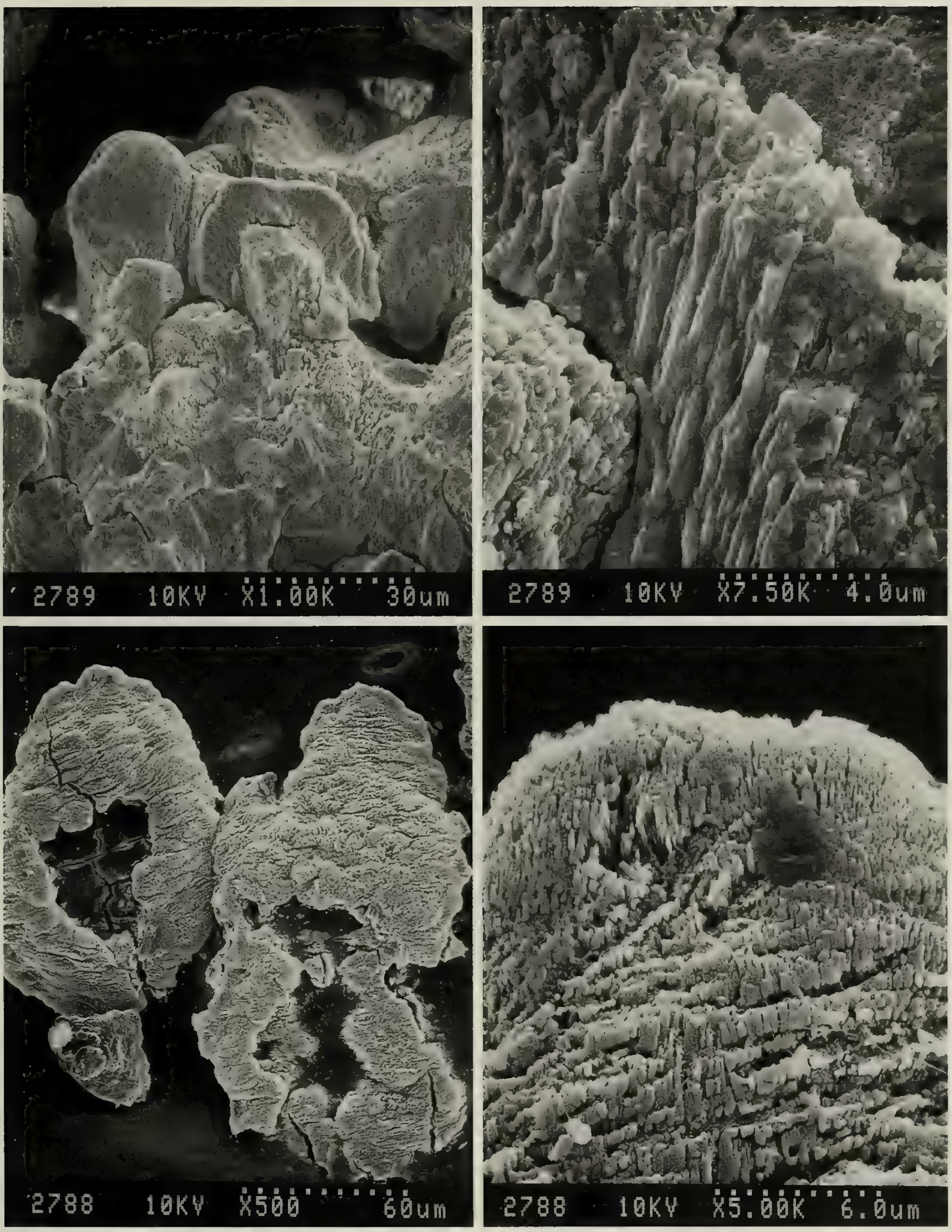

Fig. 23. Mineral of holdfast of *Rumphella aggregata.* Top left, Fracture surface of component granules of Mg-calcite (SEM 2789); Top right, Fracture surface showing calcite crystals (SEM 2789); Bottom left, Incompletely formed granules of calcite on surface of organic lamella near edge of holdfast (SEM 2788); Bottom right, calcite crystals of incomplete granule of holdfast (SEM 2788).

Table 1.—Gorgonian skeletal mineralogy.

Species	Locality/depth	Holdfast	Axis
	HOLAXONIA		
	Keroeididae		
Keroeides pallida 25366	Hawaii/252–256 m	not collected	calcite 9.2 mole% $MgCO_3$
	Acanthogorgiidae		
Acanthogorgia armata 17239	Newfoundland/380 m	no mineral	no mineral
	Paramuriceidae		
Paramuricea placomus 14491	Georgia/644 m	no mineral	no mineral
Swiftia exserta 94393	Bahamas/180–190 m	no mineral	no mineral
	Plexauridae		
Eunicea tourneforti 50275	Florida/reef	aragonite	no mineral
Muricea muricata 50314	Curaçao/reef	not analyzed[2]	no mineral
Muriceopsis flavida 14374	Nassau/reef	aragonite	no mineral
Plexaura flexuosa 51769	Yucatan//reef	aragonite	no mineral
Plexaura homomalla 50689	Andros/reef	aragonite	no mineral
Plexaurella grisea 6917	Florida/reef	aragonite	calcite 15.7 mole% $MgCO_3$
Plexaurella nutans a/c 322031	Florida/reef	aragonite	calcite 15.7 mole% $MgCO_3$
Pseudoplexaura porosa 1629	Florida/reef	aragonite	no mineral
	Gorgoniidae		
Eugorgia ampla 8967	Baja California/shallow	CHAp	CHAp
Eugorgia aurantiaca 52317	California/shallow	CHAp	CHAp
Eugorgia aurantiaca a/c 16679	Panama/shallow	CHAp	CHAp
Eugorgia rubens 50032	LaJolla, Cal./31–37 m	CHAp	CHAp
Eunicella cavolini 89285	Genoa/39 m	no mineral	no mineral
Eunicella filiformis 82909	Mauretania/35–50 m	no holdfast[1]	no mineral
Gorgonia flabellum 51766	Cozumel/reef	CHAp	CHAp
Gorgonia mariae 93965	Grenada/13 m	CHAp	CHAp
Gorgonia ventalina 55027	Dominican Rep./17–22 m	not analyzed[2]	CHAp
Leptogorgia cardinalis 50052	Off Captiva/80 m	not analyzed[2]	CHAp
Leptogorgia cardinalis 49711	Off Palm Beach/37 m	calcite[3] 11.4 mole% $MgCO_3$	CHAp
Leptogorgia caryi 57157	Str. Juan de Fuca/73 m	no mineral	no mineral
Leptogorgia gilchristi 59824	Mozambique/55 m	not analyzed[2]	CHAp
Leptogorgia lemasti 52730	W. Mexico/shallow	CHAp	CHAp

Table 1.—Continued.

Species	Locality/depth	Holdfast	Axis
Leptogorgia riodouroi 82910	Mauretania/35–50 m	no holdfast[1]	CHAp
Leptogorgia sanguinolenta 82904	Off Ivory Coast/20 m	CHAp	CHAp
Leptogorgia setacea 43245	Virginia/24 m	no holdfast[1]	CHAp
Leptogorgia stheno (white) 49781	Off Louisiana/64 m	no holdfast[1]	CHAp
Leptogorgia stheno (pink) 49782	Off Louisiana/49 m	no holdfast[1]	CHAp
Leptogorgia stheno (pink) 50033	Off Louisiana/55–70 m	no holdfast[1]	CHAp
Leptogorgia styx 98800	NE of Clipperton I/1900 m	CHAp	CHAp
Leptogorgia viminalis 82905	Off Liberia/46–49 m	not collected	CHAp
Leptogorgia virgulata 49690	Apalachee Bay/6 m	CHAp	CHAp
Olindagorgia marcgravii 73426	Brazil/3 m	aragonite	CHAp
Pacifigorgia cribrum 1677	C. San Lucas/shallow	CHAp	CHAp
Pacifigorgia media 57905	I. Maria Magdalena/10–12 m	CHAp	CHAp
Pacifigorgia stenobrochis 49366	Panama/shallow	CHAp	CHAp
Phycogorgia fucata 56886	Chile/45 m	CHAp	CHAp
Phyllogorgia dilatata 5247	Brazil/shallow	CHAp	CHAp
Pseudopterogorgia americana 53582	Belize/4–5 m	not collected	CHAp
Pseudopter. australiensis 82139	W. Australia/8 m	not collected	CHAp
Pseudopter. australiensis 80952	Darwin/weed reef	CHAp	CHAp
Pseudopter. australiensis 80953	NW Shelf Australia/37–39 m	CHAp	CHAp
Pseudopterogorgia bipinnata 96216	Eleuthera/7.63 m	aragonite	CHAp
Pterogorgia anceps 50057	Sarasota/2 m	aragonite	no mineral
Pterogorgia guadalupensis 51311	Aruba/reef	aragonite	no mineral
Pterogorgia guadalupensis 52029	St. John, V.I./reef	not collected	no mineral
Pterogorgia citrina 51028	Anegada/1 m	aragonite	no mineral
Rumphella aggregata 86004	Gilbert Is./2–5 m	calcite 12.7 mole% $MgCO_3$	no mineral
	CALCAXONIA		
	Ellisellidae		
Junceella gemmacea not cat.	Philippines/shallow	calcite 13.8 mole% $MgCO_3$	calcite 14.0 mole% $MgCO_3$
Ellisella barbadensis 50610	Off Pensacola/75 m	calcite 11.2 mole% $MgCO_3$	calcite 11.1 mole% $MgCO_3$
	Ifalukellidae		
Ifalukella yanii 50142	Caroline Is./3 m	aragonite calcite[3] 11.2 mole% $MgCO_3$	aragonite
Plumigorgia hydroides 59811	Cuyo Ids, Sulu Sea/15 m	aragonite calcite[3] 12.3 mole% $MgCO_3$	aragonite

Table 1.—Continued.

Species	Locality/depth	Holdfast	Axis
	Chrysogorgiidae		
Chrysogorgia spiculosa 52851	Key West/1281 m	calcite 6.4 mole% $MgCO_3$	calcite 11.7 mole% $MgCO_3$
Radicipes gracilis 11913	Georges Bank/3259 m	calcite 8.3 mole% $MgCO_3$	calcite 8.3 mole% CO_3
	Primnoidae		
Ainigmpatilon edisto 54491	Ross Sea/611 m	calcite 6.4 mole% $MgCO_3$	calcite 10 mole% $MgCO_3$
Ainigmaptilon antarcticum 82871	S. Shetland Is./88–112 m	calcite 5.9 mole% $MgCO_3$	calcite 9.8 mole% $MgCO_3$
Calyptrophora trilepis 57445	Blake Plateau/814 m	aragonite	aragonite
Candidella sp. 56774	Hawaii/374 m	aragonite	aragonite
Fanellia tuberculata 30029	Japan/187 m	calcite 9.9 mole% $MgCO_3$	calcite 13.8 mole% $MgCO_3$
Fannyella rossii 77360	Antarctic Peninsula/110 m	calcite 6.3 mole% $MgCO_3$	calcite 7.9 mole% $MgCO_3$
Narella n. sp. a/c 272779	Hawaii/ca. 250 m	aragonite	aragonite
Primnoella scotiae 77370	Argentina/ca. 400 m	calcite 6.9 mole% $MgCO_3$	calcite 7.9 mole% $MgCO_3$

[1] Colonies lie prone on soft substrate, not forming a holdfast.

[2] Not analyzed because holdfast could not be separated from substrate.

[3] Probably contamination from substrate.

which, in some cases, is extensively perforated by a boring sponge. The mineral is deposited in the form of irregular granules that fuse into a solid mass (Fig. 22 top left); fracture surfaces clearly reveal the aragonite crystals of the component granules (Fig. 22 top right). The outer surface of the mineralized holdfast is granular, with pores opening into the sponge galleries (Fig. 22 bottom left), the walls of which show the usual pitted surface characteristic of sponge borings (Fig. 22 bottom right).

The axis of the Indo-Pacific genus *Rumphella* has no mineral component but the holdfast is reinforced with massive crystalline $CaCO_3$. Unlike the case in *Pterogorgia,* the mineral form is Mg-calcite containing 12.7 mole% magnesium carbonate. The surface of the mineralized holdfast is coarsely granular as is the case in *Pterogorgia* but the individual granules are more distinctly separated, stacked one upon another and fusing proximally (Fig. 23 top left); fracture surfaces reveal the orientation of the calcite crystals (Fig. 23 top right). The surface of a holdfast near what must have been an actively thickening margin shows incompletely formed nodules (Fig. 23 bottom left) composed of crystalline Mg-calcite (Fig. 23 bottom right) on the surface of the organic lamella.

Conclusion

This detailed study of the skeletal mineralogy of axes and holdfasts of 58 species of Gorgonacea further documents the presence of aragonite (Lowenstam 1964), amorphous carbonate hydroxylapatite (Macintyre et al. 2000), and Mg-calcite (Lowenstam 1964) in these structures. In contrast, octocoral sclerites as far as known are composed of Mg-calcite (Chave 1954, Lowenstam 1964, Milliman 1974). Apatite, though unusual in modern invertebrates, is said to be common in invertebrates in the fossil record. Hence, Macintyre et al. (2000) interpreted its occurrence in the family Gorgoniidae to be a vestige of an earlier history of phosphatic skeletal mineralization among coelenterates.

The distribution of skeletal minerals in the various octocoral species studied suggests that the patterns are taxonomically rather than environmentally controlled. This is particularly well demonstrated by the enigmatic occurrence of carbonate hydroxylapatite, which is found only in the family Gorgoniidae over its entire geographic and bathymetric ranges. It also raises the question about the significance of mineralogical differences among genera and species in one family traditionally defined on the basis of morphological characteristics.

The possible relationship between skeletal mineralogy in the axes and holdfasts of octocorals and their taxonomy could prove to be useful in resolving problems in octocoral systematics. Future descriptions of octocoral species should therefore consider the mineralogy that may exist in axes or holdfasts.

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Preparation of this paper has severely tested the patience of numerous colleagues. William T. Boykins performed innumerable analyses by X-ray diffraction, M. Amelia V. Logan provided analyses on the electron microprobe, Donald Dean prepared samples for microprobe analysis, Kenneth P. Towe, Eugene Jarosewich, and H. Catherine W. Skinner gave invaluable advice and information regarding chemistry. Walter R. Brown and Susann Braden provided essential expertise with the scanning electron microscope.

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114(1):346–348. 2001.

Errata

The following are corrected Figures (Figs. 1, 6 & 7) for: Littmann, Burr, & Nass. 2000. Proc. Biol. Soc. Wash. 113(4): 900–917. The map printed as Fig. 6 (113: 912) is cited correctly in the text and should have been identified as Fig. 5. These mistakes were no fault of the authors.

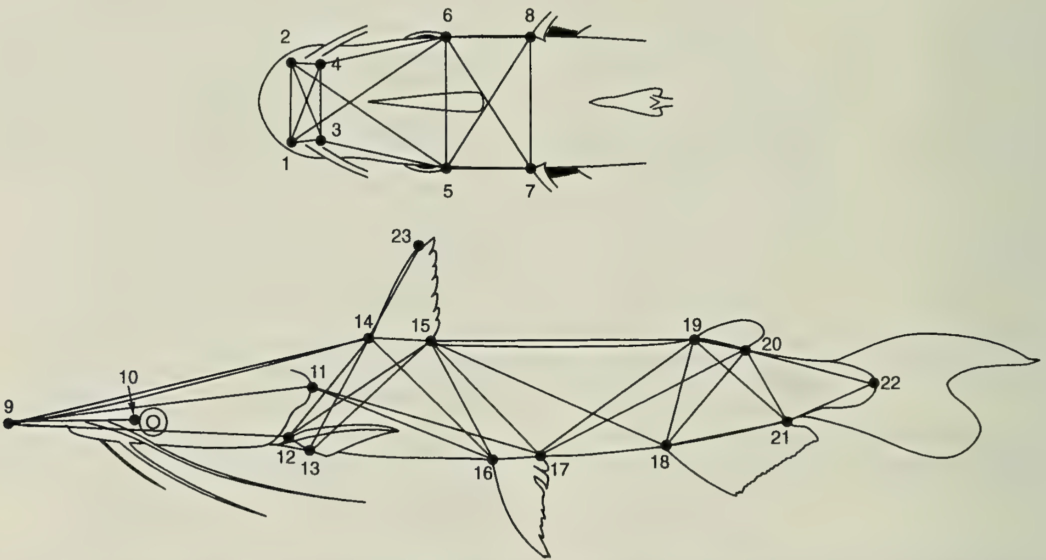

Fig. 1. Diagrammatic representation of 15 head measurements, 31 body measurements, and truss network used in sheared principal component analyses of the species of *Sorubim*. Descriptions of distance measures are provided in Table 2.

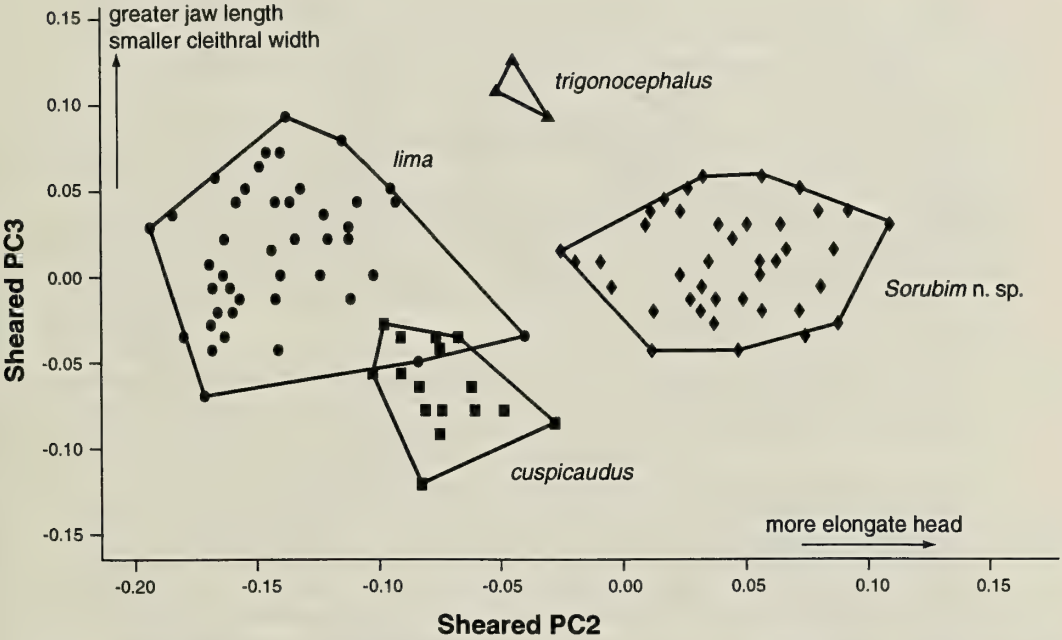

Fig. 5. Record stations in South America of *Sorubim cuspicaudus* n. sp. Open symbol is type locality in Río Magdalena, Puerto Soplaviento, Colombia. Dots may represent more than one lot or locality. Base map by M. Weitzman.

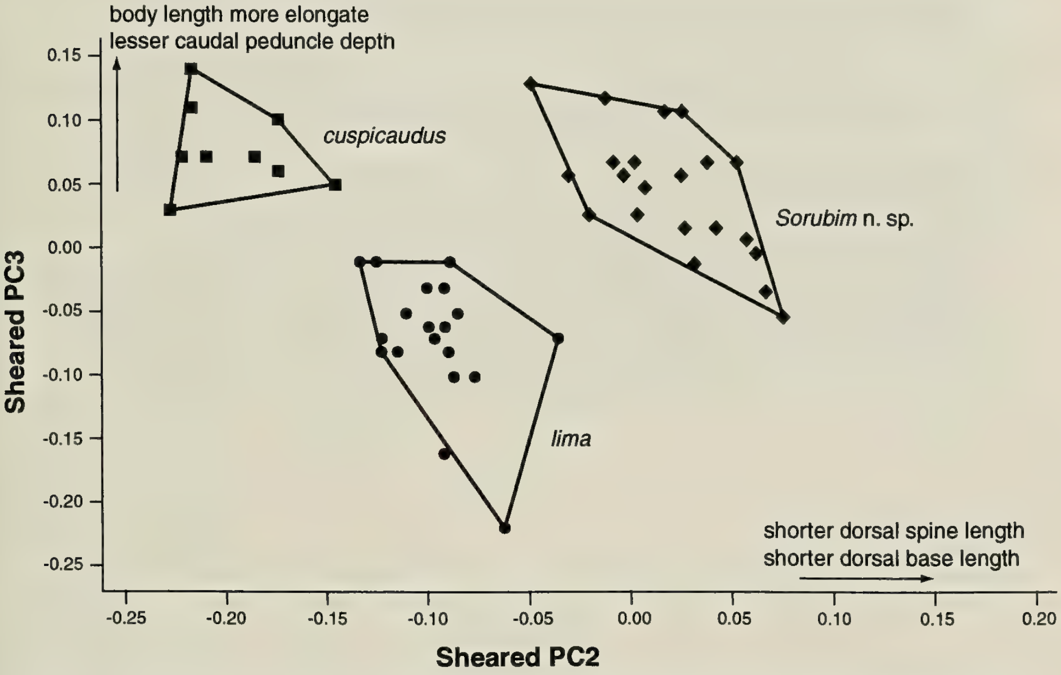

Fig. 6. Morpometric scores of head measurements on sheared PC axes 2 and 3 for 45 specimens of *Sorubim lima,* 43 specimens of *Sorubim* n. sp., 17 specimens of *S. cuspicaudus* n. sp., and three specimens of *S. trigonocephalus.*

Corrections to "*Grievella shanki,* a new genus and species of scolecitrichid calanoid copepod (Crustacea) from a hydrothermal vent along the southern East Pacific Rise"—Proceedings of the Biological Society of Washington 113: 1079–1088 [Frank D. Ferrari & E. L. Markhaseva, 2000].

Page 1080, column 2, line 4: and extra digit was inadvertently added to the catalogue number of the holotype; the correct catalogue number is USNM 261784. The length of the female holotype and only specimen was omitted; the dissected female is 2.15 mm, with a prosome of 1.61 mm and a urosome of 0.54 mm.

Page 1081, the last sentence of the figure legend should read: "Scale lines for A & B are 1.0 mm, for C–J 0.1 mm."

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New species of antipatharians (Cnidaria: Anthozoa) from Madeira, with the establishment of a new genus

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Abstract.—A new genus, *Tanacetipathes*, and two new species of antipatharian corals, *T. cavernicola* and *T. wirtzi*, are described from the waters off Madeira. Included in the new genus are the species *T. tanacetum* (Pourtalès, 1880), *T. hirta* (Gray, 1857), *T. barbadensis* (Brook, 1889), *T. thamnea* (Warner, 1981), and *T. spinescens* (Gray, 1857). Species in the genus are differentiated by the branching pattern of the corallum; the number, length, and arrangement of the primary pinnules, the degree of subpinnulation, and the size and density of the spines.

Several years ago a large collection of antipatharian corals was sent to the Smithsonian Institution by Dr. Peter Wirtz of the University of Madeira. Included in this collection were representatives of two undescribed species hand-collected from a submarine cave off Madeira at a depth of 9–15 m. It was determined that these species are closely related to several other Eastern and Western Atlantic species, and that together they merit recognition at the genus level.

The type specimens of the new species have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Family Antipathidae
Tanacetipathes, new genus

Type species.—*Antipathes tanacetum* Pourtalès, 1880. Type locality: Western Atlantic, Lesser Antilles; see Opresko (1972), for a complete description of the species.

Diagnosis.—Corallum monopodial or branched. Stem and branches complexly pinnulate, producing a bottlebrush appearance. Primary pinnules arranged in four to six rows along the axis and also in alternating biserial groups of varying regularity. Posterior-most primary pinnules with 1–3 orders of subpinnules; secondary and higher order pinnules present on abpolypar, and sometimes polypar side of lower order pinnules. Anterolateral and anterior primary pinnules (when present) simple or with secondary and sometimes higher order subpinnules.

Remarks.—The genus is characterized by the presence of four, sometimes five, and occasionally six rows of primary pinnules and at least one order of subpinnules (secondary pinnules). Subpinnules always occur (with varying frequency) on the abpolypar side and near the base of the posterior-most primary pinnules, and in some species they may also be present on the polyp side. Species in the genus are differentiated by the branching of the corallum; the number, length, and arrangement of the primary pinnules; the degree of subpinnulation; and the size and density of the spines. The genus includes the type species, *Tanacetipathes tanacetum* (Pourtalès), as well as *T. hirta* (Gray, 1857), *T. barbadensis* (Brook, 1889), *T. thamnea* (Warner, 1981), *T. spinescens* (Gray, 1857), and the two new species described below.

Etymology.—The genus name, is derived from "*tanacetum*" (Latin; composite, tansy), the species name of the type species.

Fig. 1. *Tanacetipathes cavernicola,* n. sp., holotype, USNM 96956; height 17 cm.

Geographic distribution.—The genus is known from the northeastern and northwestern Atlantic. Specimens of species that may be assigned to *Tanacetipathes* have also been collected from Ascension Island and the northeast coastline of South America (undescribed material in the USNM).

Tanacetipathes cavernicola, new species
Figs. 1–4

Material examined.—Madeira, Canico de Baixo, 9 m, on vertical wall of cave (type locality); P. Wirtz, August, 1995 (holotype, USNM 96956). Madeira, Canico de Baixo, 10 m, in cave, 27 Apr 1995, P. Wirtz, (paratypes, USNM 96959, several branches).

Diagnosis.—Corallum branched to 5th order or more; stem and branches pinnulate in bottlebrush pattern with up to three orders of pinnules. Primary pinnules arranged in 4 (sometimes 5 and very rarely 6) rows, of varying regularity, and in alternating biserial groups, consisting of one lateral (or posterolateral), one anterolateral (or lateral), and one anterior pinnule (not always present). Usually one, sometimes two and rare-

Fig. 2. *Tanacetipathes cavernicola,* n. sp., holotype, USNM 96956. A. Cross sectional view of branch with pinnules; ×2.5. B. Lateral view of branch with pinnules, ×2.5.

ly three uniserial secondary pinnules on some posterior-most primaries. Secondary pinnules occasionally present on anterolateral primaries. Secondary pinnules usually confined to abpolypar side of primaries and inclined distally relative to the primary. Tertiary pinnules very rarely present on secondary pinnules on posterior-most primaries. Primary pinnules usually less than 1.5 cm long, inclined and/or curved distally (distal angle 70°–80°); secondary pinnules usually not more than 1 cm long, extending out laterally in the plane delineated by the primaries in each bilateral group; tertiary pinnules usually less than 0.5 cm in length. Spines on pinnules simple, elongate, conical, acute, very finely papillose, and inclined distally; polypar spines mostly 0.2–0.25 mm (from midpoint of base to apex), but up to 0.3 mm tall; abpolypar spines smaller, narrower, and more distally inclined than polypar spines. Spines arranged in rows extending along length of axis; 4–6 rows visible from one aspect; 4.5 to 5.5 spines per millimeter in each row. Polyps 0.65–0.70 mm in transverse diameter, arranged uniserially on lateral, or upper or lower side of the pinnules; 9–12 polyps per centimeter.

Description of holotype.—The holotype (USNM 96956) is 17 cm high, 16 cm wide, and about 4 cm thick (Fig. 1). The stem just above the basal plate is about 3.5 mm in diameter. The corallum is branched with up to 5 orders of sub-branches. A cluster of six primary branches arises from the lowermost 2.5 cm of stem. Several of the major branches extend from the lower part of the stem to the top of the corallum; the largest is about 18 cm long and about 1 mm in diameter near its midpoint. The larger branches form two overlapping planes; the smaller ones tend to be placed laterally, at varying distances, usually 1–2 cm or more apart. The branches are straight or curved; the distal branch angles range from 45° to 90°. Over most of the corallum the primary pinnules occur in 4 rows of varying regularity and in alternating bilateral groups of two each (Fig. 2); occasionally a fifth primary occurs on the anterior side of the axis, and very rarely a sixth is also present on the anterior side, resulting in bilateral groups of 3 pinnules each. Within each row the pinnules are spaced about 2 mm apart resulting in 5–6 per centimeter. In each lateral group, the posterolateral pinnules are placed on the same level or slightly below (proximal to) the adjacent lateral pinnule. The primary pinnules are not uniform in size; the largest, which occur on the mid to lower portions of the branches, are mostly

1 to 1.5 cm long (rarely up to about 2.0 cm). The anterolaterals are usually slightly shorter than the posterolaterals. The maximum basal diameter of primary pinnules is 0.45–0.50 mm (including spines). The secondary pinnules, which occur on the abpolypar side and near the base of the primary pinnules, are generally 5–10 mm in length and are about as thick as the primary pinnules. There is usually only one secondary per primary, but occasionally there are two, and rarely three. A single secondary pinnule sometimes occurs on an anterolateral primary pinnule, usually on the lateral (abpolypar) side. Tertiary subpinnules are usually absent; when present they occur on the lowermost secondary pinnules, are less than 5 mm in length, and slightly smaller in diameter than the secondaries and primaries. The tertiary pinnules can be in the same plane as the secondaries or they can be directed distally or basally relative to the direction of the branch.

The axial spines (Figs. 3, 4) are relatively large, conical, acute, slightly compressed laterally, and faintly papillose. They are unequal in size around the circumference of the axis; those on the polyp size of the axis are larger than those on the abpolypar side. The polypar spines near the tips of the pinnules (axial diameter about 0.07 mm) are about 0.15 mm tall (as measured from the midpoint of base to apex); on the middle to lower portions of the pinnules (axial diameter 0.20–0.30) the polypar spines are mostly 0.20–0.25 mm but reach 0.30 mm in places. The abpolypar spines are 0.12–0.20 mm. The pinnular spines are arranged in rows along length of the axis; 4–6 rows are visible in lateral view excluding rows in which the spines are only partially visible). The distance between adjacent spines in each row ranges from 0.23 to 0.36 mm, resulting in 4.5–5.5 spines per millimeter in each row. The spines on stem and larger branches are more acicular than those on pinnules. On the basal plate they are very narrow, up to 0.4 mm tall, and some are forked at their apex.

The polyps are very slightly elongated along the transverse axis; they are 0.65–0.70 mm in transverse diameter (from the distal edge of distal lateral tentacles to the proximal edge of proximal lateral tentacles). The polyps are arranged in a single row, usually on the lateral side of the pinnules, but occasionally the row is offset towards the upper or lower side of the pinnules. The inter-polyp space is about 0.3 mm, and there are 9–12 polyps per centimeter.

Field notes.—Colonies of *T. cavernicola* are reported to be light gray in color when viewed in situ and the branches are rather flexible and difficult to break (P. Wirtz, pers. comm.).

Comparisons.—*Tanacetipathes cavernicola,* n. sp. resembles *T. tanacetum* (Pourtalès) in the pattern of subpinnulation; however, the latter species has more secondary and tertiary pinnules. Furthermore, colonies of *T. tanacetum* are usually monopodial or only branched to the first order; whereas colonies of *T. cavernicola* are branched more extensively. *Tanacetipathes cavernicola* is also similar to *A. spinescens* (Gray, 1857). The latter species forms large, densely branched colonies, with the pinnules more crowded, distally directed, and arranged in close spirals (Brook, 1889). As described and illustrated by Brook (1889), the subpinnulation in *T. spinescens* is more extensive, and is more pronounced on the side of the primary pinnules in the direction of the spiral. The primary pinnules are up to 1.5 cm long and the polypar spines, as estimated from the illustration given by Brook (1889), are about 0.19 mm.

Etymology.—The species name, *cavernicola* is derived from "*caverna*" (Latin, cave) and "*cola*" (Latin, inhabitant), in reference to the preferred habitat.

Distribution.—The species is only known from Madeira; 9–10 m.

Tanacetipathes wirtzi, new species
Figs. 5–8

Material examined.—Madeira, Canico de Baixo, 9 m, in cave, P. Wirtz, August, 1995

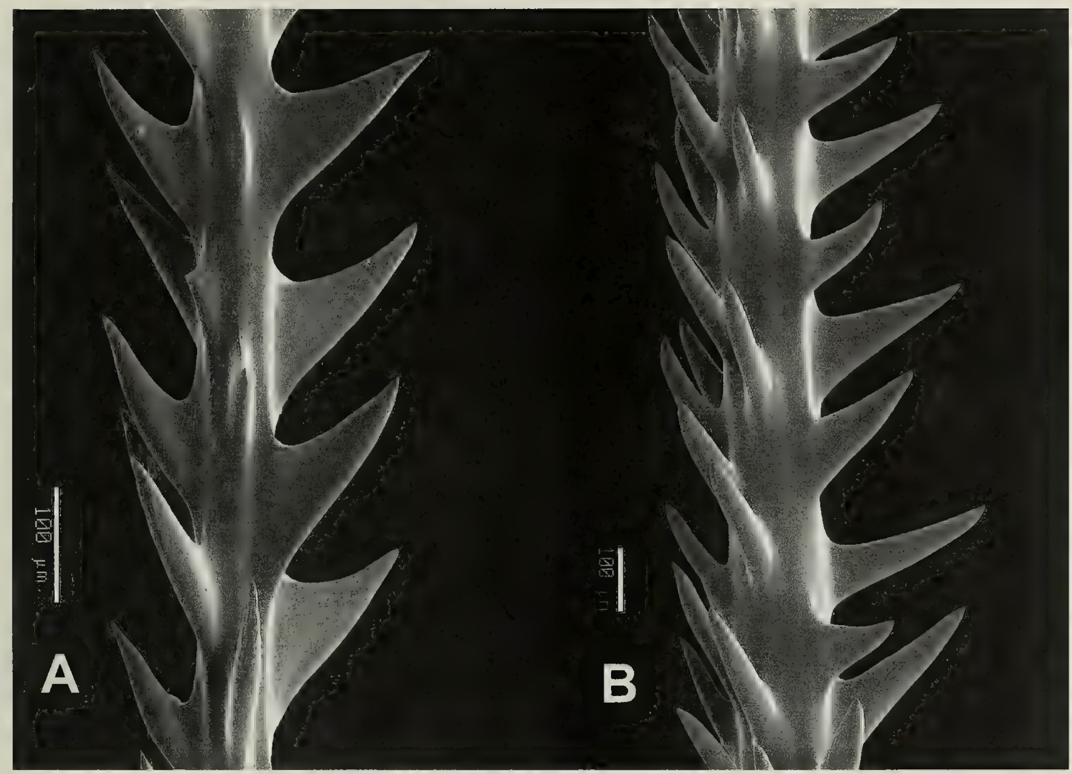

Fig. 3. *Tanacetipathes cavernicola,* n. sp., holotype, USNM 96956. A. Spines on distal section of pinnule. B. Spines on midsection of pinnule.

(holotype, USNM 96955). Madeira, Canico de Baixo, 15 m, in cave (type locality), P. Wirtz, April, 1994 (paratype, USNM 96954); Madeira, Canico de Baixo, 10 m, in cave, P. Wirtz, August, 1995 (paratype, USNM 96960).

Diagnosis.—Corallum branched sparsely, some branches arising from near base of stem, and extending to top of corallum. Stem and branches pinnulate in bottlebrush fashion. Primary pinnules up to 2.5 cm long; arranged in 4–6 axial rows and in alternating bilateral groups consisting of one posterolateral, one anterolateral, and one anterior pinnule (when present). Posterolateral pinnules usually simple or occasionally with one (rarely two) secondary pinnules on abpolypar side of axis, and usually occurring near base, but sometimes on distal portion of primary. Secondary pinnules 0.5–1.0 cm in length, inclined distally relative to the primary pinnule. Tertiary pinnules absent. Anterolateral and anterior pinnules almost always simple, without secondary pinnules. Largest primary pinnules 1.5–2.5 cm in length, 0.7–0.8 mm in diameter at base (including spines), and inclined distally (distal angle 70°–80°) relative to the branch or stem. Spines on pinnules conical, acute, slightly compressed, faintly papillose, and inclined distally. Polypar spines on lower portion of pinnules 0.24–0.30 mm from center of base to apex; abpolypar spines up to 0.2 mm, narrow and inclined distally. Spines arranged in 5–8 axial rows (as viewed from one aspect), with 4–6 spines per millimeter in each row. Polyps mostly 0.7–0.8 mm in transverse diameter; interpolypar space 0.2–0.3 mm; 8–10 polyps per centimeter.

Description of holotype.—The holotype (USNM 96955) is about 7 cm high and

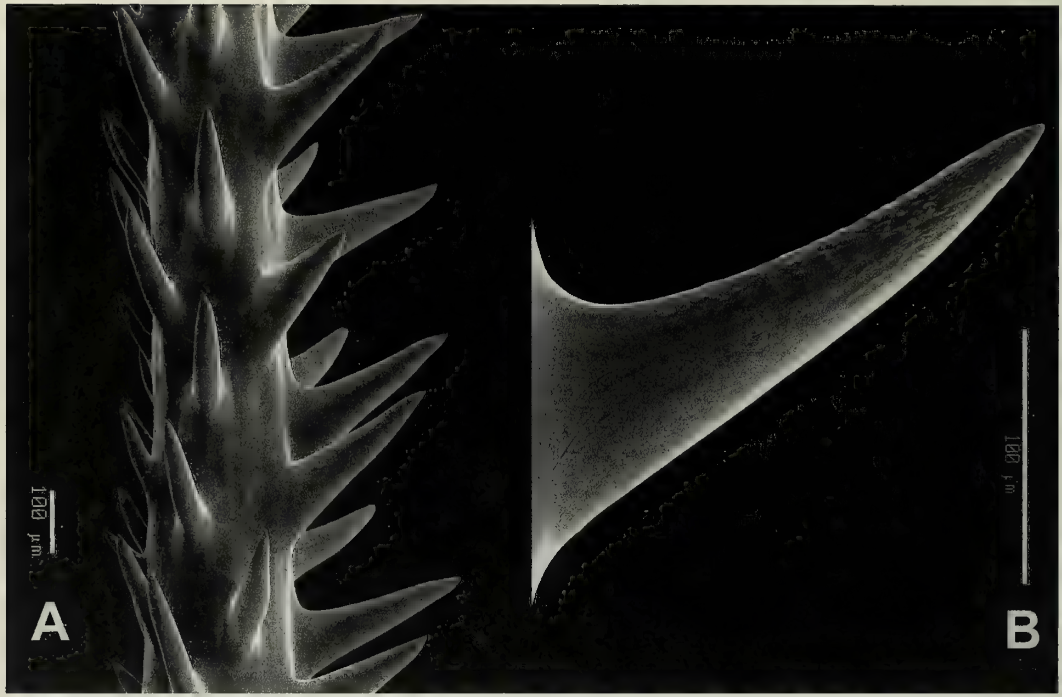

Fig. 4. *Tanacetipathes cavernicola,* n. sp., holotype, USNM 96956. A. Spines on basal section of pinnule. B. Single polypar spine.

about as wide (Fig. 5); it has a stem diameter of 1.2 mm just above the basal plate. The corallum is branched to the second order, with three branches arising directly from the stem; one of these bears a secondary branch. The lowest branch occurs 2 mm above the basal plate, and all three main branches arise within the first 1 cm. Several of these branches are nearly as long as the stem and extend to the top of the corallum (Fig. 5).

The primary pinnules are straight and stiff and arranged in 4 to 6 axial rows and in alternating bilateral groups. Within each row the pinnules are spaced 2–2.5 mm apart, resulting in 5–6 per centimeter. The distal angle formed between the pinnules and the branch or stem from which they originate is 70–80°. The smaller pinnules tend to be straight, the larger ones are curved upward toward the distal end of the branch. In each lateral group, the primary pinnules are placed at nearly the same level or slightly offset from one another; however, they are not arranged in a regular semi-spiral pattern. The maximum length of the primary pinnules is 2.2 cm, and the diameter near the base is about 0.40 mm without spines and about 0.75 mm with spines. The longest primary pinnules are usually those in the posterolateral rows, the shortest are those in the anterior rows (when these are present).

Most of the primary pinnules are simple. A single, simple, secondary pinnule is present on a small number of posterolateral primary pinnules. The secondary pinnules are generally less than 1 cm long; most arise at a point less than 1 mm from the base of the primary. Rarely, two secondaries occur on the same primary. Secondary pinnules are not normally found on the anterior or anterolateral primary pinnules. Tertiary pinnules are absent.

The axial spines (Figs. 6, 7) are large, conical, acute, and slightly papillose. The polypar spines near the tip of a pinnule (axial diameter 0.05 mm) are about 0.1 mm tall

Fig. 5. *Tanacetipathes wirtzi,* n. sp., holotype, USNM 96955; height 7 cm.

(from middle of base to apex). Where the axial diameter is 0.1 mm, the polypar spines measure about 0.2 mm, and where the axis is 0.3–0.4 mm (near the base of the pinnule), the polypar spines are up to 0.3 mm. The abpolypar spines are generally smaller than the polypar spines by 0.02–0.04 mm; they are also narrower and can be strongly inclined distally. The spines are arranged in 5–8 rows as seen in one lateral view of a pinnule. The distance between adjacent spines in each row is usually 0.2–0.3 mm. The spines on the branches are more acicular than those on the pinnules, and those on the lower part of the stem and on the basal plate are very narrow and up to 0.30 mm tall; several on the basal holdfast are forked at the tip.

The polyps are slightly elongated along the transverse axis; the distance from distal edge of the distal lateral tentacles to proximal edge of the proximal lateral tentacles is 0.7–0.8 mm; the interpolypar space is about 0.3 mm, resulting in 8–10 polyps per centimeter. The polyps are arranged uniserially on the pinnules and occur primarily on the lateral sides relative to the direction of the branch on which the pinnules occur.

Remarks.—One paratype (USNM 96954) is a single branch 14 cm long (Fig. 8A), and the second (USNM 96960) is a small colony about the same size as the holotype. Both paratypes show the same general pinnulation pattern as the holotype, with most of the primary pinnules being simple, a few posterolaterals with a single secondary pin-

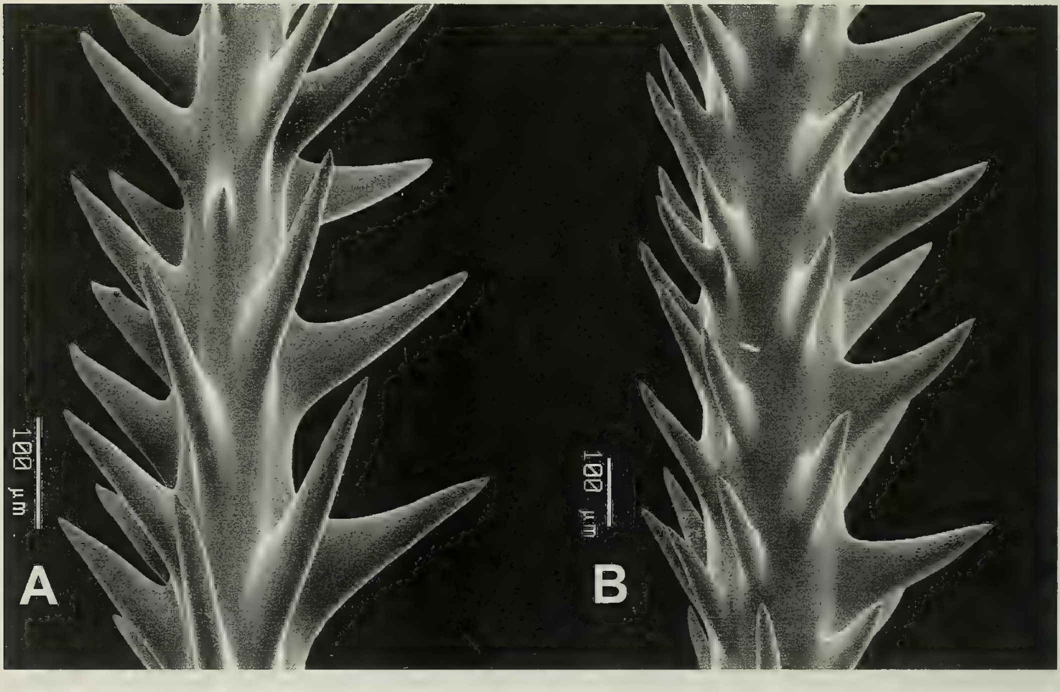

Fig. 6. *Tanacetipathes wirtzi*, n. sp., holotype, USNM 96955. A. Spines on distal segment of pinnule. B. spines on mid section of pinnule.

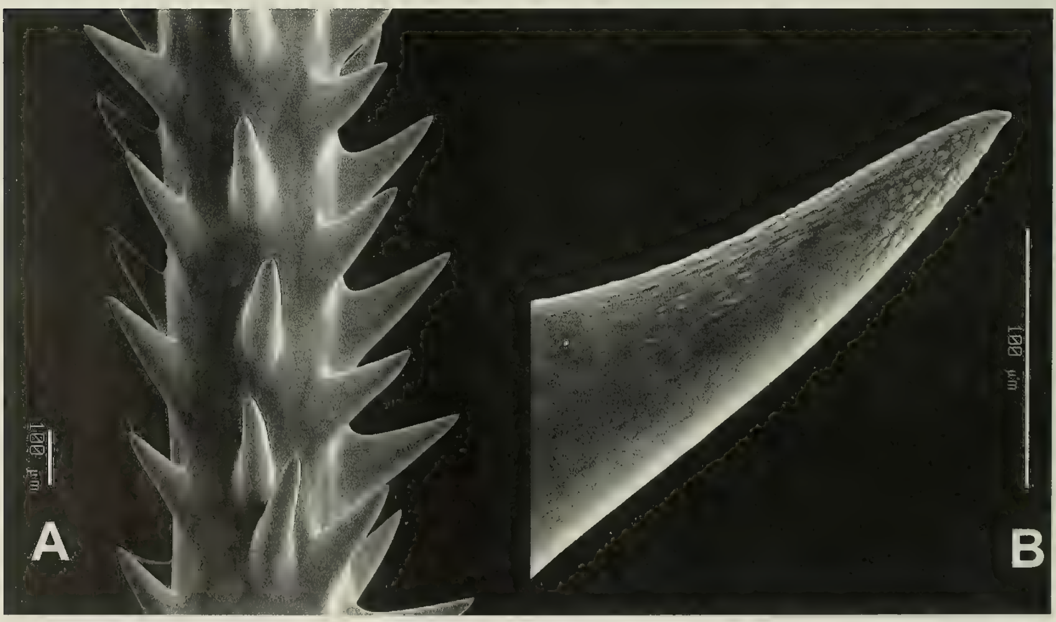

Fig. 7. *Tanacetipathes wirtzi*, n. sp., holotype, USNM 96955. A. Spines on basal section of pinnule. B. Single polypar spine.

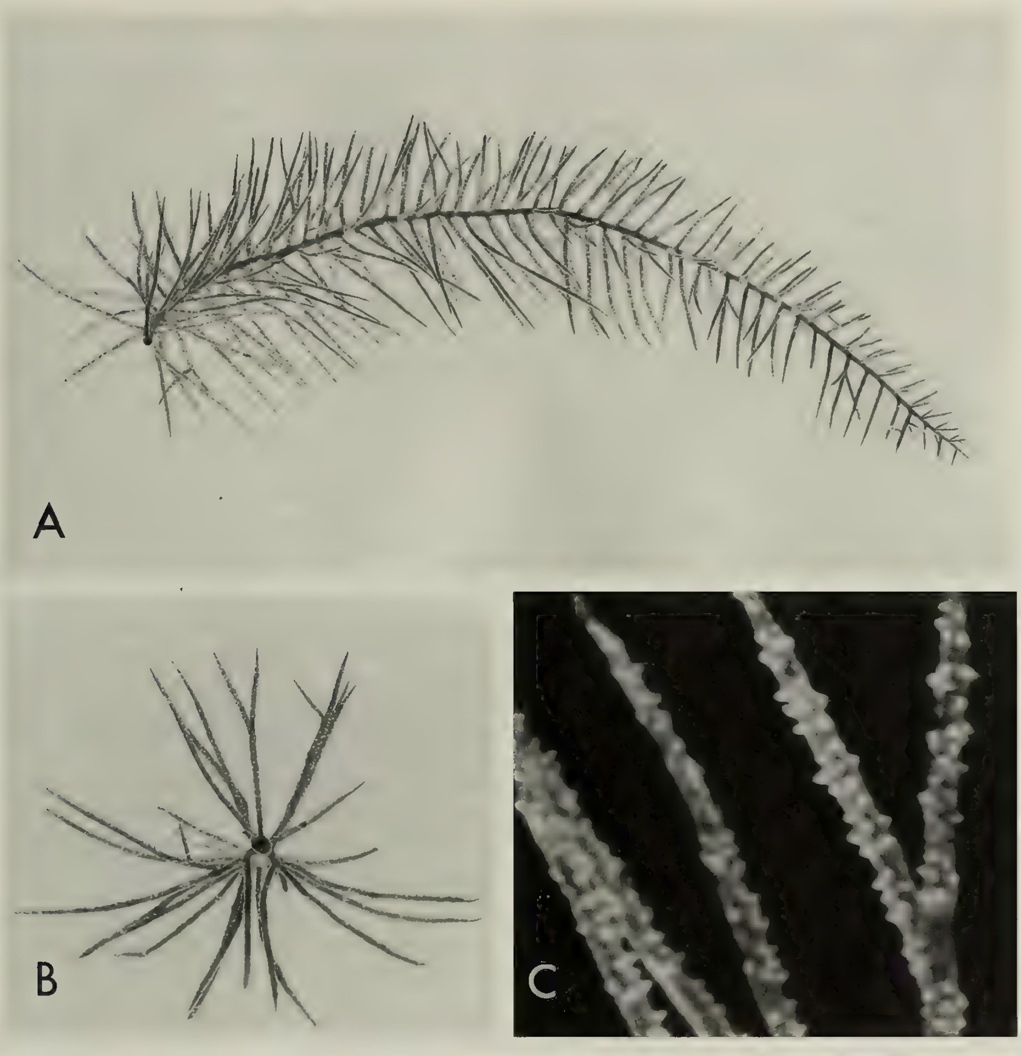

Fig. 8. *Tanacetipathes wirtzi,* n. sp., paratype, USNM 96954. A. Entire corallum. B. Cross section of branch. C. Polyps on pinnules; ×4.7.

nule near the base, and with a secondary pinnule sometimes occurring on the distal portion of a primary pinnule (Fig. 8B). The primary pinnules on both paratypes reach a maximum length of about 2.5 cm. In one paratype (USNM 69660), the spines on the stem reach a larger maximum size (about 0.4 mm) and many are multi-forked at their tip. The polyps (Fig. 8C) are 0.7–0.8 mm in transverse diameter; the interpolyp space varies from 0.2 to 0.3 mm, and there are 9–10 polyps per centimeter.

Field notes.—Colonies of *T. wirtzi* are reported to be dark brown in color when viewed in situ and rather brittle and easy to break (P. Wirtz, pers. comm.).

Comparisons.—*Tanacetipathes wirtzi* is closely related to *T. cavernicola,* n. sp., and the two species are difficult to differentiate on the basis of the size or morphology of the spines or polyps. The major differences between the two species lie in the maximum length of the primary pinnules (2–2.5 cm in *T. wirtzi* and 1.5–2.0 cm in *T. cavernicola*), and in the degree of subpinnulation. In *T. wirtzi* most of the primary pinnules are simple, and the secondary pinnules, when present, are simple and usually occur near the base of the posterolateral primaries, although here and there a secondary pinnule may also occur on the distal segment of a lateral or anterolateral primary. In *T. cavernicola* secondary pinnules commonly occur on the posterolateral primaries, and in places, especially in the older portions of the corallum, tertiary pinnules may also be present.

Tanacetopathes wirtzi resembles *T. barbadensis* (Brook, 1889) in having only a few secondary pinnules on the posterolaterals; however, the pinnules in *T. wirtzi* are shorter than those in *T. barbadensis* (2.5 cm vs. 4 cm or more). Furthermore, colonies of *T. barbadensis* are monopodial or only sparsely branched, and the branches, when present, are relatively long and occur primarily on the upper portion of the corallum. In *T. wirtzi* the branching takes place on the lower part of the corallum, just above the basal plate.

Etymology.—The species is named after Peter Wirtz of the University of Madeira who collected the specimens and made them available for study.

Distribution.—The species is only known from Madeira; 9–10 m.

Acknowledgments

The author wishes to thank Peter Wirtz for collecting the material and kindly making it available for study; S. Cairns for providing research space at the Smithsonian Institution; S. Braden of the Smithsonian Institution for preparing the samples for the SEM; and S. Gardiner for editing the manuscript. This work was supported in part by the Smithsonian Institution and by Oak Ridge National Laboratory, Oak Ridge, TN.

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Description of *Agelas cerebrum*, a new species and re-description of *A. dilatata* (Porifera)

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Abstract.—Recent collections of sponges made in the Bahamas revealed the occurrence of two species of *Agelas,* which we could not assign to any of the currently recognised *Agelas* of the Western Atlantic. A comparison with literature records and extensive collections of *Agelas* incorporated in several major musea led us to conclude that several specimens belong to a species new to science, *Agelas cerebrum.* This species differs from the repent ramose form of *A. conifera* (Schmidt, 1870) in possessing a massively erect tube shape, thinner spicules and a higher number of whorls of spines. From the tubular form of *A. conifera* the new species differs in having much thicker tube walls with a system of convolutions and meandering grooves, and likewise differences in spicular dimensions. *Agelas cerebrum* differs from *A. tubulata* Lehnert & Van Soest, 1996 in having much thicker convoluted tubes and shorter spicules. A single thickly flabellate specimen we assign to *A. dilatata* Duchassaing & Michelotti, 1864, a species so far considered incertae sedis, because of compelling similarities with its original description and depiction. Our specimen differs from *A. clathrodes* in having a smooth plate form rather than an irregularly pitted wall-shape, and in having much more heavily cored primary fibres. It differs from *A. inaequalis* Pulitzer-Finali, 1986 because it is not cup-shaped and the spicules have more whorls of spines. It appears closest to *A. flabelliformis* (Carter, 1883) in shape and surface characteristics, but Carter's species forms very thin blades of 5 mm, whereas *A. dilatata* is 25–30 mm thick. *Agelas flabelliformis* has distinctly shorter and thinner spicules.

Sponges of the genus *Agelas* are common and dominant species in Caribbean reef communities. To date 21 nominal species have been described (Table 1) from this area. Compared to other areas of the world, the diversity of *Agelas* in the Caribbean is unusually high: elsewhere, only 12 nominal species from the whole of the Indo-Pacific, and 1 species from the Mediterranean (*Agelas oroides*), have been described. Although the genus is easily recognised, the systematics of *Agelas* at the species level appears problematic because of observed in-congruence of macroscopic features (shape, surface appearance and colour) and microscopical characters (arrangement of fibres and spicules, size and ornamentation of spicules) (Lehnert & Van Soest 1999). A revision of the genus is becoming urgent because of growing interest in the impact of *Agelas* on the reef community (e.g., Reiswig 1976, Hoppe 1988, Pawlik et al.1995, Chanas et al. 1996), as well as for its promising bioactive properties (Assmann et al. 1999, Assmann et al. 2000). The chemistry described for *Agelas* is characteristic, with

Table 1.—Nominal *Agelas* species recorded from the Caribbean. *A. dispar* has been reported in two distinct color forms indicated as (1) and (2).

Agelas arborescens	Lamarck, 1813 as *Spongia*
Agelas cervicornis	Schmidt, 1870 as *Chalinopsis*
Agelas citrina	Alcolado, 1984
Agelas clathrodes	Schmidt, 1870 as *Chalinopsis*; Carter, 1883 as *Ectyon sparsus*; Topsent, 1920 as *Agelas oroides*; De Laubenfels, 1949 as *Agelas sparsus*; De Laubenfels, 1953 as *Agelas oroides*; Collette & Rützler, 1977; Gomez & Green, 1984; Wintermann-Kilian & Kilian, 1984; Pulitzer-Finali, 1986; Zea, 1987; Gomez, 1992; Lehnert, 1993; Lehnert & Van Soest, 1996; Lehnert & Van Soest, 1998
Agelas clavaeformis	Carter, 1883 as *Ectyon sparsus* var.
Agelas conifera	Schmidt, 1870 as *Chalinopsis*; Wintermann-Kilian & Kilian, 1984; Pulitzer-Finali, 1986; Zea, 1987; Lehnert, 1993; Lehnert & Van Soest, 1996; Lehnert & Van Soest, 1998
Agelas cylindricus	Carter, 1883 as *Ectyon*
Agelas dilatata	Duchassaing & Michelotti, 1864
Agelas dispar (1)	Duchassaing & Michelotti, 1864 (orange); sensu Van Soest, 1981; Pulitzer-Finali, 1986; Lehnert, 1993; Lehnert & Van Soest, 1998 (= ?*Agelas clathrodes*)
Agelas dispar (2)	Duchassaing & Michelotti, 1864 (brown); Solé-Cava et al. 1981; Boury-Esnault, 1973; Wiedenmayer, 1977; Wintermann-Kilian & Kilian, 1984; Zea, 1987
Agelas flabelliformis	Carter, 1883 as *Ectyon*
Agelas inaequalis	Pulitzer-Finali, 1986
Agelas longissima	Pulitzer-Finali, 1986
Agelas marmarica	sensu Wintermann-Kilian & Kilian, 1984 (not: Lévi, 1958)
Agelas repens	Lehnert & Van Soest, 1998
Agelas rudis	Duchassaing & Michelotti, 1864
Agelas sceptrum	Lamarck, 1813 as *Alcyonium*; Topsent, 1933 as *Ectyon*; Lamarck, 1813 as *Spongia arborescens*; Topsent, 1931 as *Ectyon cervicornis*; Schmidt, 1870 as *Chalinopsis cervicornis*; Carter, 1883c as *Ectyon cylindricus*; Pulitzer-Finali, 1986 as *Agelas longissima*; Zea, 1987; Lehnert, 1993; Lehnert & Van Soest, 1998
Agelas schmidti	Wilson, 1902; Wintermann-Kilian & Kilian, 1984; Zea, 1987; Lehnert & Van Soest, 1998
Agelas sparsus	Gray, 1867; Hechtel, 1976
Agelas sventres	Lehnert & Van Soest, 1996; Lehnert & Van Soest, 1998
Agelas tubulata	Lehnert & Van Soest, 1996
Agelas wiedenmayeri	Alcolado, 1984

monomeric or dimeric molecules of brominated pyrrole-2-carboxylic acid derivatives uniformly present in all investigated species (Braekman et al. 1992). In addition, several species possess unusual diterpenic compounds. Investigations of *Agelas* species collected in the Bahamas, revealed the occurrence of many previously described forms (*A. cervicornis, A. clathrodes, A. dispar, A. sceptrum, A. wiedenmayeri*), as well as specimens which did not belong to those commonly recorded representatives of the genus. A comparison with literature records and extensive collections of Caribbean *Agelas* sponges incorporated in the collections of the Zoological Museum of Amsterdam and other museums, led us to conclude that the Bahamas material contained specimens of a species new to science. Furthermore, one specimen appeared to be so similar to old literature images and descriptions of *Agelas dilatata* Duchassaing & Michelotti, 1864 that we propose to revive this species. The purpose of the present study is to provide descriptions of these two *Agelas* species including comparative notes on species appearing similar.

Specimens of the new and the revived species were collected by the first author during a cruise of the R/V *Seward Johnson* to the Bahamas in July/August 1999. Large fragments were incorporated in the collections of the Zoological Museum of Amsterdam (numbers and locality data are provided below in conjunction with the descriptions) remaining parts of the specimens were used for extraction and chemical analysis. Specimens examined for comparison were obtained from the collections of the Zoological Museum of Amsterdam (ZMA), the United States National Museum, Washington (USNM), and the Natural History Museum, London (BMNH). For identification of sponges small fragments were cut off and stored in 70% ethanol. Spicule slides were studied using a JEOL JSM-35C scanning electron microscope.

Order Agelasida

Family Agelasidae Verrill, 1908

Agelas Duchassaing & Michelotti, 1864

Agelas cerebrum, new species

Fig. 1

Material examined.—Holotype ZMA POR. 15603, deep reef slope of Chub Cay, Bahamas, MAB96, 30 Jul 1999, 29.1 m.

Description.—Macroscopical features. Habit and surface characteristics: the type specimen consisted of two fused tubes (Fig. 1B, C), other specimens observed were only partly fused (Fig. 1A) or single. The height is up to 33 cm and 16 (single tube) to 22 cm (fused tubes) in diameter. Two vents (Fig. 1C), one 4.5 cm, the other 4–5 cm in diameter, leading to lumina of the same diameter penetrating deep into the sponge. The lumina come together at about 15 cm depth and continue to the base of the sponge as one hole. The inner wall contains numerous oscules flush with the smooth surface. The outer surface of the sponge is rough to the touch and is characteristically convoluted (Fig. 1A, B, D). About 20 convolutions appear over the whole length. Individual convolutions are 2.5–6 cm long and 1–3 cm wide. In the central part of the convolutions scattered smaller oscules are present (Fig. 1D). Separating convolutions on the surface are meandering groves, which are at least 2–3 cm in depth and a few mm in width. The color of the sponge is light brown to greyish brown in life. The consistency is tough, spongy, firm, and almost incompressible.

Microscopical features. Spicules: verticillated acanthostyles (Fig. 1E–G) as usual for the genus; they are quite variable in length and number of whorls; spicule sizes: 99-165 by 5–10 μm; number of whorls: 13–24, with 6 spines per whorl. Skeleton: mesh sizes vary 100–700 μm. Primary fibres are well developed, and easily recognised over long distances (200–600 μm). They are about 80–170 μm in diameter and are cored throughout the skeleton by 3–10 echinating spicules per 500 μm length of fibre. Both secondary and tertiary fibres are 60–120 μm in diameter, uncored, and echinated by 12 spicules per 500 μm length of fibre.

Remarks.—Among the described *Agelas* species of the Caribbean, the new species appears closest in gross morphology to *A. conifera* (Schmidt, 1870) and *A. tubulata* Lehnert & Van Soest, 1996.

Comparison with Agelas conifera.—Schmidt (1870) described *Chalinopsis conifera* as branch-like individuals with 8 mm wide oscula (Schmidt, 1870). Our material does not agree with this description. We were able to ascertain that the type specimen in the Copenhagen Museum conforms closely to Schmidt's description and is similar to the dominant form encountered among specimens identified by one of us (RvS) in the ZMA collections. We chose to compare the type of *A. cerebrum* with four ZMA specimens of similar growth form as Schmidt's type:

ZMA POR. 14197, Curaçao, "octopus-type", repent-ramose with volcanoe-shaped oscules: skeleton is a well-developed sys-

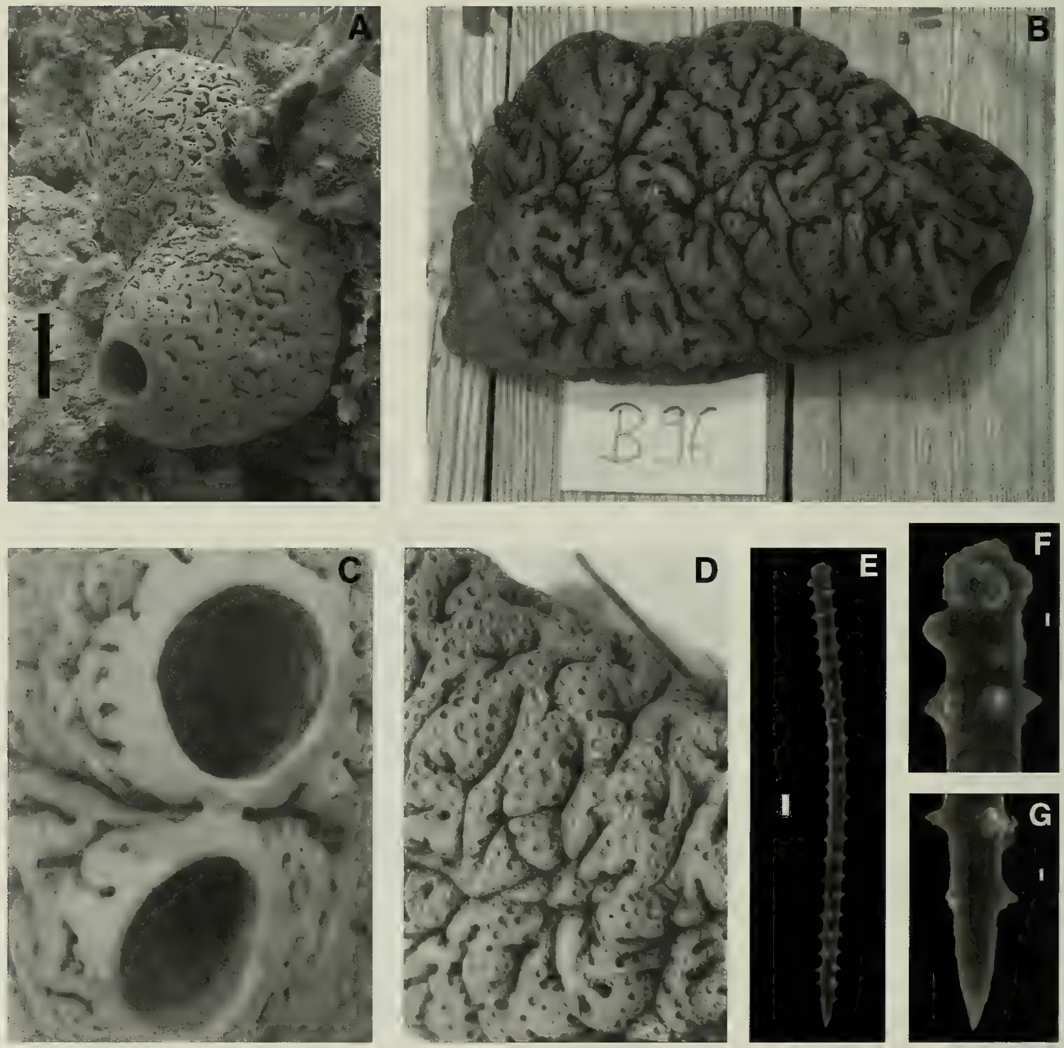

Fig. 1. *Agelas cerebrum* new species. A, habit photographed in situ (scale = 10 cm); B–D, holotype ZMA POR. 15603 (size quoted in text); E, acanthostyle of holotype (scale = 10 μm); F–G, details of acanthostyle (scale = 1 μm).

tem of primary and secondary fibres, easy to detect, penetrating deep into interior; primary fibres lie at distances of 400–700 μm and are cored with 5–9 spicules in cross section; thickness of primary fibres 60–100 μm; they are echinated by 6–7 spicules per 500 μm fibre length; secondary fibres are uncored, 30–60 μm in thickness; the echination of secondary fibres is about 8–12 per 500 μm fibre length. Meshes are 250–600 μm. Spicule sizes vary from 126–192 by 10–13 μm, with 11–15 whorls.

ZMA POR. 14170, Curaçao: similar to above, spicule sizes: 117–156 by 10–13 μm, with 11–16 whorls.

ZMA POR. 12778, Jamaica: similar to above, spicule sizes: 138–180 by 10–13 μm, with 11–14 whorls.

ZMA POR. 7783, Bahamas: similar to above, spicule sizes: 126–186 by 9–13 μm, 11–15 whorls.

There appears to be a consistent difference in spicule thickness and number of whorls, and they appear less variable, compared to *Agelas cerebrum.* We also compared our sample with two specimens identified as *A. conifera* from Belize and Colombia displaying a tube form in growth. These tubes assigned to *A. conifera* are not grooved nor convoluted:

USNM unnumbered, Belize, P110, Carrie-Bow Cay, Belize, IMSWE Project, fore reef slope, 15–30 m, Rützler, col., id. 4 May 1973, on loan from the National Museum of Natural History, Smithsonian Institution: in total four tube individuals, up to 46 cm high, 8 cm in diameter, lumen 4 cm, surface is undulating but smooth, covered with zoanthids. Spicule sizes: 140–180 by 15–16 μm, with 11–16 whorls.

ZMA POR. 6148, Colombian Caribbean: 25 cm high, diameter of 6 cm, lumen of 3 cm in diameter, surface is undulating but smooth. Spicule sizes: 148–177 by 12–17 μm, 14–17 whorls.

In both *Agelas conifera* growth forms the spicules appear shorter and fatter, with a lower number of whorls, than in *A. cerebrum,* new species. The thickness overlaps only marginally with that of *A. cerebrum,* new species, spicules.

Comparison with Agelas tubulata *Lehnert & Van Soest, 1996.*—Specimens from Jamaica are long, brown, branching tubes (ZMA POR. 11323, ZMA POR. 13560), with individual tubes ca. 20–37 cm long, 3.5–5 cm in diameter, central aperture 2–2.5 cm in diameter. Numerous small (<1 mm) pores scattered over the smooth surface. A few larger (2–4 mm) apertures are visible. Choanosomal skeleton a reticulation of primary fibres, 40–70 μm in diameter, cored by 1–4 spicules, diverging to the surface, lying at distances of 300–400 μm apart, and interconnecting secondary fibres 20–50 μm diameter, forming almost square meshes. Spicule sizes: 78–210 by 5–12 μm, with 10–32 whorls. The major differences with *Agelas cerebrum* are thinner tubes, smooth unmarked surface and the greater upper length of the spicules.

Agelas dilatata Duchassaing & Michelotti, 1864
Fig. 2

Agelas dilatata Duchassaing & Michelotti, 1864: 77, pl. II fig. F, XIV fig. 1; van Soest et al., 1983: 197.

Material examined.—ZMA POR. 15604, Little San Salvador, Bahamas, MAB118, 3 Aug 1999, 23.4 m.

Description.—Macroscopical features. Habit and surface characteristics (Fig. 2A–D): flabellate; wedge-shaped; pedunculate. The height of the specimen is up to 35 cm and 41 cm in diameter, thickness 2.5–3 cm. One side (upper side, Fig. 2C) with 15 oscules per 25 square cm. Width of the oscules is 4–5 mm in diameter and they are flush with the smooth surface. Stalk (Fig. 2B) with few oscules, width of oscules 7–9 mm in diameter. The other side (Fig. 2D) with scattered fields of small apertures, slightly rough, uneven, with shallow depressions. The color of the upper side is orange brown, whereas the underside is bright orange in color. The consistency is slightly compressible, tough, spongy, firm, almost incompressible.

Microscopical features. Spicules (Fig. 2E, G): verticillated acanthostyles as usual for the genus; they are quite variable in length and number of whorls; spicule sizes: 78–195 by 5–9 μm; number of whorls: 11–21, with 6 spines per whorl. Skeleton: special ectosomal skeleton is absent, choanosomal fibres protrude at the surface, causing the slightly rough feel of the surface. Skeleton consists of a reticulation of spongin fibres. General aspect of the skeleton is irregular without prominent primary fibres, only in the periphery they are easily recognisable, the reason of their in-distinctness is their frequent anastomosing and subdividing, individual fibres only detectable over a short stretch, in other places the skeleton is dense and irregular. Primary fibres are not well developed. They contain a core of 0–6 spicules in a cross section. In the periphery the primary fibres lie at distances of

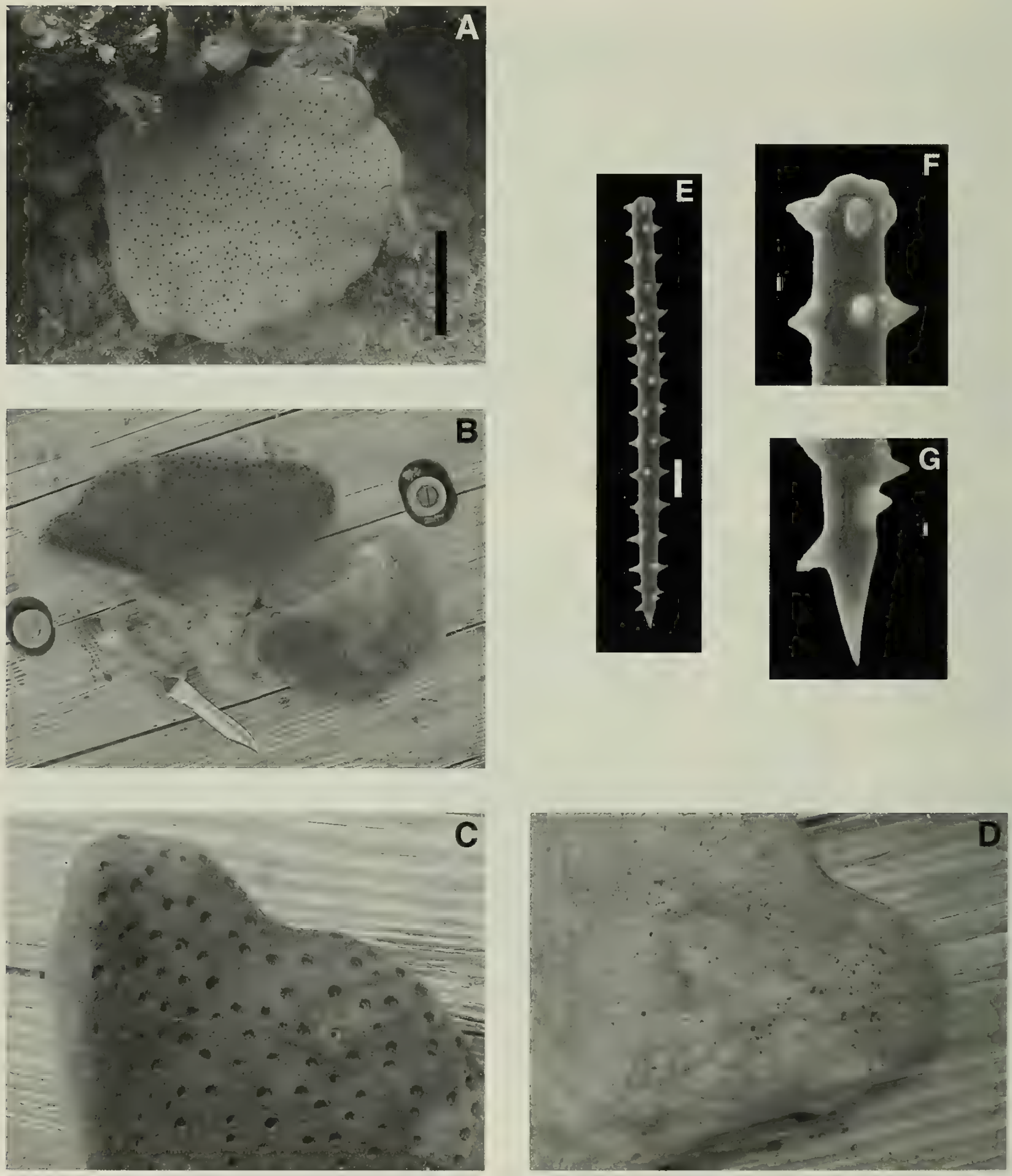

Fig. 2. *Agelas dilatata.* A, habit photographed in situ (scale = 10 cm); B–D, ZMA POR. 15604 (size quoted in text); E, acanthostyle (scale = 10 μm); F–G, details of acanthostyle (scale = 1 μm).

250–800 μm; thickness of the fibres 60–115 μm, they are echinated by 4–6 spicules over a distance of 500 μm fibre length. Although most primary fibres are only recognisable over short distance, occasionally they show a greater length. Interconnecting/secondary and tertiary fibres: they are arranged very irregularly and densely, they are mostly uncored but occasionally are cored by a single spicule; they are echinated by 6–12 spicules over a distance of 500 μm fibre length; sizes are largely similar to primaries: 25–100 μm, but quite variable. Meshes 50–400 μm.

Remarks.—We assign our specimen to *Agelas dilatata* because of the overall similarity with the Duchassaing & Michelotti's plate XIV fig. 1 (Duchassaing & Michelotti 1864). Also, their crude line drawings of the skeleton and the spicule (their pl. II fig. F) are more or less similar to microscopical details of our specimen. The one line description does not allow further confirmation, and unfortunately type material is no longer extant (Van Soest et al. 1983). No matching description so far appeared in the literature and we are confident that this is a valid species with characteristic morphology.

Comparison with similar species.—Among the described *Agelas* species of the Central West Atlantic, *A. dilatata* appears closest in gross morphology to *A. clathrodes* (Schmidt, 1870), *A. inaequalis* Pulitzer-Finali, 1986 and *A. flabelliformis* (Carter, 1883).

Agelas clathrodes (Schmidt, 1870 as *Chalinopsis*) is not likely to be our species. Schmidt's description refers to a bumpy surface and cavernous interior (Schmidt 1870). This description allows many interpretations, however, our specimen differs from it by the thin-bladed growth form, smooth surface, regularly and densely scattered oscules concentrated on one side only. The skeleton could be compared with a slide of a fragment of one of the types of *A. clathrodes* from the Copenhagen Museum. Compared with our *A. dilatata* specimen, it shows a less dense and much more regular reticulation, with clearly developed fibres: coring of primary fibres 6–12 spicules; primary fibres lie at distances further away from each other, 800–1100 μm; thickness of primary fibres about 100 μm; echination of fibres 6–7 spicules per 500 μm fibre length; secondary fibres are uncored; echination of secondary fibres: 7–10 spicules per 500 μm fibre length; thickness of secondary fibres: 40–70 μm; meshes: 100–500 μm.

Our specimen is not likely to belong to *Agelas inaequalis* Pulitzer-Finali 1986, because this is cup-shaped. The convex side is entirely perforated by apertures of 0.5–1 mm and 1–1.5 mm apart; on the inner side there are numerous oscules, sparse multiple oscules 5–10 mm wide, rather irregular. The fibres are only 45–90 μm thick, are abundantly echinated; coring spicules are observed only occasionally. Spicule sizes: 65–149 by 3.5–7 μm, with only 10–12 whorls with 3–4 spines each (Pulitzer-Finali 1986).

The present material is probably close to Carter's (1883) *Ectyon flabelliformis*. The type specimen only (not Carter's pictured specimen, which is probably *Agelas clathrodes*), BMNH 1884.4.14.9, was examined. It is likewise a thin-bladed species with scattered oscules on one side. However, the type specimen is three-lobed and the blade thickness is only 5 mm. We compared the skeleton of this species using a slide made from the type: it is similar in having a dense and irregular reticulation of spongin fibres; low spicular density, coring of main fibres is sparse, 0–3 spicules in a cross section; main fibres 50–90 μm in diameter; secondary fibres: 40–80 μm; echinating spicules about 12 over a distance of 500 μm fibre length. A distinct difference are the spicules. Compared with those of our *A. dilatata* specimen, they appear to be much shorter and thinner: 50–120 μm in length and by 3–6 μm width; sparsely developed whorls, spines irregularly distributed, here and there, 6–15 whorls.

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New species of *Calyptrophora* (Coelenterata: Octocorallia: Primnoidae) from the western part of the Atlantic Ocean

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Abstract.—Three new species of the gorgonacean genus *Calyptrophora* from the western Atlantic are described and compared with the previously known *C. trilepis* (Pourtalès, 1868). All are illustrated by scanning electron micrographs. The status of several Indo-Pacific specimens indentified in the literature as the type species, *C. japonica* Gray, 1866, is discussed, and a new drawing of Gray's specimen is provided.

Kinoshita (1908:58) early recognized the sharp distinction of the species of *Calyptrophora* having ringlike body sclerites as in *C. japonica* Gray, 1866, from those having unfused pairs of sclerites surrounding the polyps as in *C. kerberti* Versluys, 1906. He proposed for the latter group the subgenus *Paracalyptrophora,* including *C. mariae* Versluys, *C. josephinae* Lindström, 1877, and *C. kerberti* Versluys, 1906, and at the same time the nominate subgenus *Calyptrophora* s.s. for *C. japonica* Gray, 1866, *C. wyvillei* Wright, 1885, and *C. agassizii* Studer, 1894. Although subsequently ignored by other specialists, the validity of *Paracalyptrophora* can hardly be doubted. Recent discoveries not only support it, but even justify its elevation to full generic rank (Bayer 1981:937, Bayer & Stefani 1988:455).

Until now, ten species of *Calyptrophora* with abaxial body scales inseparably fused to form rings have been described: *C. japonica* Gray, 1866, *C. trilepis* (Pourtalès, 1868), *C. angularis* (Nutting, 1908), *C. clarki* Bayer, 1951, *C. juliae* Bayer, 1952, *C. spinosa* Pasternak, 1984, and *C. microdentata* Pasternak, 1985, with polyps bending upward, and *C. wyvillei* Wright, 1885, *C. agassizii* Studer, 1894, and *C. versluysi* Nutting, 1908, with polyps bending downward. All of these species inhabit the Indo-Pacific as far east as Hawaii except for *C. trilepis* (Straits of Florida), *C. microdentata* (Rockaway Seamount, North Atlantic) and *C. agassizii* (Galápagos). Recent operations of oceanographic research vessels in the northwestern Atlantic have obtained three species with solidly fused rings in addition to *C. trilepis* and *C. microdentata.*

Differences in branching pattern, development of marginal spines of the sclerite rings, form of the opercular scales, number of polyps per whorl and spacing of whorls along the branches have resulted in the recognition of distinct but obviously related species. These suggest the existence of at least two lineages of *Calyptrophora* with fused rings: one with polyps facing upward as in *C. japonica,* the other with polyps facing downward as in *C. wyvillei.* The former, here treated as a "*japonica*-complex," contains two species groups, one with polyps having a pair of marginal spines on the basal ring and smaller spines, denticles or pointed lobes on the free margin of the buccal ring as in *C. japonica,* the other with polyps having at most a pair of short marginal points or lobes, and little or no ornamentation on the much narrower free margin of the buccal ring as in *C. trilepis.*

Family Primnoidae

Calyptrophora Gray, 1866

Calyptrophora Gray, 1866:25, fig. 1; 1870: 42, fig. 13.—Studer [& Wright], 1887:

48.—Wright & Studer, 1889:xlvii, 50.—Versluys, 1906:104 (part).—Kinoshita, 1908:54.—Kükenthal, 1919:468 (part); 1924:317 (part).—Deichmann, 1936:171 (part).—Bayer, 1951:40 (part); 1956: F221 (part); 1981:937 (in key only).—Bayer & Stefani, 1989:455 (in key only).

Type species.—*Calyptrophora japonica* Gray, 1866, by monotypy. As this species is central to the understanding of *Calyptrophora* worldwide, a new drawing of Gray's type specimen is provided and some descriptive remarks about other similar material are included with the following descriptions of western Atlantic species.

Diagnosis.—Primnoidae with verticillate polyps enclosed in two annular sclerite rings each composed of two inseparably fused abaxial scales. Tentacles of most species with small curved scales.

Descriptions.—Colonies are planar or nearly so, the branching dichotomous, bipectinate or lyrate, in one species in whorls from the main stem but subsequently dichotomous, in a few species unbranched and flagelliform, with polyps always arranged in whorls and in most species directed upward.

The polyps are encased in two ring-like sclerites, each composed of two semiannular sclerites inseparably fused abaxially and adaxially to form solid rings surrounding the body; in most species a pair of curved infrabasal scales lies between the basal ring and the sclerites of the coenenchyme, but in a few the basal ring articulates directly with the coenenchymal plates. Eight roughly triangular scales close the aperture of the distal body ring, forming an operculum covering the retracted tentacles; in some species, the tentacles have numerous small, narrow, curved scales. The coenenchyme contains a layer of tessellate or imbricating plates. In this material from the western Atlantic, sclerites are composed of magnesian calcite containing from 6.4 mole% to 8.1 mole% $MgCO_3$ as determined by X-ray diffraction.

The axis is stiff, brittle, heavily calcified with aragonite, weakly grooved longitudinally, proximally brownish or blackish, becoming paler distally, sometimes with bronze or golden metallic sheen; the holdfast also is composed of aragonite, irregularly discoidal, attached to solid substrate, only rarely obtained owing to its firm attachment to solid substrate.

Distribution.—Indian Ocean; Pacific Ocean from the Malay Archipelago to the Galápagos and the Gulf of Panama; Atlantic Ocean. In depths of 228–1463 m.

Calyptrophora trilepis (Pourtalès, 1868)
Figs. 1, 2b

Primnoa trilepis Pourtalès, 1868:130.

Calyptrophora trilepis.—Gray, 1870:42.—Lindström, 1877:7.—Deichmann, 1936: 171, pl. 25, fig. 1, pl. 26, fig. 4.

Stachyodes trilepis.—Versluys, 1906: 122.—Kükenthal, 1919:465; 1924:316.

Not *Stachyodes trilepis.*—Studer, 1901:41, pl. 5, pl. 11, figs. 3, 6, 7 (=*Stachyodes bellissima* Kükenthal, 1915).

Material examined.—Blake Plateau, off Savannah, Georgia: 31°49′40″N, 78°19′16″W, 625 m, R/V *Cape Hatteras* cruise SA-6, dredge 5, 7 May 1987, one incomplete colony, USNM 79764.

Blake Plateau, off Brunswick, Georgia: 31°07′N, 79°08.5′W, 631 m, R/V *Gosnold* cruise 74, sta. 2478, 17 Sep 1965, one colony lacking holdfast, and fragments, USNM 57300.

Blake Plateau, off Brunswick, Georgia: 31°01.5′N, 78°19′W, 911 m, R/V *Gosnold* cruise 74, sta. 2382, 27 Aug 1965, one colony lacking holdfast, USNM 57299.

Blake Plateau, off Brunswick, Georgia: 30°59′N, 78°14′W, 480 fathoms (=878 m), R/V *Atlantis* sta. 266–41, 15 Jul 1961, three colonies without holdfast, USNM 57446.

Blake Plateau, off Fernandina, Florida: 30°57.2′N, 78°54.6′W, 779 m, R/V *Gosnold* cruise 74 sta. 2385, 27 Aug 1965, one colony lacking holdfast, USNM 56893.

Blake Plateau, off Fernandina, Florida:

30°53′N, 78°47′W, 445 fathoms (=814 m), R/V *Atlantis* sta. 266–40, 13 Jul 1961, three colonies one lacking holdfast, and fragments, USNM 57445.

Straits of Florida off Sebastian Inlet, Florida: 27°57′N, 78°56′W, 779 m, R/V *Gerda* sta. G-181, 2 Jul 1963, one colony 17 cm tall and one small colony 7 cm tall, both lacking holdfast, USNM 52744 (SEM 70, 245).

Straits of Florida "off Bahia Honda," Florida, [24°14′20″N, 80°59′40″W, 324 fathoms (=593 m), U.S. Coast Survey Exploration of the Gulf Stream, U.S. Coast Survey steamer *Bibb,* 12th dredging, Pourtalès sta. 22P, 4 May 1868], dry fragment, holotype, MCZ 4812.

Diagnosis.—Dichotomously branched, lyrate *Calyptrophora* with polyps about 1.5 mm tall, directed upward, in whorls of 3–4, 13–17 whorls in 3 cm of axial length; infrabasal scales well developed; basal ring with a pair of inconspicuous blunt, short marginal processes; free margin of buccal ring narrow, smooth; outer surface of annuliform sclerites ornamented by crowded, smooth granules, interior with crowded complex tubercles.

Description.—Colonies are lyrate, dichotomously branched in one plane, attached to solid substrates by a roughly discoidal holdfast; terminal branches are long and very flexible. The polyps are in regular whorls of 3 or 4, sometimes in opposite pairs, predominantly directed upward but with occasional strays facing down; 13–17 whorls occur in 3 cm, but commonly 15.

The polyps are protected by 2 ringlike sclerites each composed of two inseparably fused semicircular scales, a pair of large, crescentic infrabasal scales situated between the basal ring and the coenenchymal scales, and the usual 8 triangular operculars; sometimes the members of the basal ring fail to meet adaxially, but the abaxial symphysis is always solidly fused. The tentacles have numerous small, narrow scales curved in conformity with their locations. The outer surface of the annular body sclerites is covered with sharp, simple granules, and the inner surface with crowded, complex tubercles. The opercular scales have a longitudinal apical keel on the inner surface, most strongly developed on the abaxials, becoming less prominent toward the axis.

The axis is dark brown with bronze lustre proximally, gradually becoming paler with a golden gloss distad, and almost white near the twig tips; inconspicuous longitudinal ribbing is present on the proximal parts of the axis, becoming obsolete distad. The terminal twigs are unusually flexible, especially in small specimens.

The sclerites are composed of magnesian calcite; USNM 52744 was found to have 6.6 mole% $MgCO_3$, USNM 57445 with 7.4 mole% $MgCO_3$. The mineral component of axis and holdfast consists of aragonite.

Distribution.—Blake Plateau south to Straits of Florida between the Florida Keys and Cuba, 593–911 m.

Comparisons.—*Calyptrophora trilepis,* with its inconspicuous marginal processes of the basal ring and smooth margin of the buccal ring, resembles the Hawaiian *C. angularis* (Nutting). Its body sclerites are more strongly sculptured and much less fragile than those of *C. angularis,* which are nearly smooth and very easily damaged. *C. trilepis* is branched dichotomously, whereas *C. angularis* is bipectinate.

Remarks.—The sole surviving fragment of the type specimen in the Museum of Comparative Zoology was kindly made available by the late Dr. Deichmann for preparation of the drawing presented here.

Deichmann (1936:172) misquotes the original description by Pourtalès (1868: 130) by adding the words "downward bent," which are not in the published text. Examination of a part of the original specimen shows that the polyps are directed upward, not downward, and have two, not three, ringlike scales. However, Pourtalès obviously overlooked the fact that the members of the infrabasal pair of scales are not inseparably fused to form a ring as the

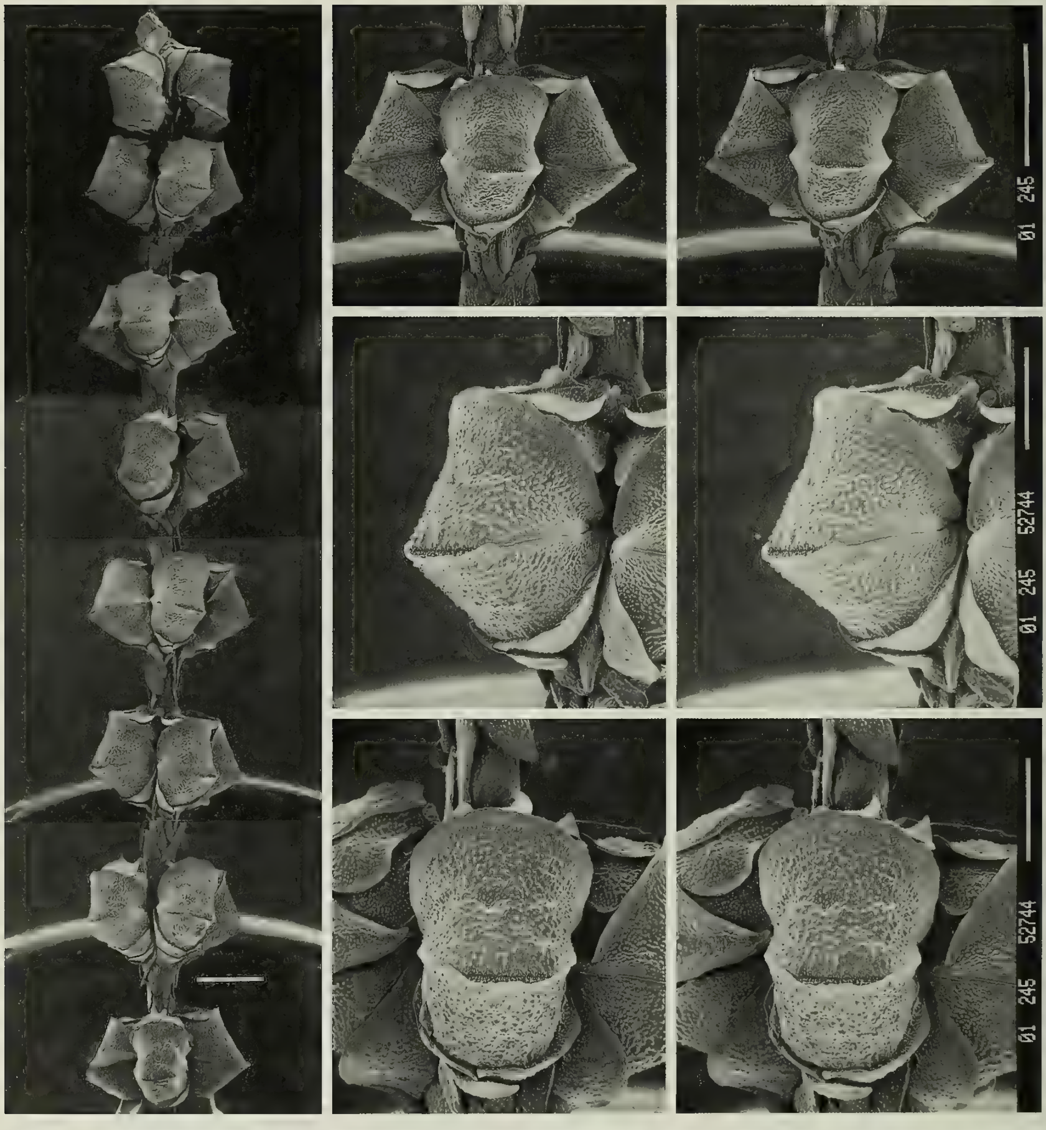

Fig. 1. *Calyptrophora trilepis* (Pourtalès), USNM 52744 (SEM 245). Left. Part of terminal branch with whorls of polyps (scale bar = 1.0 mm); Right. Single whorl of polyps, stereo pair (scale bar = 1.0 mm); oblique and abaxial aspects of polyp, stereo pairs (scale bar = 0.5 mm).

basal and buccal pairs are, so the polyps have two, not three ringlike scales; the alleged downward orientation of the polyps is an error introduced by Deichmann and represented by her illustrations (1936: pl. 25, fig. 1, pl. 26, fig. 1). Verrill's original unpublished illustration intended for his projected "Blake Report" shows the correct upward orientation of polyps.

Calyptrophora pillsburyae, new species
Fig. 3

Material examined.—Leeward Islands, Lesser Antilles, west of Montserrat: 16°55′N, 62°43′W, 686–1125 m, R/V *Pillsbury* sta. P-954, 18 Jul 1969, one incomplete colony, holotype, USNM 52743 (SEM 247, 1699).

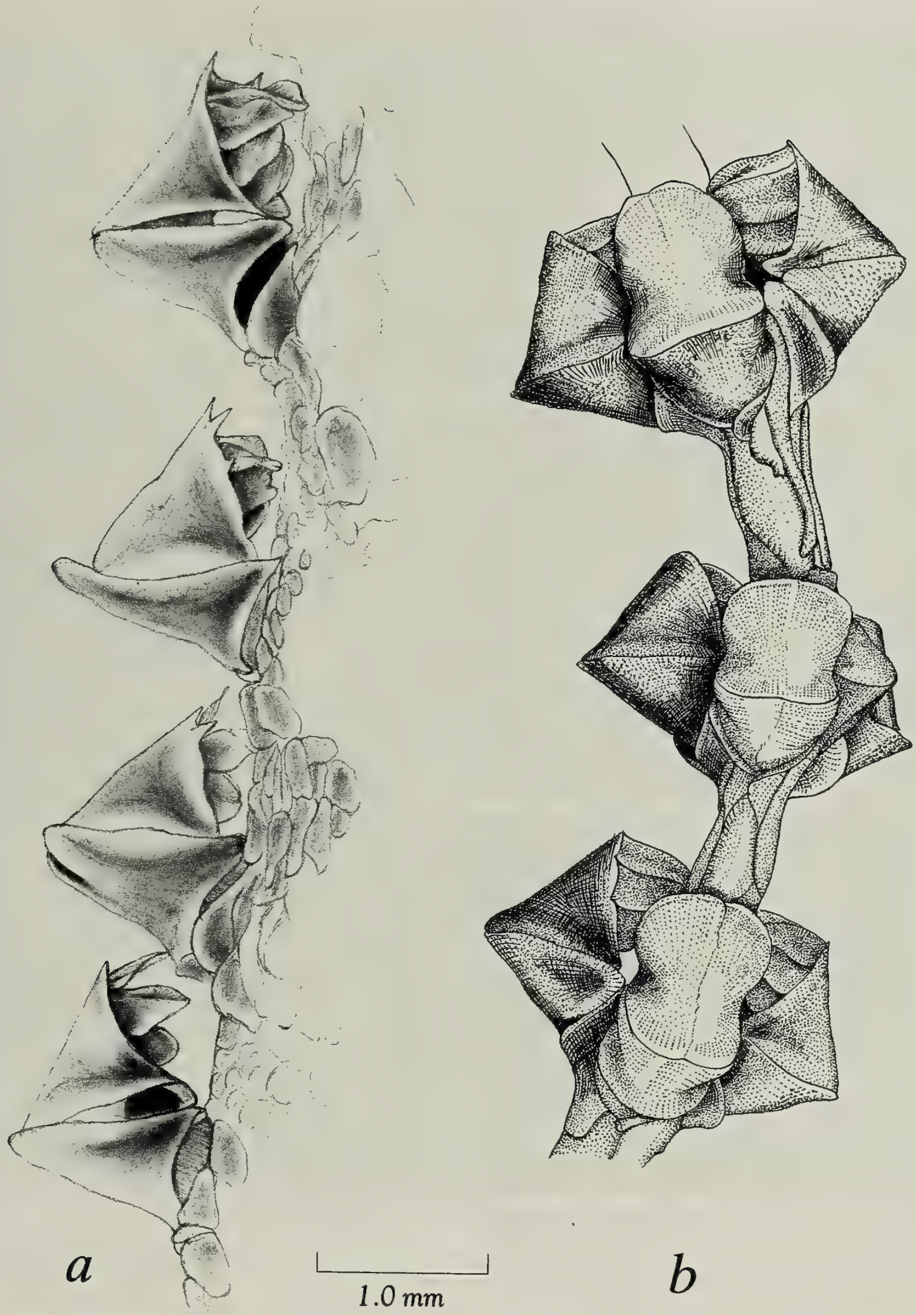

Fig. 2 a, *Calyptrophora japonica* Gray, holotype, BMNH 1866.1.8.2. b, *Calyprophora trilepis* (Pourtalès), holotype, MCZ 4812. Scale bar applies to both drawings.

Diagnosis.—Dichotomous *Calyptrophora* with polyps about 1.5 mm tall, directed upward in whorls of 4, 11–12 whorls in 3 cm of axial length; infrabasal scales well developed; basal ring having a pair of smooth, sharp marginal spines; buccal ring with narrow free margin having 4–6 conspicuous marginal denticles; outer surface of annuliform sclerites ornamented by crowded, smooth granules.

Description.—The colony is narrow, upright, about 32 cm tall, branched dichotomously in one plane, 25–85 mm between bifurcations, with almost straight terminal branches up to 12 cm long. The polyps are directed upward, placed in regular whorls of 4 except on the lower parts of the proximal branches where there may be 5; 11–12 whorls occur in 3 cm. Whether this specimen represents a colony complete save for holdfast, or only a branch from a larger, openly lyrate colony, is not known.

The polyps are enclosed in two ringlike sclerites consisting of the solidly fused basal and buccal pairs of scales. A pair of conspicuous, crescent-shaped infrabasal scales is present between the scales of the coenenchyme and the basal sclerite ring, which bears a pair of short, smooth, sharp marginal spines. The annuliform solidly fused buccal scale pair has only a narrow free margin that does not hide the opercular scales from abaxial view; the buccal margin has 4–6 small but distinct smooth spines and sometimes one or more inconspicuous intermediate points. The opercular scales are roughly triangular with rounded angles, decreasing in size from the abaxials to the adaxials. They have a strong apical keel on the inner surface and corresponding though on the outer; the keel is marked by closely placed, narrow serrate ridges. The tentacles contain narrow, flattened scales with granular sculpture and tapered ends, placed crosswise and curved to fit their location in the tentacle. The coenenchyme contains a layer of elongate scales with rounded ends and somewhat overlapping margins.

The sclerites are composed of magnesian calcite containing 6.5 mole% $MgCO_3$. The axis is strongly mineralised with aragonite.

Etymology.—Named in honor of R/V *John Elliott Pillsbury,* research vessel of the University of Miami, in recognition of the rich contributions to knowledge of the American deep-sea fauna made possible by operations conducted aboard that ship.

Comparisons.—This species differs from both *Calyptrophora gerdae* and *C. antilla* by its smooth, rather short basal spines, and the small, well-differentiated, smooth spines of the buccal margin. The polyps of *C. pillsburyae* bear a striking resemblance to those of the type specimen of *Calyptrophora japonica* Gray from Japan in the Natural History Museum, London, Register number 1866.1.8.2. In 3 cm of axial length it has 16 whorls of 6 polyps; on the largest part of the branch, the whorls are composed of 8–11 polyps.

My observations and drawings of Gray's specimen differ somewhat from those of Versluys (1906:113, figs. 153–155) made prior to 1906. My drawing (Fig. 2a), made with the aid of a camera lucida, does not show the basal spines as long as drawn by Versluys (1906: figs. 153, 154), apparently free-hand, and I did not find basal spines as long as shown in his figure 153.

To judge by Versluys' excellent drawings of the specimens that he considered to be variants of *C. japonica,* all probably belong to other species. They differ among themselves in much the same way as do *C. gerdae, pillsburyae,* and *antilla,* which I cannot regard as representing a single variable species. Versluys's specimens no. 3 of "Form B" seems to be very close to Nutting's (1908:578) *Calyptrophora japonica* from *Albatross* sta. 4007 off Ukula (=Puolo) point, Kauai, Hawaii, which subsequently was described as a distinct species, *C. clarki* (Bayer, 1951:40).

The specimens from Hawaii and Japan identified as *C. japonica* by Nutting (1908, 1912) are of biplanar, bipectinate growth form. The type specimen of *japonica* is dichotomous (see Gray 1866, fig. 1 and 1870, fig. 13) but, as it is incomplete, it is impossible to determine whether it is only a dichotomous distal branch of a uniplanar bipectinate colony such as Versluys's specimen no. 2, shown on his plate 10, fig. 27, of a biplanar bipectinate colony such as Kinoshita (1908,

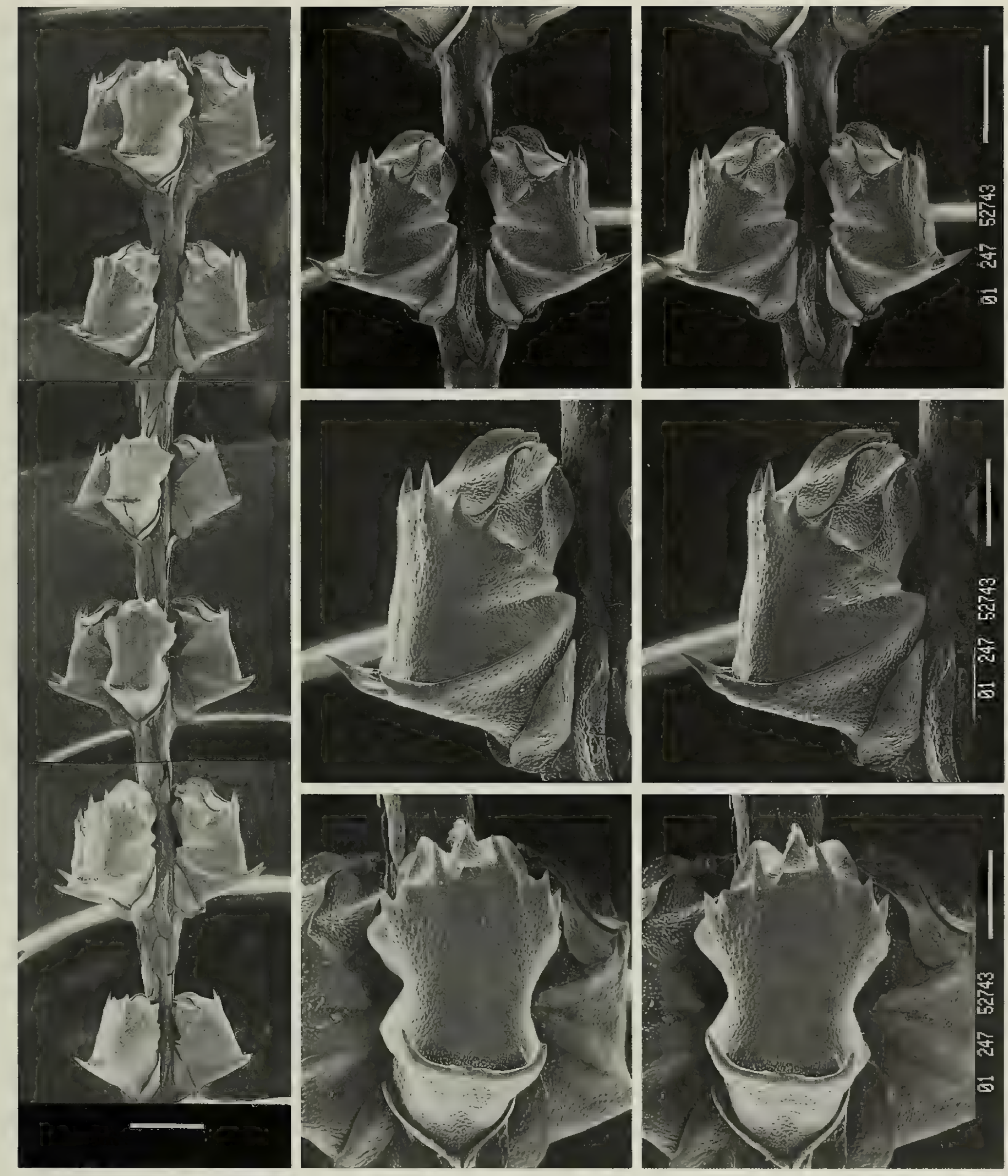

Fig. 3. *Calyptrophora pillsburyae*, new species, USNM 52743, holotype (SEM 247). Left. Part of terminal branch with whorls of polyps (scale bar = 1.0 mm); Right. Single whorl of polyps, stereo pair (scale bar = 1.0 mm); Lateral and abaxial aspects of polyp, stereo pairs (scale bar = 0.5 mm).

plate 4, fig. 33) illustrated, or part of a regularly dichotomous colony.

Nuttings's specimen from *Albatross* sta. 4924 off Nagada Saki (USNM 30027) has polyps corresponding closely with those of Gray's type and is therefore deemed to be genuine *japonica.* The colony is severely damaged, but retains ample evidence of biplanar bipectinate growth form. A biplanar bipectinate colony taken in 1900 at *Albatross* sta. 3749 off Suno Saki, identified as *C. japonica* (USNM 49323) by Nutting but not included in his report on the material from the 1906 cruise, has polyps agreeing closely with Versluys's specimen no. 10 of his Form C, which he thought might represent a new species distinct from *japonica* (1906:122). Biplanar bipectinate colonies from *Albatross* sta. 3882 between Maui and Molokai, reported as *japonica* by Nutting (1908:578), have polyps of the *gerdae* type, with irregular, broad, more or less pointed lobes on the free margin of the buccal ring.

A few specimens taken by the *Albatross* in Philippine waters with the general features of the "*japonica* complex" conform well neither with Gray's type specimen nor with Versluys's Forms B and C. One of the *Albatross* specimens established as a distinct species, *C. juliae* Bayer (1952:82) (incorrectly synonymized with *C. japonica* by Pasternak (1984), is now presumed to have an unbranched growth form similar to flagelliform specimens from New Caledonia in the Muséum National d'Histoire Naturelle in Paris, which remain to be described.

Pasternak (1985:30) described a new species, *Calyptrophora microdentata,* from south of Rockaway Seamount in 940–950 m (30°30.5′N, 52°00.5′W), which differs from *C. pillsburyae* in the paired arrangement of polyps, which were reported to be 1.7–2.0 mm long. Being larger than the polyps of *C. pillsburyae,* they must be more closely placed along the axis than is the case with *C. pillsburyae.* The margin of the buccal ring of *C. microdentata* was reported to have 4 broad, acute projections which sometimes are needle-like, occasionally with smaller intermediate spines resulting in a dentate appearance. Pasternak commented on the resemblance of *C. microdentata* to *C. japonica,* a comparison that applies also to *C. pillsburyae* as mentioned above.

In view of the small size and probable immaturity of the unique specimen of *C. microdentata,* and the single but well developed specimen of *C. pillsburyae* now available, it cannot be ruled out that further analysis may demonstrate that the two are conspecific when additional specimens of both become available for study.

Calyptrophora antilla, new species
Fig. 4

Material examined—Windward Passage between Cuba and Haiti: 20°09′N, 73°29′W, 1399 m, R/V *Pillsbury* sta. P-1146, 14 Jan 1970, severely damaged syntypic fragments, USNM 52914 (SEM 1697, 1698, 1740).

Diagnosis.—Dichotomous *Calyptrophora* with polyps about 2 mm tall, directed upward in whorls 4 or more, 7–11 whorls in 3 cm of axial length; infrabasal scales well developed; basal ring with a pair of prominent, sharp, serrated marginal spines; free margin of buccal ring narrow, with 4 conspicuous marginal spines and sometimes two or more small intermediate spinules; outer surface of annuliform sclerites ornamented by sharp granules arranged in rows radiating away from depositional centers.

Description.—The severely damaged specimen is broken in many pieces, the largest of which is dichotomously branched in one plane, showing that the colony is lyriform, with internodes 2–3 cm long and nearly straight terminal branches that may exceed 6 cm in length. The polyps are about 2 mm tall, directed upward and arranged in regular whorls of 4 (but more on the large branches), of which 7–11 occupy 3 cm of axial length. The axis is stiff and brittle, nearly circular in cross section, the basal parts with inconspicuous irregular longitudinal grooves; it is brownish in color with distinct metallic bronze luster, darker proximally and becoming paler distad until in the slenderest terminal branches it is smooth, cream white with pearly reflections.

The polyps are encircled by two annular sclerites each composed of two curved scales inseparably fused along the abaxial midline and at the narrow adaxial symphysis. A pair of semilunate infrabasal scales lies between the coenenchyme and the basal ring. The basal ring bears a pair of strong, serrate, slightly curved marginal spines. The buccal ring has only a narrow free margin, with four slender, sharp marginal spines, and sometimes two or more smaller spinules. The closed operculum projects prominently from the buccal aperture, composed of 8 tall, bluntly triangular scales with a strong apical keel on the inner surface corresponding with an external furrow. The outer surface of the annular sclerites is ornamented by sharp granules arranged in lines radiating out from the depositional center of the component scales, extending as sharp, serrated ridges along the marginal spines. The tentacles contain many small, flattened, oval scales with granular sculpture. The coenenchyme contains a layer of thin, flat, irregularly oval scales ornamented externally by simple granules, internally by complex tubercles.

The sclerites are composed of magnesian calcite containing 6.4 mole% $MgCO_3$. The axis is heavily mineralized with aragonite.

Etymology.—*Antilla,* noun in apposition, referring to the Antilles, islands surrounding the Caribbean Sea.

Comparisons.—*Calyptrophora antilla* differs from *C. gerdae* in having short, serrate spines on the narrow free margin of the buccal ring, and much longer serrate spines on the basal ring; it differs from *C. pillsburyae* in having the spines of both basal and buccal rings distinctly serrate rather than smooth.

Calyptrophora gerdae, new species
Figs. 5, 6

Material examined.—Straits of Florida off Jupiter Inlet, Florida: 27°01′N, 79°21.5′W, 275–229 m, R/V *Gerda* sta. G-169, 29 Jun 1963, one immature colony with three branches, lacking holdfast, USNM 52740, paratype.

Straits of Florida off Southwest Point, Grand Bahama: 26°27′N, 78°40′W, 514–556 m, R/V *Gerda* sta. G-707, 22 Jul 1965, one colony lacking holdfast, USNM 52741, paratype (SEM 1717).

Straits of Florida off Memory Rock, Little Bahama Bank: 26°52′N, 79°11′W, 536 m, R/V *Gerda* sta. G-1314, 31 Mar 1971, one colony lacking holdfast, USNM 52742, holotype (SEM 246); two colonies lacking holdfast, USNM 100744, paratypes.

Diagnosis.—Dichotomous *Calyptrophora* with polyps about 1.5 mm tall, directed upward in whorls of 4–6, 16–20 whorls in 3 cm of axial length; infrabasal scales well developed; basal ring having a pair of prominent, broad, flattened, serrate marginal spines; buccal ring with free margin wide, divided into several irregular, more or less pointed, broad lobes; outer surface of annuliform sclerites ornamented by fine, closely crowded smooth granules arranged in radial rows diverging from depositional centers.

Description.—The colonies are dichotomously branched in one plane and apparently do not attain large size as the largest is only approximately 14 cm high and wide; in the proximal parts of the colonies the axis is the color of pale bronze with distinct metallic luster, marked by fine, irregularly longitudinal ridges and grooves, distally becoming smooth, paler, with golden metallic iridescence. The polyps are about 1.5 mm tall, directed upward and arranged in regular whorls of 5–6, except near the tips of branches where 4 is a common number; 16–20 whorls occur in 3 cm of axial length.

The polyps have a pair of crescent-shaped infrabasal scales between the coenenchymal plates and the basal pair of body scales; the basal scales form a solid ring bearing a pair of strong, echinulate marginal spines. The scales of the buccal pair are also inseparably fused to form a ring the wide free margin of which extends beyond the abaxial opercular scales, nearly or completely obscuring them from abaxial view. The buccal margin is divided into two or more broad lobes, sometimes more or less pointed, sometimes smoothly rounded. The opercular scales are broadly triangular in

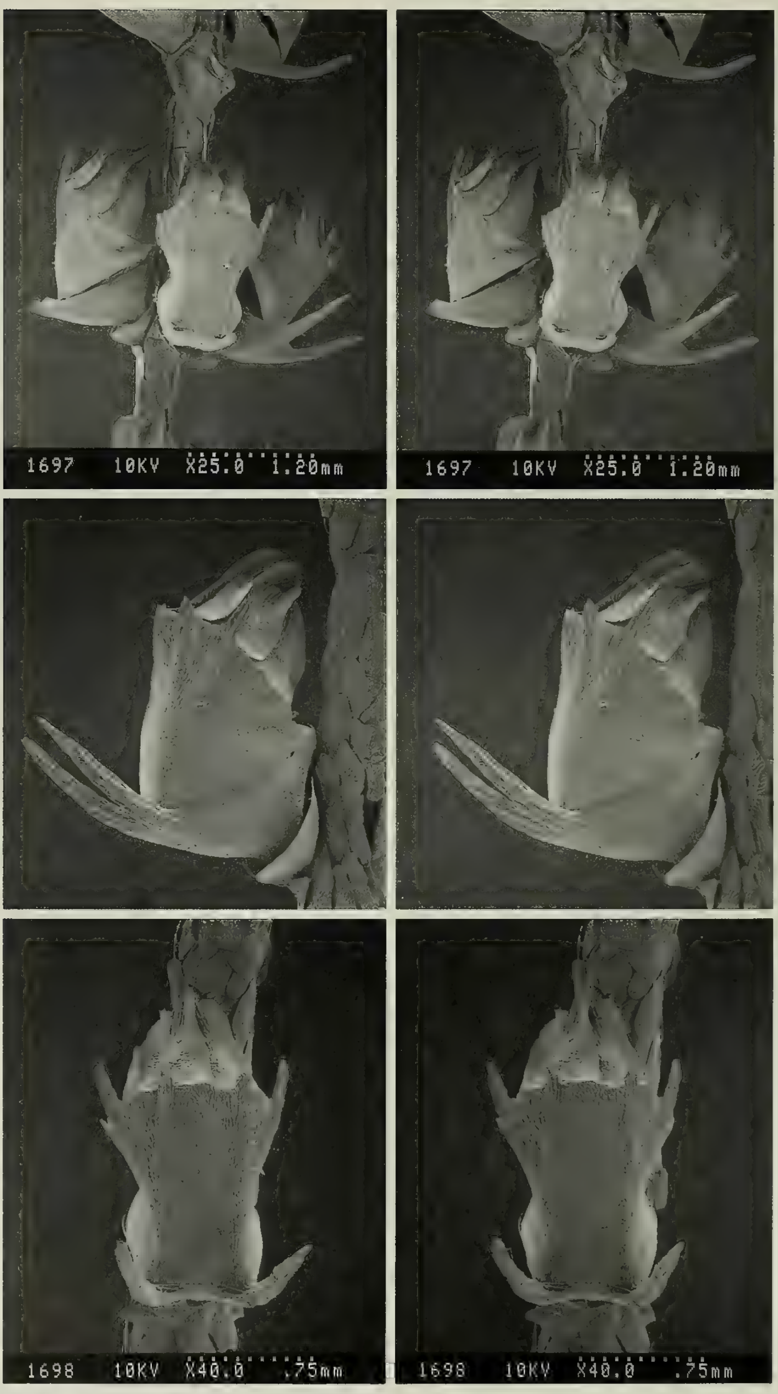

Fig. 4. *Calyptrophora antilla,* new species, USNM 52914, syntypic fragments. Top. Single whorl of polyps, stereo pair (SEM 1697); Bottom. Lateral and abaxial aspect of polyp, stereo pairs (SEM 1698). Magnifications as indicated by scales.

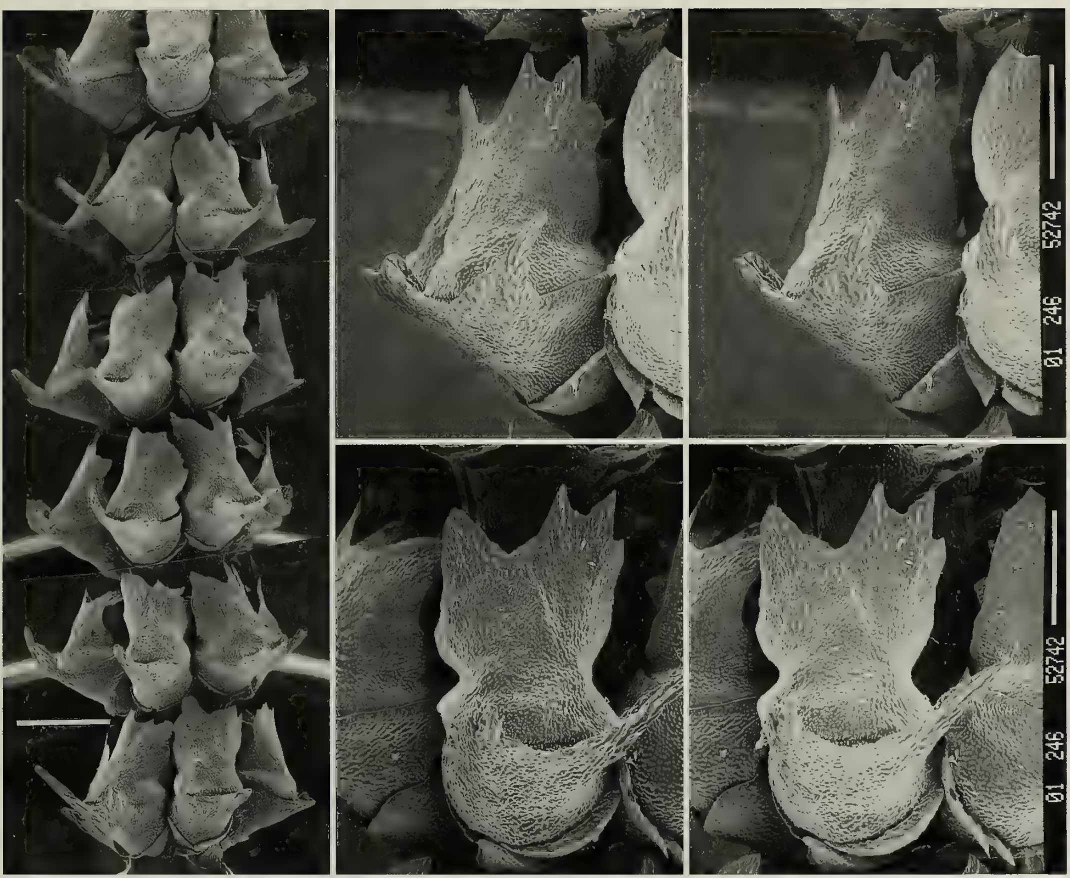

Fig. 5. *Calyptrophora gerdae*, new species, USNM 52742, holotype (SEM 246). Left. Part of terminal branch with whorls of polyps (scale bar = 1.0 mm); Right. Oblique and lateral aspects of polyp, stereo pairs (scale bar = 0.5 mm).

shape, with rounded angles and a strong apical keel on the inner surface. The operculars decrease in size from the abaxials to the adaxials; the keel of the abaxial scales has two or more narrower longitudinal crests, and the apex of the largest abaxial may be conspicuously bilobed. The outer surface of the body rings and operculars is covered with small, simple granules, and the inner surface with complex tubercles; the marginal spines of the basal ring have several narrow, serrate longitudinal ridges. The tentacles contain small, narrow, flattened, tuberculate scales with rounded ends, placed crosswise and curved to fit the contour of the rachis. The coenenchyme contains a layer of polygonal plates of very variable shape.

Sclerites are composed of magnesian calcite containing 8.1 mole% $MgCO_3$. The axis is heavily mineralized with aragonite.

Etymology.—Named for R/V *Gerda*, for years the workhorse vessel of the Marine Laboratory, University of Miami.

Comparisons.—This species differs from *C. pillsburyae* in having serrate rather than smooth basal spines, wide buccal margins with broad, flat marginal lobes rather than narrow buccal margins with small, smooth spines, and strong, longitudinally crested apical keels on the abaxial operculars. *C. antilla* differs in having a narrow buccal

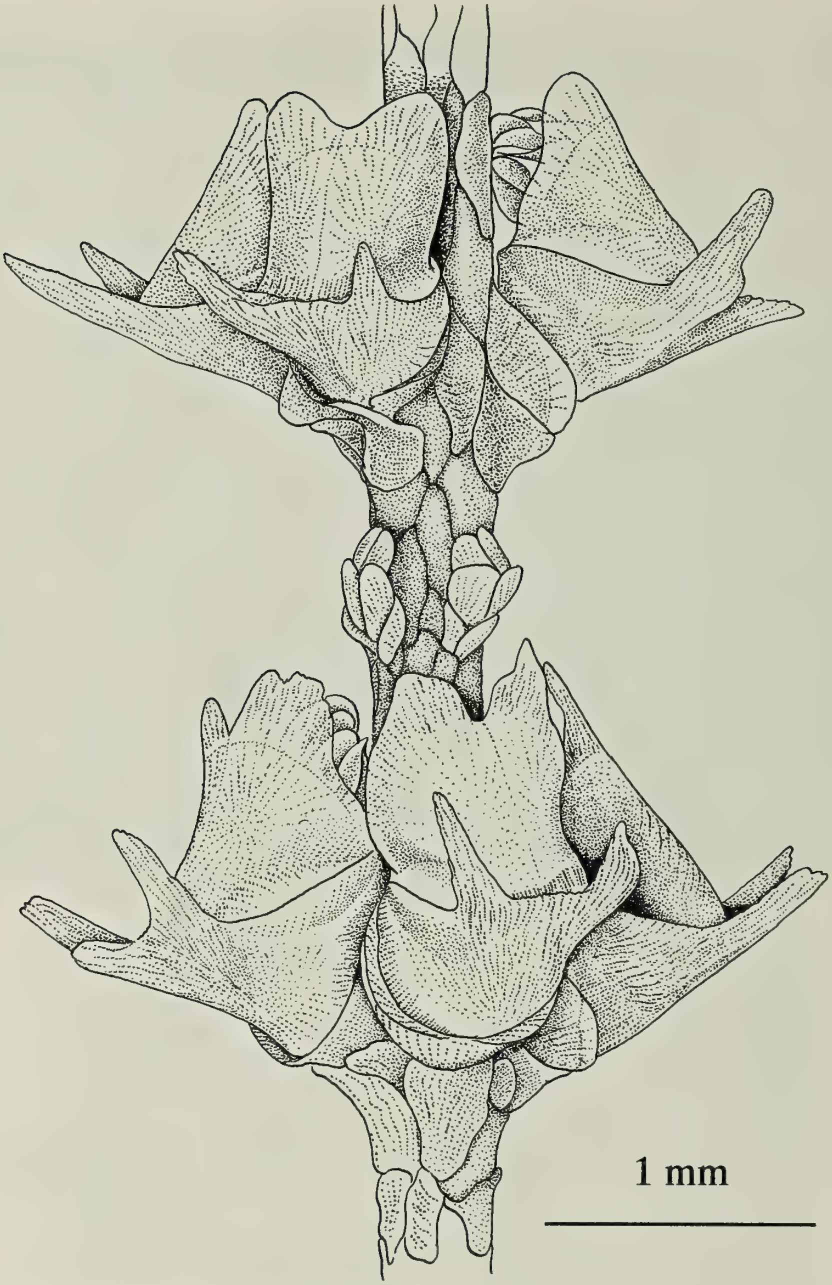

Fig. 6. *Calyptrophora gerdae,* new species, USNM 52742, holotype. Whorl of new polyps between fully developed whorls. Camera lucida drawing.

margin with four strong, serrate spines, and very long, serrate basal spines.

The polyps of a specimen of *Calyptrophora* from Hawaii identified as *C. japonica* Gray by Nutting (1908:578; USNM 25369) are extraordinarily similar to those of *C. gerdae,* differing most conspicuously in having smooth rather than granulate body scales. Moreover, the large fragments of Hawaiian material show conclusively that the colonies are stiffly bipectinate rather than regularly dichotomous as in *C. gerdae.*

Remarks.—The small size of specimens of *Calyptrophora gerdae* collected at three different localities over a period of nine years suggests that the species may not produce colonies as large as do other species of the genus.

Whorls of new polyps are present here and there between whorls of fully developed individuals. On the specimen from off Grand Bahama (USNM 52741) they occur in two cases between the second and third whorls of a bifurcation on one half of the dichotomy; in another case the new polyps occur between fully developed whorls on part of a terminal branch removed for illustration. The body scales of the young polyps are arranged in three unfused pairs, suggesting that the infrabasal scales of fully developed polyps are polyp scales rather than coenenchymal scales, and demonstrating that the inseparable ringlike fusion of basal and buccal scale pairs is a function of age. As no examples of young polyps were found on a preparation made for examination by SEM (No. 246), the drawing made prior to availability of scanning microscopy is presented here (Fig. 6) to illustrate this developmental phenomenon.

Key to the western Atlantic species of *Calyptrophora*

1. Basal body ring with two projecting spines 2
1. Basal body ring without projecting spines, or at most two short, blunt lobes; buccal ring with distal margin entire, not widely flared around operculum .... *trilepis* (Pourtalès)
2. Polyps arranged in pairs .... *microdentata* Pasternak
2. Polyps arranged in whorls of 3–6 or more 3
3. Spines of basal ring smooth; buccal ring with only a narrow free margin not widely extending beyond bases of opercular scales, with six or more small smooth, sharp spines .... *pillsburyae,* new species.
3. Spines of basal ring serrate 4
4. Buccal ring with a wide free margin extending beyond bases of opercular scales and produced into two broad, more or less pointed lobes, one or both of which may be divided in two; 16–17 whorls in 3 cm of axis .... *gerdae,* new species.
4. Buccal ring with a narrow free margin extending little beyond bases of opercular scales, with four strong, well differentiated, echinulate spines; 11–12 whorls in 3 cm of axis ..... *antilla,* new species.

Acknowlegments

Many of the specimens used in the preparation of this report were collected by operations aboard research vessels of the University of Miami during a deep-sea biology program directed by the late Dr. Gilbert L. Voss. Over many years, the late Dr. Elisabeth Deichmann made available the classic collections of octocorals at the Museum of Comparative Zoology. The late Dr. W. J. Rees of the British Museum (Natural History) placed collections in his charge available to me during my visit to London in 1958. Dr. Manfred Grasshoff of the Forschungsinstitut und Naturmuseum Senckenberg has been a constant source of advice in matters dealing with the systematics of gorgonians and other octocorals. Stephen D. Cairns made numerous helpful comments on a draft of this text. George Steyskal and Svetlana Maslakova translated pertinent parts of Pasternak's Russian publications. The scanning electron micrographs illustrating this paper were made with the technical skills of Walter R. Brown, former head of the SEM Laboratory of the National Museum of Natural History, Smithsonian Institution. Ian J. Macintyre kindly provided mineral determinations made by X-ray diffraction analyses conducted by William T. Boykins.

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Eulalia gemina (Phyllodocidae: Polychaeta), a new species from Shirahama, Japan

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Abstract.—*Eulalia gemina,* a new phyllodocid species, is described from intertidal rocks at Shirahama, Honshu, Japan. It is characterized by a specific pigmentation pattern and by a unique combination of characters. The new species is compared to a series of other *Eulalia* Savigny *in* Lamarck, 1822, which it approaches in pigmentation patterns, body shape, and/or shape of the dorsal cirri. *Eulalia ornata* Saint-Joseph, 1888 and *E. myriacycla* (Schmarda, 1861) are considered most similar. *Eulalia pacifica* (Imajima, 1964), new combination, is transferred from *Steggoa* Bergström, 1914.

In terms of species richness, *Eulalia* Savigny *in* Lamarck, 1822 is one of the largest genera of phyllodocids, including ca. 80 nominal species (Pleijel 1991). In Japanese waters four species have previously been recorded (Uchida 1988), five with the inclusion of *Steggoa pacifica* Imajima, 1964 (see below). Here we describe a new species of *Eulalia* from the Pacific side of southern Japan, occurring intertidally in deep crevices in pudding stone. In spite of being distinctive both by its large size (over 15 cm in length) and in its striking pigmentation (yellow green with two transverse, dorsal green bands on each segment), the new taxon has previously been overlooked, presumably due to the poorly studied habitat where it occurs.

Materials and Methods

Specimens were collected intertidally from crevices in pudding stone (conglomerate: clastic sedimentary rock composed by rounded stones in a cement of calcareous material), relaxed in 10% magnesium chloride, fixed in calcium carbonate-buffered formalin in sea water (10%) for at least 24 hrs, rinsed in fresh water, and transferred to 70% ethanol. Drawings were prepared from preserved specimens with a camera lucida.

Museums are indicated by the following abbreviations: Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan (ZIHU); Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Eulalia gemina, new species
Figs. 1–3

Material examined.—Holotype (ZIHU 1333), 10 paratypes (ZIHU 1334–1343), 6 paratypes (MNHN-POLY64, Shirahama, Wakayama, Honshu, Japan, 33°41′N, 135°20′E, intertidal rocky shore, 13 May 1998; 3 paratypes (ZIHU 1344–1346), same locality, 19–20 Apr 1995.

Description.—Holotype complete ovigerous female, 138 mm long and 1.0 mm wide at middle of body (including parapodia but excluding chaetae), for 457 segments. Largest paratype specimen 176 mm long and 1.2 mm wide at middle of body, for 530 segments (lacking posterior end; see Fig. 3 for other paratypes).

Body long and slender, ventrally flattened, of almost uniform width. Prostomium rounded rectangular, slightly wider than long, with delineated protuberance at base of paired antennae (Fig. 1A). Eyes rounded, ca. 1/5 to 1/6 as wide as prostomium, situated near posterior margin of prostomium. Paired antennae cylindrical, slightly shorter than prostomium (Fig. 1A–C). Median antenna similar to paired ones in length, slightly narrower, situated anterior to eyes medially on prostomium (Fig. 1A). Nuchal organs not observed.

Entire surface of proboscis covered with diffusely distributed, rounded papillae (examined by dissection). Terminal proboscis ring with 13–18 papillae.

Dorsal tentacular cirri cylindrical, ventral ones slightly flattened (Figs. 1B, C, 2A–C). Segment 1 dorsally and ventrally fully developed. Tentacular cirri of segment 1 reaching segment 4–5; dorsal and ventral tentacular cirri of segment 2 reaching segments 8–9 and 5, respectively; dorsal tentacular cirri of segment 3 reaching segment 8–10. Segment 2 lacking neuropodial lobes and chaetae (Fig. 2B). Segment 3 with neuropodial lobes and ca. 7 chaetae (Fig. 2C). Ventral cirri of segment 3 similar in shape to but slightly smaller than those of following segments, which gradually increase in size.

Dorsal cirri of anterior and median segments lanceolate, ca. twice as long as broad, with pointed tips (Fig. 2D–G); dorsal cirri of posterior segments shorter, more conical and inflated (Fig. 2H, I). Neuropodial lobes short, rounded, supra-and subacicular lips of equal size, with ca. 10 chaetae. Rostrum of chaetal shaft symmetrical, with large number of teeth, decreasing in size proximally. Chaetal blades short. Ventral cirri of anterior and median segments oval, longer than neuropodial lobes (Fig. 2E, G); ventral cirri of posterior segments rounded triangular (Fig. 2I).

Pygidial cirri cylindrical, tapered, 3 to 4 times as long as broad (Fig. 1E). Pygidial papilla absent.

Color.—Live specimens with yellow green body and two transverse green bands dorsally on each median segment; anterior segmental bands narrower than posterior ones (Fig. 1A, D). Segment 1 without transverse bands; anterior bands absent from anterior- and posteriormost segments. Prostomium with green pigmentation between and lateral to eyes. Dorsal tentacular cirri of segments 2 and 3 and dorsal side of dorsal cirri with green pigmentation. Eyes dark brown. Ovigerous females with green eggs. Preserved specimens brown with dark brown bands; eyes blackish. Pigmentation pattern well preserved in ethanol.

Habitat.—Intertidally in deep crevices in pudding stone.

Distribution.—Known only from Shirahama, southern Japan.

Reproduction.—Several mature males and females collected in April and May; egg size 60–70 μm in diameter (possibly not yet of full size).

Remarks.—The present species is assigned to *Eulalia* based on the following combination of characters: five antennae, prostomium with delineated protuberance, proboscis with diffusely distributed rounded papillae, four pairs of tentacular cirri (1+2+1), all anterior segments developed and separate, chaetae present from segment 3, chaetigerous lobes symmetrical, and rostrum of chaetal shafts with large number of teeth which decrease in size proximally. These characters agree with the diagnosis of *Eulalia* given by Pleijel (1991) and largely (with due adjustment for *Steggoa* as a junior synonym of *Eulalia*; see Pleijel 1987) with those given by Bergström (1914) and Uschakov (1972).

Distinctive pigmentation patterns occur in many members of *Eulalia,* such as *E. bilineata* (Johnston, 1840), *E. tripunctata* McIntosh, 1874, *E. aurea* Gravier, 1896, and *E. ornata* Saint-Joseph, 1888. Among these, *E. gemina* most closely resembles the European *E. ornata,* which has two transverse segmental bands similar to those of *E. gemina.* The two taxa, however, differ in a number of details in the pigmentation: the anterior trans-

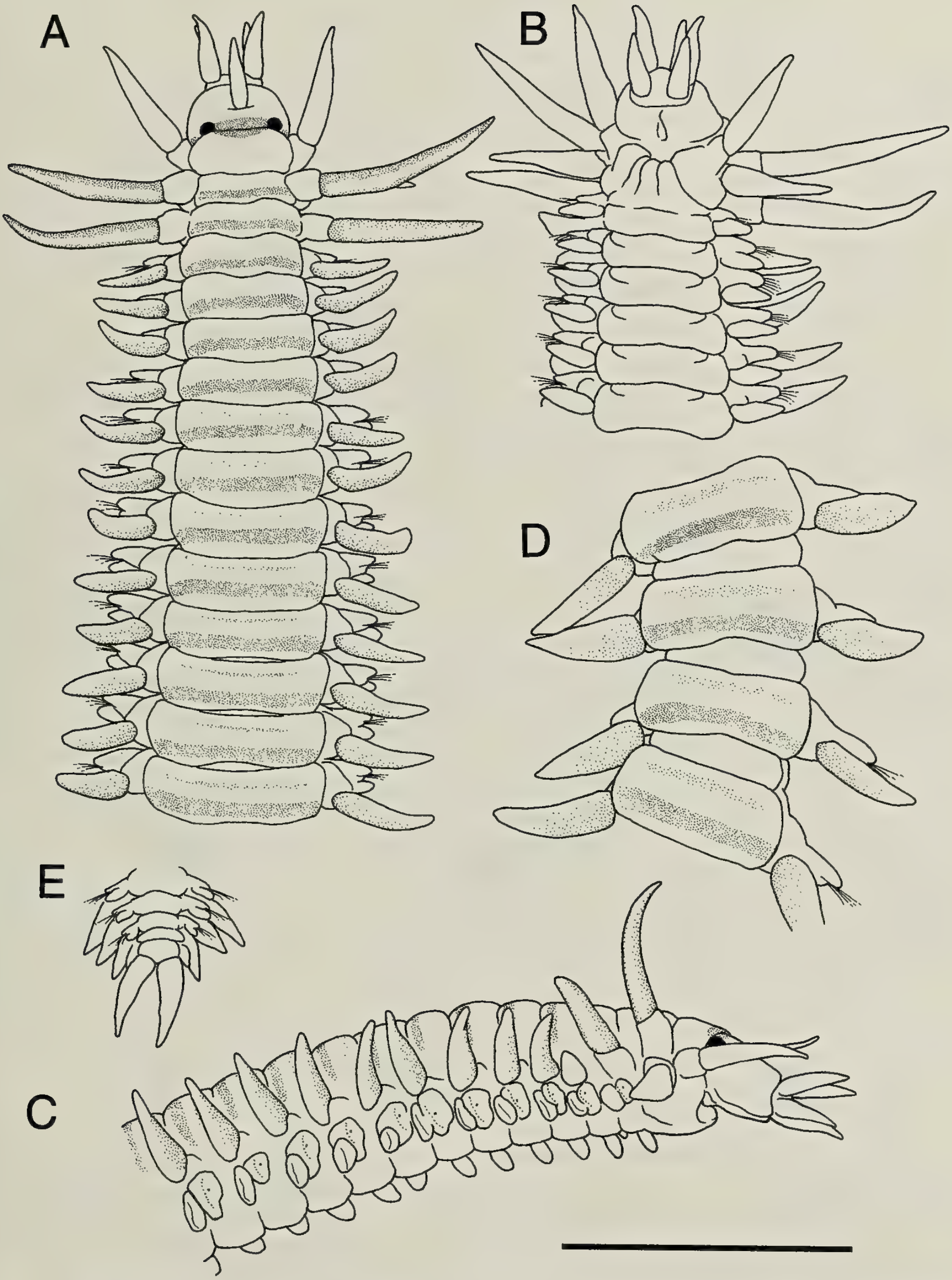

Fig. 1. *Eulalia gemina,* new species. Holotype. A, anterior end, dorsal view; B, anterior end, ventral view; C, anterior end, lateral view; D, median segments, dorsal view; E, posterior end, ventral view. Scale line: 1 mm.

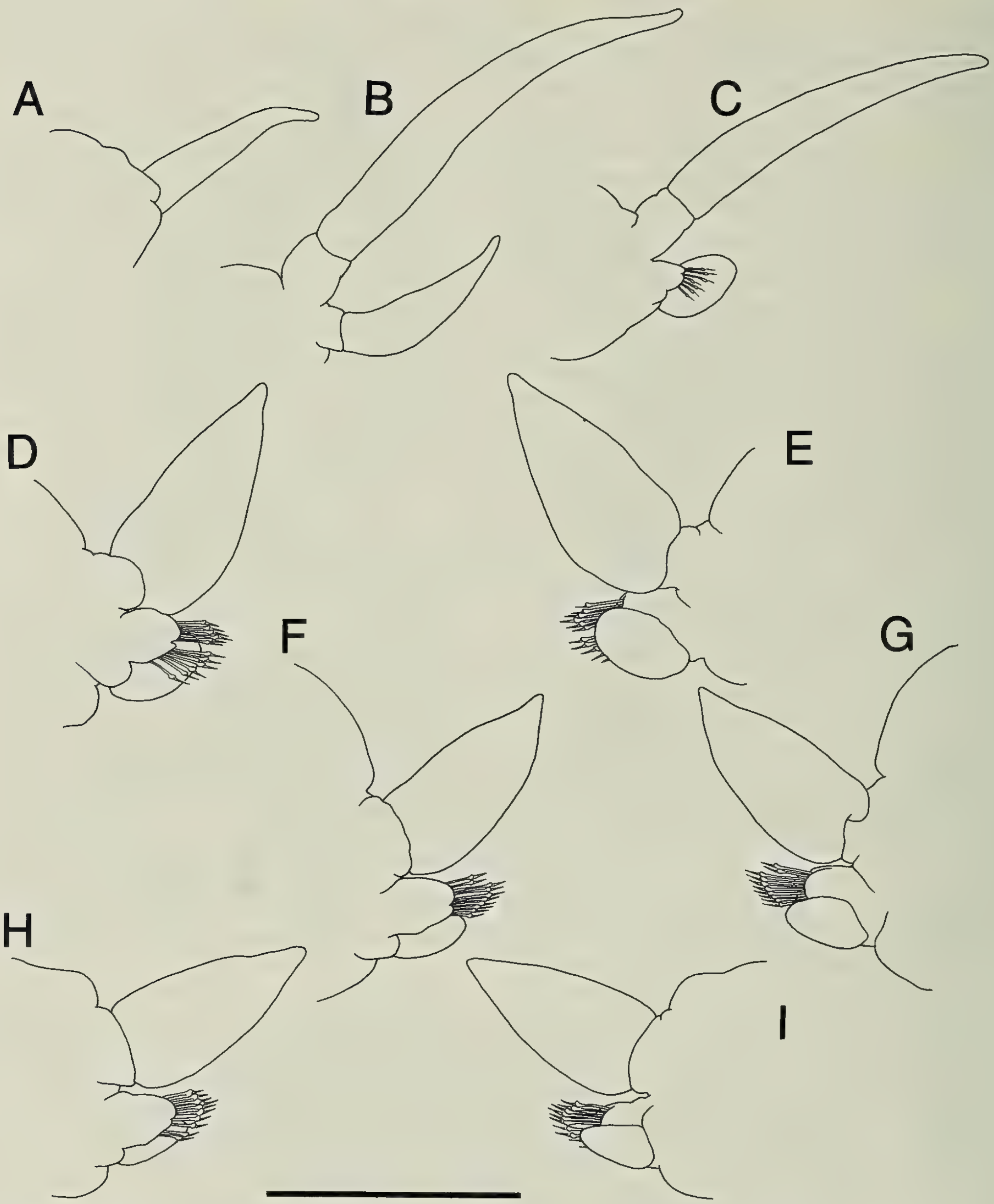

Fig. 2. *Eulalia gemina,* new species. Paratype. A, segment 1, anterior view; B, segment 2, anterior view; C, segment 3, anterior view; D, parapodium segment 23, anterior view; E, parapodium segment 23, posterior view; F, parapodium segment 206, anterior view; G, parapodium segment 206, posterior view; H, parapodium segment 402, anterior view; I, parapodium segment 402, posterior view. Scale line: 500 µm.

verse segmental bands in *E. gemina* are narrower than the posterior ones and absent from anterior and posterior segments, while in *E. ornata* these bands are similar and present on all segments; there is a pair of dark spots medially on each segment in *E. ornata,* but these are absent in *E. gemina*; there are green spots between and laterally to the eyes in *E. gemina,* whereas in *E. ornata* there is only faint yellow pigmentation laterally on the prosto-

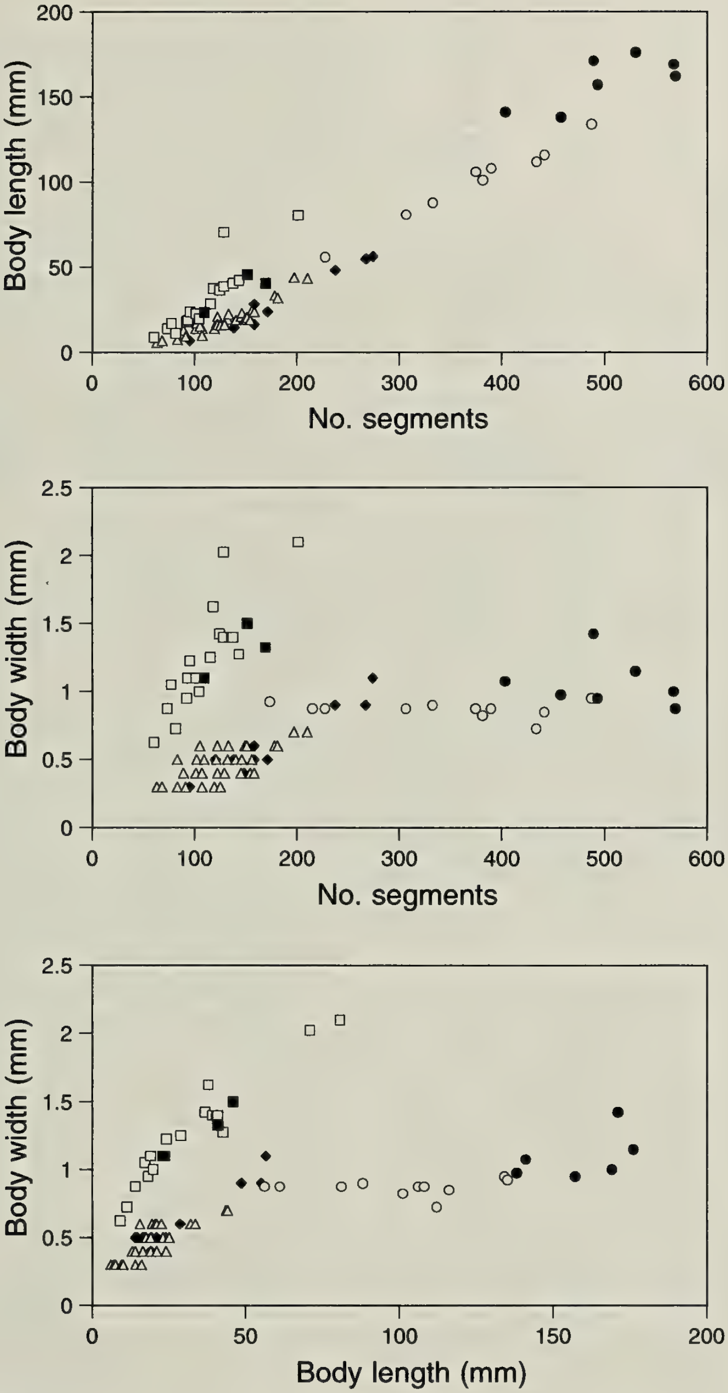

Fig. 3. Relationship between body length, body width and number of segments in *Eulalia gemina, E. ornata, E. bilineata* and *E. tripunctata.* Closed circles represent mature and open circles immature specimens of *E. gemina,* closed squares represent mature females and open squares males and immature specimens of *E. ornata* from Brittany, France, triangles represent *E. bilineata* from the Faeroes and Iceland, and diamonds *E. tripunctata* from England and Italy.

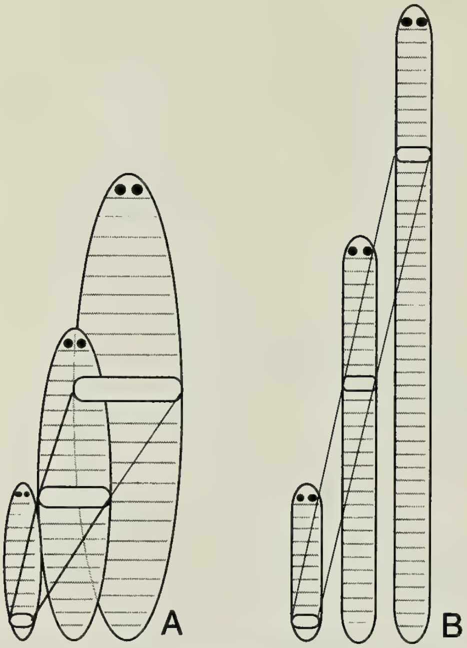

Fig. 4. Models of two growth patterns in *Eulalia.* As in other annelids, new segments are formed from the prepygidial region. A illustrates species with fusiform body shapes such as *E. viridis* and *E. ornata,* where median segments continue to increase in size during the ontogeny. B illustrates uniformly slender species such as *E. gemina* and *E. bilineata,* where newly generated segments reach their final size soon after formation.

mium; the transverse dorsal bands in *E. gemina* are narrower on anterior segments than further back, but in *E. ornata* it is the anterior bands what are widest. *Eulalia gemina* is also similar to *E. quadrilineata* Saint-Joseph, 1898 from Brittany, France, both in pigmentation and in the shape of the dorsal cirri. Unfortunately, in the absence of a detailed description and of types as well as other specimens, *E. quadrilineata* must be considered a nom. dub. (Pleijel 1991). With reference to Saint-Joseph's original description, it differs from *E. gemina* in having dorsal longitudinal violet bands, and in having neuropodia and chaetae on segment 2.

If body shape is considered, two groups can be identified within *Eulalia* (with intermediates), where *E. viridis* (Linnaeus, 1767) may exemplify taxa where median segments apparently continue to increase in size throughout the life time of the animal. This growth pattern yields body shapes with tapering anterior and posterior ends, here labeled fusiform. The second group is exemplified by *E. bilineata* or *E. myriacycla* (Schmarda, 1861), where all segments appear to reach their final size soon after formation, with little subsequent growth. This growth pattern instead yields long and slender body shapes of almost uniform widths. The two patterns are illustrated in Fig. 4. *Eulalia gemina* obviously belongs to this second group (Fig. 3). It also obtains a larger number of segments than any other measured *Eulalia* with the exception only of *E. myriacycla.* This latter taxon differs from *E. gemina* in having 5 dark dorsal longitudinal bands and in having pointed ventral cirri and elongated, slightly flattened pygidial cirri (Eibye-Jacobsen 1992).

If shape of dorsal cirri is considered, two groups can again be identified within *Eulalia.* Taxa such as *E. bilineata* and *E. mustela* Pleijel, 1987 have rounded dorsal cirri which are symmetrical along the longitudinal axis. *Eulalia viridis, E. ornata* and *E. myriacycla,* among others, have dorsal cirri which instead are pointed and asymmetrical along the longitudinal axis as seen in anterior or posterior view. The shape of the dorsal cirri in *Eulalia gemina* is similar to this second group.

In summary, in pigmentation *E. gemina* resembles *E. ornata,* in body shape it is similar to a group including *E. bilineata* and *E. myriacycla,* and in the shape of the dorsal cirri it resembles a group including *E. viridis, E. ornata* and *E. myriacycla.* Apart from details in pigmentation, *E. gemina* is not characterized by any single unique feature but has a specific combination of characters which separates it from all other known members of the genus. A summary of characters and character distributions among relevant species of *Eulalia* is provided in Table 1. Possibly, *E. gemina* may be closely related to *E. ornata* and/or *E. myriacycla,* but a closer investigation of its position would require a full revision of *Eulalia.*

Table 1.—Characters and character distributions among relevant species.

Species	Sources of information	Body shape	First chaetiger	Shape, symmetry, dorsal cirri	Shape ventral cirri	Shape pygidial cirri	Pigmentation pattern	Transverse segmental bands	Paired dark brown middorsal segmental spots	Paired longitudinal violet bands
Eulalia gemina, new species	holotype, 19 paratypes from Shirahama, Japan	slender	segment 3	lanceolate, asymmetrical	rounded	tapered with pointed ends	2 transverse dorsal segmental bands	dark green, anterior bands narrower than posterior bands	absent	absent
E. aurea	Pleijel 1993, ca. 30 spms from North Atlantic	stout	segment 3	lanceolate, symmetrical	rounded	tapered with pointed ends	4 longitudinal bands; 2 red and 2 dark	absent	absent	absent
E. bilineata	Pleijel 1993, ca. 40 spms from North Atlantic, ca. 30 spms from Japan	slender	segment 2	oval, symmetrical	rounded	cylindrical with rounded ends	2 longitudinal dark bands	absent	absent	absent
E. myriacycla	Eibye-Jacobsen 1992, 2 spms from California	slender	segment 3 or 4	lanceolate, asymmetrical	pointed	elongated oval with rounded ends	5 longitudinal bands	absent	absent	absent
E. ornata	Pleijel 1993, 47 spms from Brittany, France	stout	segment 3	lanceolate, asymmetrical	rounded	tapered with pointed ends	2 transverse dorsal segmental bands	dark green, of equal size	present	absent
E. quadrilineata	Saint-Joseph 1898	unknown	segment 2	lanceolate, symmetry unknown	rounded	flattened, probably with rounded ends	2 transverse dorsal segmental bands	color unknown, probably of equal size	absent	present
E. tripunctata	Pleijel 1993, ca. 10 spms from North Atlantic and Mediterranean	slender	segment 2	oval, asymmetrical	rounded	cylindrical with rounded ends	3 black spots on each segment	absent	absent	absent
E. viridis	Pleijel 1993, ca. 180 spms from Japan	stout	segment 2 or 3	lanceolate, asymmetrical	rounded	tapered with pointed ends	uniformly green	absent	absent	absent

Five species of *Eulalia* have hitherto been recorded from Japanese waters: *E. bilineata, E. microphylloides* Hartmann-Schröder, 1979, *E. tenax* (Grube, 1878), *E. viridis* and *E. pacifica* (Imajima, 1964), new combination (Okuda 1940, Imajima 1964, Imajima & Hartman 1964, Uchida 1988). *Eulalia pacifica* was originally referred to *Steggoa,* a generic name which Pleijel (1987) considered a junior synonym of *Eulalia.* Judging from its original description this species also belongs to *Eulalia.* The issue as to whether *E. bilineata* and *E. viridis,* both described from European waters, actually are conspecific with those recorded from Japan is beyond the scope of this study. *Eulalia gemina* is, nevertheless, easily distinguished from both of these in having a slender body and lanceolate dorsal cirri; *E. bilineata* has a slender body but rounded dorsal cirri, and *E. viridis* has pointed lanceolate dorsal cirri but a fusiform body shape. *Eulalia microphylloides* and *E. tenax,* as *E. viridis,* are similar in having lanceolate dorsal cirri, but differ in having fusiform body shapes (Grube 1878, Hartmann-Schröder 1979, Pleijel 1993). *Eulalia pacifica,* a deep water species, is distinguished from *E. gemina* in lacking eyes, and in having a fusiform body shape, asymmetrical ventral tentacular cirri, and oval dorsal cirri. In addition to these differences, the pigmentation pattern of *E. gemina* is unique among all reported Japanese species of *Eulalia.*

Etymology.—The new species is named for the paired dorsal transverse bands on each segment, "*gemina*" being Latin for double, twofold.

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Two new species of *Platynereis* (Polychaeta: Nereididae) from eastern Mexican shores

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Abstract.—Two new species of *Platynereis* are described from Mexican shores, *P. hutchingsae,* new species and *P. mucronata,* new species. These species differ from others in the genus mainly by the disposition and shape of the setae.

Specific diversity in the genus *Platynereis* in Mexican littoral areas is low. Until this study, only three species were known: *P. bicanaliculata, P. dumerilii* and *P. polyscalma.* Of these, the second was found to have the widest distribution, having been found practically in all regions sampled in the Gulf of Mexico, Mexican Caribbean and the northwestern coast of Mexico (de León-González 1998). The two new species of *Platynereis* that are described herein were collected from quite different substrates. The terminology of parapodial structures is based on that proposed by Hutchings & Reid (1990).

The type material is deposited in the Polychaetological collections of both the Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León (UANL), and the Instituto de Ciencias del Mar y Limnología, U.N.A.M. (CPICML).

Platynereis hutchingsae, new species
Figs. 1, 3

Material examined.—Campeche: Col. V. Solís-Weiss and collaborators, Términos Lagoon, San Julián, 3 Mar 1984, (holotype UANL 4281), and one paratype (UANL 4282).

Description.—Holotype complete with 75 setigers, without pigmentation pattern, 16 mm long and 1.5 mm wide, including setae. Prostomium pentagonal, with pair of slender antennae slightly exceeding distal margin of palps. Two pairs of eyes in trapezial arrangement, anterior ones with lens, posterior ones rounded, partially covered by anterior margin of peristomium. Biarticulate palps ventrally directed. Peristomium as long as next segment, with four pairs of tentacular cirri, longest pair extending to posterior margin of their setiger (Fig. 1a).

Pharynx with translucent pectinate bars in following arrangement: Areas I, II, IV and V with no pectinate bars; III with 3 small pectinate bars; VI each with a pectinate bar; VII–VIII with 5 hardly visible pectinate bars (Fig. 3a, b).

Anterior parapodia with notopodium formed of triangular, distally blunt, ligule, mamilliform median ligule, superior lobe not evident; neuropodium formed of triangular, postsetal lobe, truncate inferior lobe, and subulate ventral ligule. Dorsal cirrus inserted on median posterior region of dorsal ligule, ventral cirrus inserted basally to ventral ligule, cirri subequal (Fig. 1b). Middle parapodia with triangular dorsal and median ligules, dorsal ligules smaller; neuropodium formed by conical postsetal lobe and subulate ventral ligule. Dorsal cirrus inserted at base of dorsal ligule, slightly longer than ventral cirrus (Fig. 1c). Posterior notopodium with dorsal ligule with proximal portion enlarged and distal

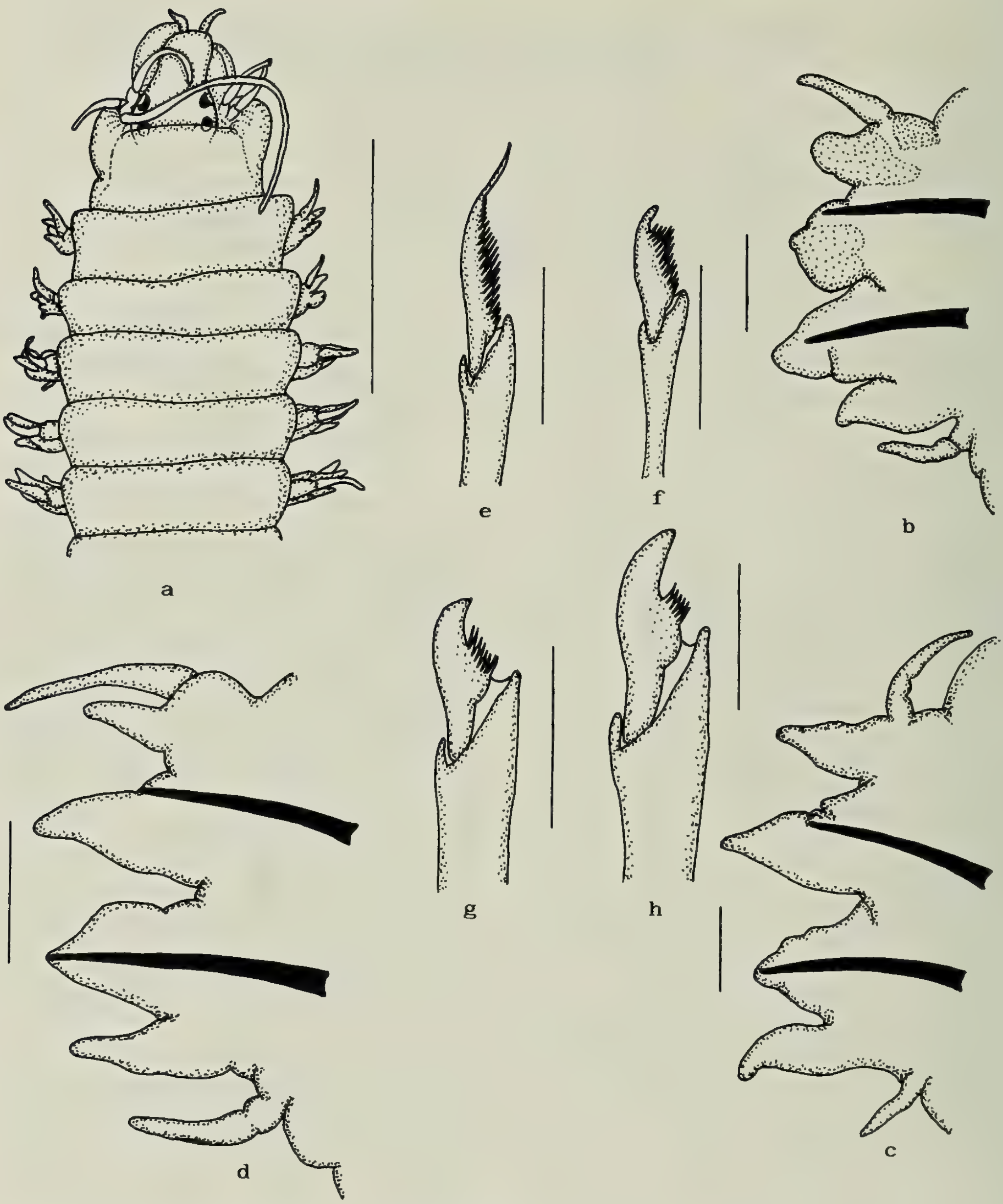

Fig. 1. *Platynereis hutchingsae* n. sp.: a, anterior region, dorsal view; b, parapodium 11; c, parapodium 31; d, parapodium 62; e, supra-acicular neuropodial spiniger, setiger 11; f, infra-acicular neuropodial falciger, setiger 11; g, neuropodial supra-acicular falciger, setiger 31; h, infra-acicular neuropodial falciger, setiger 62. Scale bars: a—1 mm; b–d—150 μm; e–h—30 μm.

portion slender; median ligule subulate, longer than dorsal ligule; neuropodium formed by proximally enlarged postsetal lobe ending in short cone; ventral ligule conical, smaller than postsetal lobe. Dorsal cirrus inserted on median posterior region of dorsal ligule, slightly longer than ventral cirrus (Fig. 1d).

Setae of anterior parapodia in following arrangement: notosetae consisting of 12 homogomph spinigers; supra-acicular neuroseta numbering seven homogomph spinigers and three heterogomph spinigers, latter with short blade, strongly spinulate on internal margin (Fig. 1e); infra-acicular neurosetae consisting of two heterogomph spinigers with long, slender blade with numerous small teeth, numerous heterogomph falcigers with blade slender and with slender dentition (Fig. 1f), and single heterogomph spiniger in inferior portion of fascicle. Setae of median parapodia in following arrangement: notosetae numbering 10 homogomph spinigers; supra-acicular neurosetae with four homogomph spinigers with long, slender blade, and two heterogomph falcigers with short and curved blade, latter with spines along half internal margin (Fig. 1g); infra-acicular neurosetae two heterogomph spinigers with long slender blade and seven heterogomph falcigers with blades similar to those of supra-acicular. Posterior notopodia with numerous homogomph spinigers; supra-acicular neuroseta three homogomph spinigers and two heterogomph falcigers; infra-acicular neurosetae heterogomph spinigers with long and slender blades, and three heterogomph falcigers with short and curved blades, latter with few teeth or spines on internal basal margin (Fig. 1h).

Pygidium with dorsal and opening and two small ventral and cirri.

Discussion.—Both *Platynereis hutchingsae* and *P. australis* (Schmarda, 1861) lack homogomph notopodial falcigers. Day (1967) and Imajima (1972) noted that in *P. australis* this type of seta can be present on the last 10 parapodia of juveniles; however, in the specimens described here notopodial falcigers are not present. *P. hutchingsae* and *P. australis* are the only species in the genus lacking homogomph notopodial falcigers, at least in the adult stage.

These species can be differenciated as follows: *P. australis* lacks pectinate bars on areas I, II and V, pectinate bars of area VI and VII–VIII are doubled, whereas *P. hutchingsae* lacks pectinate bars on areas I, II, IV and V, and pectinate bars of areas VI and VII–VIII are plain. The heterogomph neuropodial supra-acicular spinigers of anterior parapodia of *P. australis* have a long and slender blade with small teeth, while the blades of heterogomph neuropodial supra- and infra-acicular falcigers of median and posterior parapodia have an anterior recurved tooth; in *P. hutchingsae* however, the blades of these spinigers are short with long teeth; also, the distal part of the blade of the heterogomph neuropodial falcigers has no recurved teeth, and dentition of these falcigers is clearly different.

Etymology.—The species is named in honor of Dr. Patricia Hutchings, eminent polychaetologist of The Australian Museum, Sydney for her many contributions in nereidid taxonomy and for her unconditional assistance to the authors for many years.

Distribution.—Endemic. Only known from a single locality in Términos Lagoon, southern Gulf of Mexico.

Habitat.—Among sediment trapped in rhizomes of *Thalassia testudinum.*

Platynereis mucronata, new species
Figs. 2, 3

Material examined.—Tamaulipas: Col. J. A. de León-González, La Pesca, 12 Apr 1991 (Holotype UANL 3975); Col. G. Guajardo-Martínez, La Pesca, 20 May 1995 (UANL), 1 specimen; Col. J. A. de León-González, Tampico, Stn. ET-04, 8 Mar 2000 (UANL 4083), 2 specimens, Stn. ET-03, 8 Mar 2000 (UANL 4091) 7 specimens. Veracruz: Villa del Mar beach, 10 Aug 1999 (UANL 4028) 2 specimens, Villa Rica, 10 Aug 1999 (UANL 4092) 6 specimens. All records in intertidal waters. Quintana Roo: Col. V. Valadez-Rocha and A. Granados-Barba, Caetita, Cozumel Island, Stn. Cz5R2 (2 specimens), 3 m, Stn. Cz5R3 (1 specimen), 13 m (POICML).

Description.—Holotype complete with 62 setigers, without evident pigment pattern, 19 mm long and 2 mm wide, including parapodia. Prostomium pentagonal, four eyes in trapezial arrangment, the anterior-

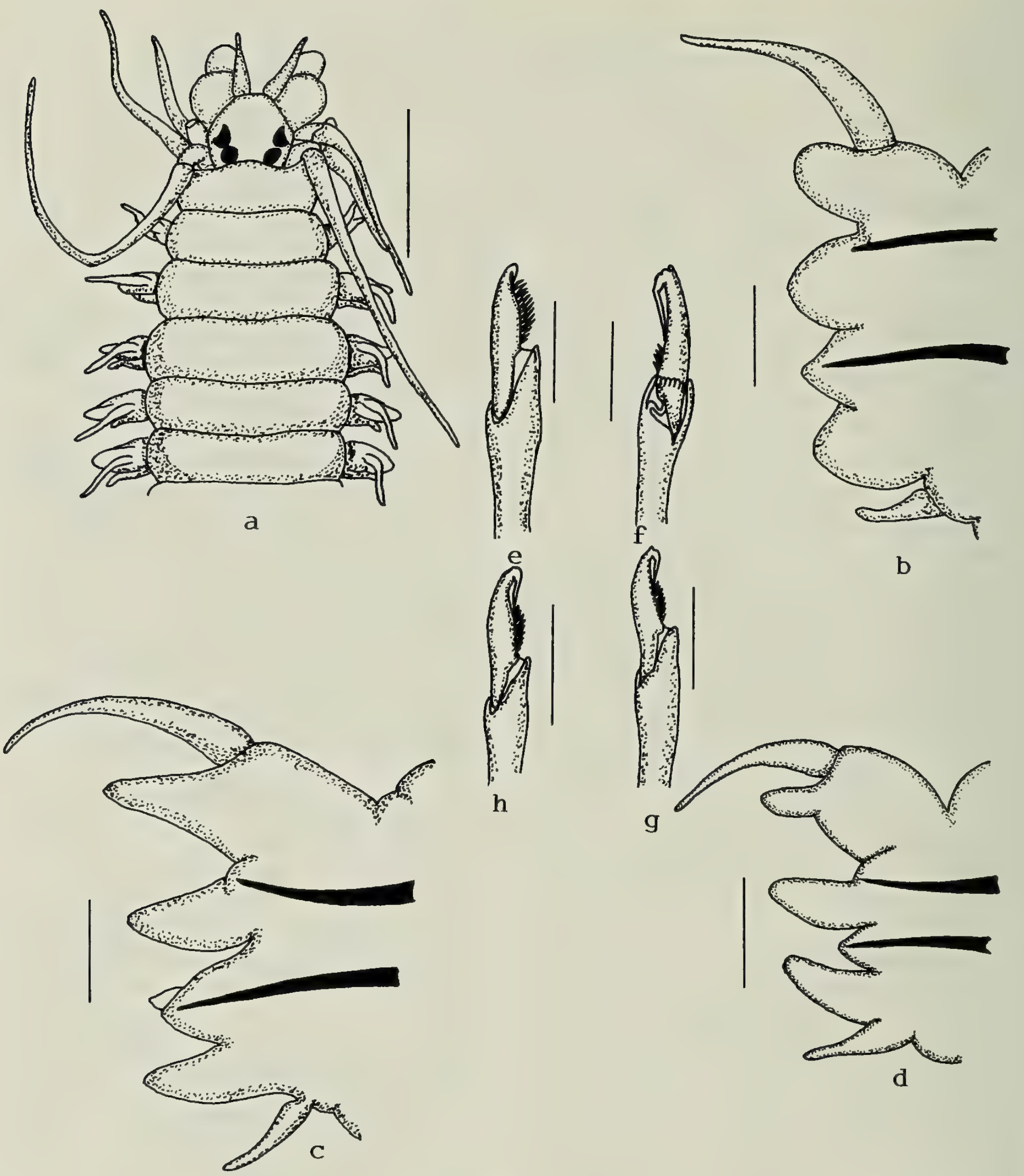

Fig. 2. *Platynereis mucronata* n. sp.: a, anterior region, dorsal view; b, parapodium 10; c, parapodium 31; d, parapodium 51; e, supra-acicular neuropodial falciger, setiger 10; f, notopodial falciger, setiger 51; g, supra-acicular neuropodial falciger, setiger 51; h, infra-acicular neuropodial falciger, setiger 51. Scale bars: a—0.5 mm; b–d—150 μm; e–h—30 μm.

most more widely separated and lensed, posterior ones rounded. Frontal antennae cirriform. Biarticulate palps stout, globular palpostyle longer than half length of total palp. Peristomium with four pairs of tentacular cirri, longest pair extending to about setiger 6 (Fig. 2a).

Pharynx with pectinate paragnaths on both rings in the following arrangement: I, II and V with no paragnaths; III 3 small

Fig. 3. *Platynereis hutchingsae* n. sp.: a, pharynx, dorsal view; b, pharynx, ventral view. *Platynereis mucronata* n. sp.: c, pharynx, dorsal view; d, pharynx, ventral view.

pectinate bars in a transverse line; IV 4 pectinate bars, 3 small and one elongate; VI 2 pectinate bars; VII–VIII 5 plain pectinate bars in a transverse line (Fig. 3c, d).

Anterior parapodia with dorsal, median and ventral ligules rounded, postsetal lobe triangular, dorsal cirrus medially inserted (Fig. 2b). Middle parapodia with dorsal ligules expanded, median and ventral ligules subtriangular, postsetal lobes conical; dorsal cirri medially inserted, ventral cirri similar, smaller (Fig. 2c). Posterior parapodia with tips of dorsal ligules globular, median ligule with tip more rounded, dorsal cirri inserted in median anterior position (Fig. 2d).

Setation in anterior parapodia as follows: notosetae homogomph supra-acicular spinigers; neurosetae supra-acicular homogomph spinigers and heterogomph falcigers, blades of latter with internal margins strongly dentate and with short distal tooth directed downward (Fig. 2e); infra-acicular setae heterogomph spinigers and falcigers similar to supra-acicular ones. Middle notopodia with supra-acicular spinigers and homogomph falcigers, blades of latter with small apical mucron and slender tooth directed downwards, and fused to internal margin of blade; 4 small teeth present on basal internal region of blade; supra-acicular neurosetae homogomph spinigers and heterogomph falcigers, infra-acicular setae only heterogomph falcigers. Posterior notopodia with homogomph spinigers and falcigers, blades of latter with apical mucron, frontally bilobate, with distal tooth directed proximally, inferior part scarcely dentate, blade linked to shaft by an "S" shaped ligament, shaft with lobulate membrane surrounding base of blade (Fig. 2f); supra-acicular neurosetae homogomph spinigers and heterogomph mucronate falcigers (Fig. 2g), infra-acicular neuroseta only heterogomph falcigers with tips of blades rounded, without mucron (Fig. 2h).

Pygidium with terminal anus and 2 long anal cirri.

Discussion.—*Platynereis mucronata,* new species, is similar to *P. dumerilii* and *P. hutchingsae,* new species, in the shape of the dorsal ligule of posterior parapodia; the two new species can be differentiated from *P. dumerilii* in the ornamentation of the pharynx: in both new species, pectinate simple bars are present on areas VI and VII–VIII, whereas in *P. dumerilii* double pectinate bars are present. *Platynereis mucronata* and *P. hutchingsae* differ from each other in the structural shape of the falcigers blade. Also, *P. coccinea* (delle Chiaje, 1841) is similar to *P. mucronata* in having an apical mucron in the tip of the blade of homogomph notopodial falcigers, but the latter differs from the former in the pharyngeal arrangement in that pectinate bars are present only on Area IV in *P. coccinea* (see Fauvel 1923).

Etymology.—Specific name refers to the mucron present on the tip of the blade of both the notopodial homogomph falcigers and the supa-acicular neuropodial heterogomph falcigers of the new species. The Latin adjetive *mucronatus* is from Latin *mucro, mucronis* = a sharp point.

Distribution.—Western Atlantic. This species has been collected in the type locality of La Pesca, Tamaulipas, Gulf of Mexico, as well as in the reef zone of Cozumel Island in the Mexican Caribbean.

Habitat.—La Pesca, Tamaulipas, among algae fixed to rocks of breakwaters; in Cozumel, Mexican Caribbean as part of the sponge cryptofauna.

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A new species of Dorvilleidae (Annelida: Polychaeta) from a cold seep site in the northeast Pacific

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Abstract.—*Parougia oregonensis,* a new species of the Dorvilleidae (Annelida: Polychaeta), is described from 5 specimens collected from a cold seep site at 600–800 m depth in the northeast Pacific at the Cascadia Margin off Oregon. This new species differs from all other species of *Parougia* in the degree of sclerotization of the mandibles, which are anteriorly smooth rather than serrated, and in morphological details of the maxillae. *Parougia oregonensis* is the first member of the Dorvilleidae to be recorded from a cold seep site.

During a joint German-Canadian-U.S. project conducted in summer 1996 to study the cold seep sites along the Aleutian convergence zone, a few days were set apart initially to deploy the Canadian ROPOS (Remotely Operated Platform for Ocean Sciences) at the Cascadia convergent margin off Oregon. In this area, an abundant deep-sea benthic community, dominated by the vestimentiferan tube worm, *Lamellibrachia barhami* Webb, 1969 and the clams, *Calyptogena* sp. and *Solemya* sp. had been observed before at a depth of ca. 2000 m (Suess et al. 1985). Investigations were performed at the Second Accretionary Ridge (=Hydrate Ridge) near ODP-site 892 where gas hydrates and active fluid venting had been shown to occur near the summit of this ridge during ODP leg 146 and cruise 109 of R/V *Sonne* (Herzig et al. 1997). Among the fauna collected were five specimens of a previously undescribed dorvilleid polychaete belonging to the genus *Parougia.* To date, the genus is represented by only six species: *P. caeca* (Webster & Benedict, 1884), *P. furcata* (Hartman, 1953), *P. batia* (Jumars, 1974), *P. eliasoni* (Oug, 1978), *P. nigridentata* (Oug, 1978), and *P. wolfi* Blake & Hilbig, 1990. *Parougia batia* is reported from deep waters of the northeast Pacific, and *P. wolfi* was described from hydrothermal vents of the Juan de Fuca Ridge, *P. caeca* from the Arctic and *P. furcata* from the Antarctic, while *P. eliasoni* and *P. nigridentata* were described from Norway and Skagerrak, respectively. The new species is the first in this genus to be recorded from cold seep environments.

Material and Methods

The material was collected during a joint German-Canadian-U.S cruise with R/V *Sonne* (SO 110 leg 1a, July 1996) to the Second Accretionary Ridge (=Hydrate Ridge) off central Oregon (Suess & Bohrmann 1997). For collecting either a TV-grab (TV-G) or the ROPOS system was used. Drawings were made using a Leitz microscope and Wild dissection microscope. The pharynx was dissected and kept in glycerin over night for better visibility of the jaws. For scanning electron microscopic (SEM) investigations, one specimen was dehydrated via a graded ethanol series, critical point dried using CO_2, coated with Au-Pd, and examined in a CamScan CS 24 SEM.

Fig. 1. *Parougia oregonensis,* new species. SEM micrographs of paratype (SMF 8898). A, anterior end, anteroventral view; B, C, furcate chaetae; D, subacicular chaetae.

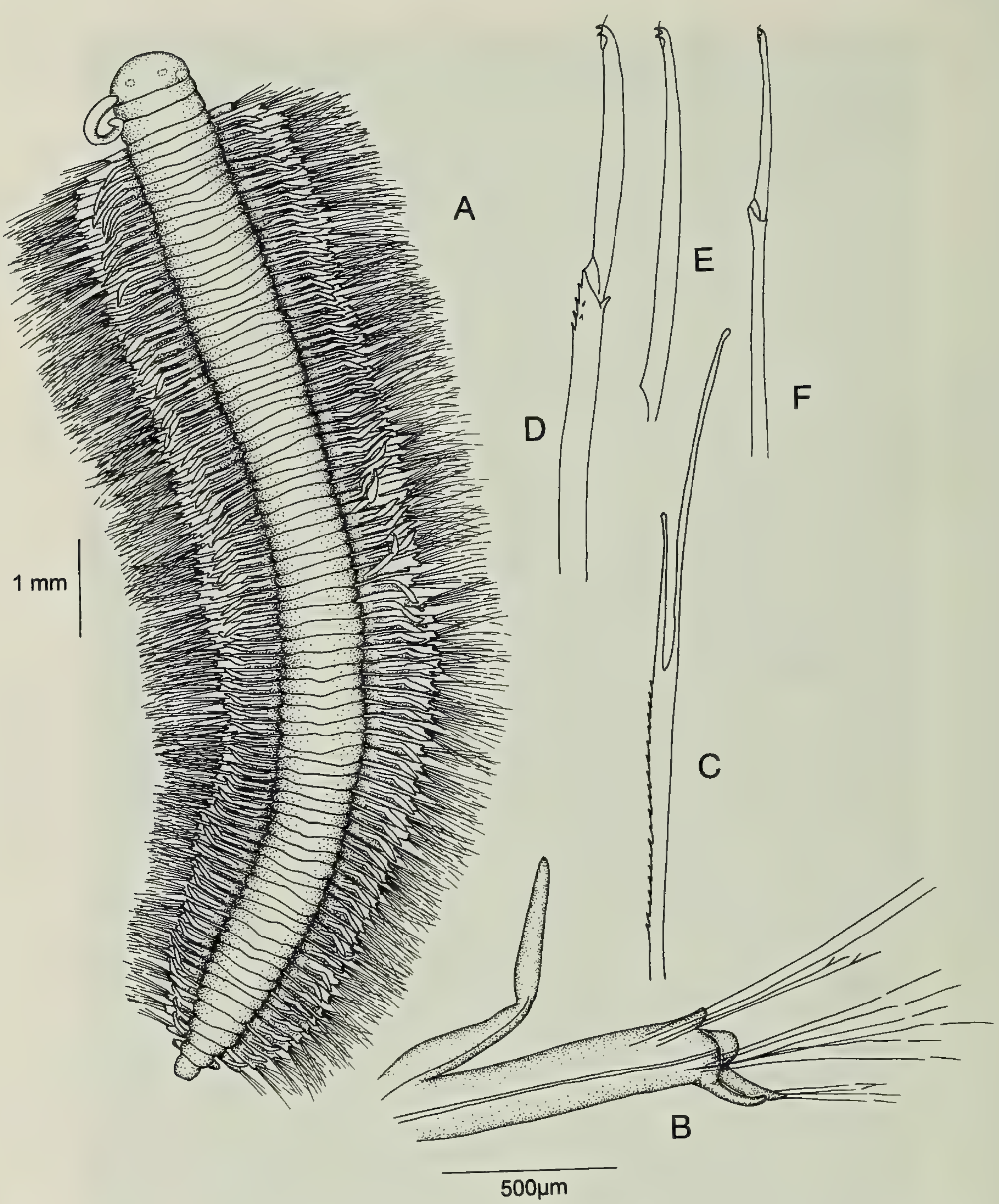

Fig. 2. *Parougia oregonensis,* new species. A, entire animal, paratype (ZIM-P24243), dorsal view; B, parapodium, middle segment, anterior view; C, furcate chaeta; D, E, subacicular, compound chaeta, shortest and longest blades of fascicle; F, small compound chaeta from tip of inferior subacicular lobe. B–C, paratype LACM-AHF Poly 1969; D–F drawn to scale.

Material has been deposited in the collections of the Zoologisches Institut und Museum, Hamburg, (ZIM), Los Angeles County Museum—Allan Hancock Foundation, Los Angeles (LACM-AHF) and the Senckenberg Museum, Frankfurt (SMF).

Family Dorvilleidae Chamberlin, 1919

Genus *Parougia* Wolf, 1986

Parougia oregonensis, new species

Figs. 1–3

Material examined.—NE Pacific, off

Oregon, Cascadia Margin, Second Accretionary Ridge (=Hydrate Ridge): SO 110/1a, ROPOS 339, 10 Jul 1996, 44°40.2′N, 125°6.5′E, 632 m, Pete Vent; holotype (SMF 8897), 1 paratype (ZIM P-23243), 1 paratype (LACM-AHF Poly 1969); SO 110/1a, ROPOS 341 SS 1 (=suction sample 1), 12 Jul 1996, 44°40.12′N, 125°05.80′E, 595 m, northern summit of Hydrate Ridge; 1 paratype + 1 posterior fragment (SEM stub 581, SMF 8898); SO 110/1a, TV-G 18, 13 Jul 1996, 44°34,235′N, 125°08.891′W, 785 m, southern summit of Hydrate Ridge; 1 paratype (SMF 8899).

Diagnosis.—Generic definition according to Wolf (1986). Parapodia with suprachaetal, acicular, postchaetal, and inferior chaetal lobes; dorsal cirri with long, tapered cirrophores, about as long as cirrostyles in middle and posterior chaetigers; furcate chaetae numerous, with long serrated subdistal portion and smooth-tipped tines; subacicular chaetae of 2 sizes, those in inferior chaetal lobe much thinner than those of acicular lobe. Mandibles smooth, delicate, winglike; maxillae without inferior basal plates, with superior basal plate and heavily sclerotized superior free denticles and delicate inferior denticles, distal ones with whiplike terminal tooth.

Description.—Holotype: length about 17 mm (coiled), width 1.0 mm, excluding parapodia, for about 85 segments; paratypes 5.5 to 12 mm long, 0.7 to 1.5 mm wide, about 47 to 80 segments. Color in alcohol uniformly pale. Prostomium broadly rounded, wider than long, slightly widening toward posterior margin, ventrally forming large, medially incised upper lip (Figs. 1A, 2A). Antennae broken off on most specimens, leaving deep, distinct scars; right antenna on one specimen simple, tapering, about 4 times as long as prostomial width (Fig.1A). Palps about twice as long as prostomial width, evenly tapered, with short, slightly clavate palpostyle, inserted lateral and slightly anterior to antennal scars; eyes absent. Nuchal organs located at posterior prostomial margin behind antennae; additional s-shaped ciliary bands running along anterior margin of palps and lateral margin of antennae. Peristomium biannular, anterior ring dorsolaterally split into 2 rings fusing again ventrolaterally and produced ventrally into crenulated lower lip; posterior ring simple, about as long as following chaetigers.

Segments short and crowded throughout, with highly arched dorsum and flat ventrum; ciliary bands restricted to dorso- and ventrolateral areas, continuing onto parapodia and dorsal cirri. Parapodia very long and slender, exceeding segmental width where best developed (Fig. 2A, B). Notopodia present from chaetiger 2, reduced to slender, tapered dorsal cirri supported by delicate acicula in cirrophore; cirrostyle short, pointed in anterior parapodia, increasing to about length of cirrophore (when fully extended) in midbody and posterior parapodia; dorsal cirri subequal in length to neuropodia when relaxed; all parapodial structures with varying proportions due to muscle contraction during fixation. Neuropodia with small digitiform suprachaetal lobe; short truncate acicular lobe; triangular, somewhat longer postchaetal lobe; conical, often retracted inferior chaetal lobe; and subterminal, digitiform ventral cirrus (Fig. 2B). Aciculae and bases of chaetae emerging from inferior chaetal lobe honey colored, other chaetae translucent.

Chaetae long and flowing, most numerous in anterior parapodia; supra-acicular chaetae of 2 types, serrated capillaries and furcate chaetae with long, slender, unequal tines and subdistal serration (Figs. 1B, C, 2C); long tine about 2.0–2.5 times longer than short tine, both with small hood-like structure on tip but not pubescent; subacicular chaetae compound with smooth shafts, distally minutely serrated (visible only with SEM), and bidentate blades of slightly varying length, tips appearing finely serrated in SEM and equipped with sheath by light microscopy (Figs. 1D, 2D, E). Small fascicle of chaetae emerging from

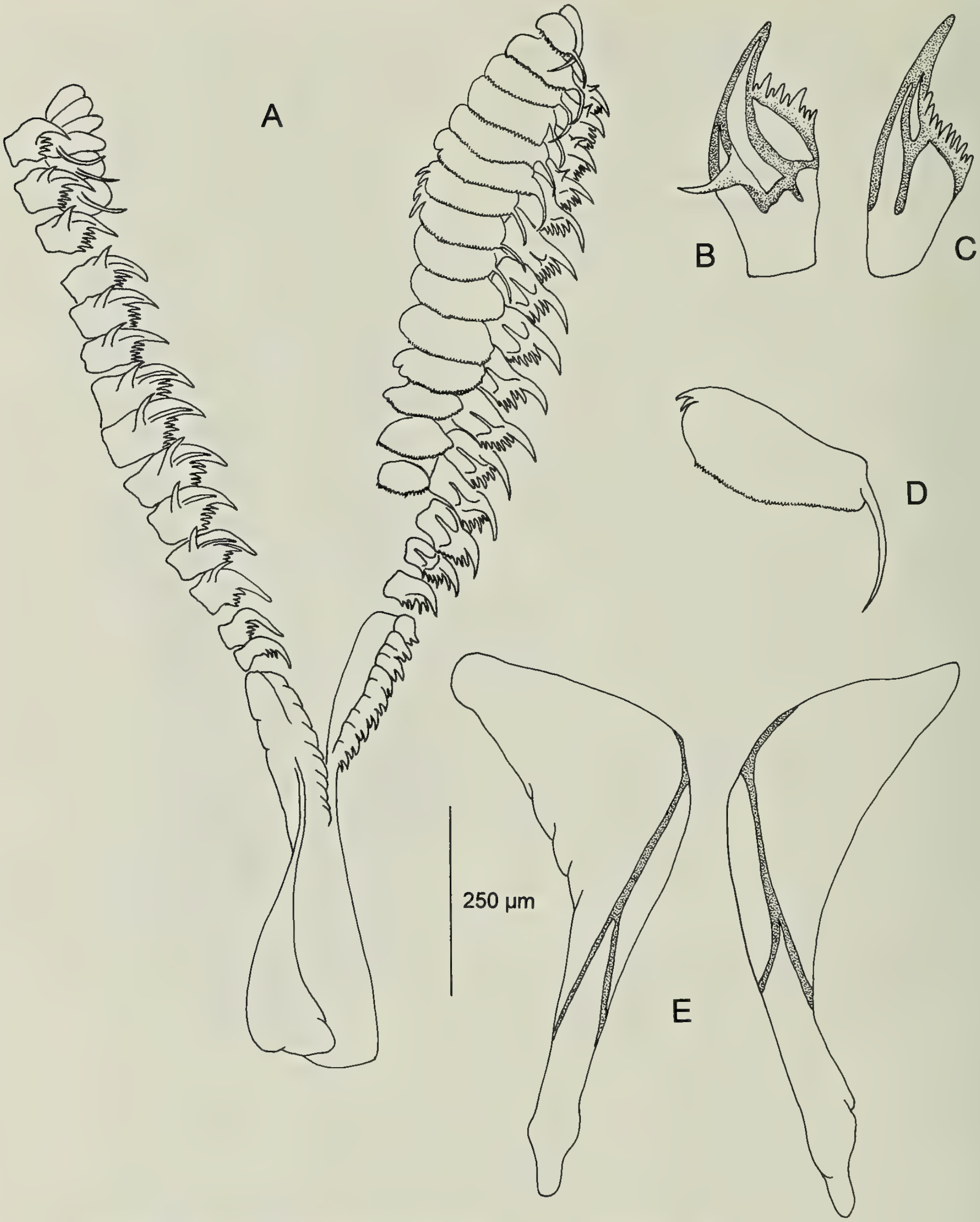

Fig. 3. *Parougia oregonensis,* new species, paratype LACM-AHF Poly 1969. A, maxillae, dorsal view, left inferior denticle row omitted; B, C, superior free denticle, dorsal and ventral view; D, upper inferior free denticle; E, mandibles; A, E drawn to scale.

tip of inferior lobe distinctly thinner and shorter than remaining chaetae (Fig. 2F).

Pygidium ring-shaped, with long, conical ventromedian style and apparently 2 ventrolateral anal cirri (all broken off, scars distinct); anus slightly dorsal.

Maxillae consisting of 2 rows of denticles, superior row with basal plates (Fig.

Table 1.—Known species of *Parougia* and differences in selected diagnostic characters.

Species	Notochaetae	Mandibles, cutting edge	Basal plates	Maxillae	
				Superior free denticles	Inferior free denticles
P. caeca (Webster & Benedict, 1884)	furcates with long unequal tines; occasionally lacking; capillaries serrated	coarse teeth	row of imbricated fused denticles	squarish, with large main tooth and serrated cutting edge	oval, with short, finely serrated cutting edge
P. furcata (Hartman, 1953)	furcates with long unequal tines, short tine pubescent; capillaries serrated	coarse teeth	row of imbricated fused denticles	squarish, with large main tooth and serrated cutting edge	oval, with long, finely serrated cutting edge
P. batia (Jumars, 1974)	furcates absent; capillaries smooth	medially serrated	row of fused denticles	rounded, with main tooth and serrated cutting edge	rounded, with finely serrated cutting edge
P. eliasoni (Oug, 1978)	furcates with long unequal tines, tips pubescent; occasionally lacking; simple setae bidentate	coarse teeth	row of large fused denticles	squarish, with large tooth and serrated cutting edge	rounded, with finely serrated cutting edge
P. nigridentata (Oug, 1978)	furcates with long unequal tines, tips pubescent; capillaries serrated	coarse teeth	row of imbricated fused denticles	elongate, with large main tooth and coarsely serrated cutting edge	oval, with short, finely serrated cutting edge
P. wolfi Blake & Hilbig, 1990	furcates with very short equal tines; capillaries absent	coarse teeth	double row of imbricated fused denticles	elongate, some with whiplike tooth and slanted cutting edge	elongate, some with slanted cutting edge
P. oregonensis, new species	furcates with long unequal tines, tips hooded; capillaries serrated	smooth	row of small fused denticles	squarish, some with heavy accessory dorsal tooth	rounded, with finely serrated cutting edge, some with whiplike tooth

3A). Basal plates relatively short, about one-fourth of total length of superior maxillary row, with toothed edge, about 16 major teeth alternating with very small ones; superior free denticles 14 or 15 on a side, heavily sclerotized oval plates with large main fang and row of alternating small and large teeth along cutting edge and sclerotized ribs across plate, some bearing additional tooth directed upward (Fig. 3B, C). Inferior basal plates absent; free denticles 17 or 18 on a side, all broadly rounded, delicate plates with very finely serrated cutting edge, from D6 on additional long, whiplike marginal tooth (Fig. 3D). Mandibles wing-shaped, with slightly divergent sclerotized handles and smooth cutting edge; wing-like anterior part of mandible with sclerotized rib between tip of handle and anterior margin (Fig. 3E).

Remarks.—Most dorvilleids described from deep water in general, and geologically active sites in particular, belong to either *Ophryotrocha* or *Exallopus* (for example, Blake & Hilbig 1990, Hilbig & Blake 1991). Species of *Parougia* reported from deep waters of the northeast Pacific are *P. batia* (Jumars, 1974), *P. caeca* (Webster & Benedict, 1884) and *P. wolfi* Blake & Hilbig, 1990, the latter being the only dorvilleid from the *Dorvillea-Ougia-Parougia* group so far described from geologically active environments, i.e., hydrothermal vent systems. *Parougia oregonensis,* new species, differs from *P. wolfi* most obviously in the presence of long-tined furcate chaetae and distally entire rather than bidentate capillaries. Furthermore, *P. oregonensis* has mandibles with a smooth rather than serrated cutting edge, and there are large differences in the shape and degree of sclerotization of the free denticles. This difference can be easily seen by examining the maxillae in situ through a middorsal incision of the anterior thorax without further dissection. *Parougia batia* is much smaller than *P. oregonensis* and has no furcate chaetae, and the maxillary denticles are delicate and few in number; *P. caeca* lacks suprachaetal parapodial lobes and has a strongly sclerotized mandible with serrated cutting edge. All other species of the genus *Parougia* also differ from *P. oregonensis* in the heavily sclerotized, anteriorly serrated mandibles and in morphological details of the maxillae. A synopsis of some important morphological characters among species of *Parougia* is given in Table 1.

Etymology.—The species is named after its type locality off Oregon.

Distribution.—Known only from cold seeps off Oregon, about 600–800 m depth.

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Revision of five species referred to *Myriochele* and *Galathowenia* (Polychaeta: Oweniidae) from the Antarctic Seas based upon type material

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Abstract.—Based on the examination of type material, five Antarctic oweniid species (Polychaeta: Oweniidae), belonging to the genus *Myriochele* and *Galathowenia,* were studied: *Myriochele scotiae* Hartman, 1978, *Galathowenia wilsoni,* Blake, 1984, *Myriochele joinvillensis* Hartmann-Schröder & Rosenfeldt, 1989, *Myriochele longicollaris* Hartmann-Schröder & Rosenfeldt, 1989 and *Myriochele terranovensis* Cantone & Di Pietro, 1998. The original description of *M. scotiae* has been emended due to the confirmation that the specimen described is a broken animal, and the shape of its anterior end is an artifact due to a breakage process. *Galathowenia wilsoni* and *M. terranovensis* are considered junior synonyms of *Galathowenia scotiae* (Hartman, 1978), new combination. *Myriochele joinvillensis* and *M. longicollaris* are regarded as valid species. Data are also given on the intraspecific variability of some body traits of high taxonomic relevancy in oweniids such as the shape of the head region, posterior end and anteroposterior variation of the hooked setae. The taxonomic status of the genus *Galathowenia* Kirkegard, 1959 is discussed, and a key to the species of the family Oweniidae recorded in Antarctic waters is provided.

Hartman (1978) described *Myriochele scotiae* from the Weddel Sea in Antarctica, with setigers 1 and 2 having notosetae only and with a unique feature which distinguished it from other oweniids—the greatly reduced, truncated prostomium with, on occasion, a partially everted proboscis. This species was also found and illustrated later by Blake (1984) from the Ross Sea and north of the Amundsen Sea. Blake also describes a new species from the same localities, *Galathowenia wilsoni,* with a well developed anterior end, truncated terminal ciliated mouth, and three thoracic setigers wider than long with notosetae only, as the only body characteristics that clearly separate it from *Myriochele scotiae. Galathowenia wilsoni* was later found by Imajima & Morita (1987) in the Japan Sea and by Hartmann-Schröder & Rosenfeldt (1989, 1991 as *Myriochele*) in South Shetland Islands (Antarctica). Recently, Cantone & Di Pietro (1998) described a new oweniid species from Terra Nova Bay in the Ross Sea, *Myriochele terranovensis,* with a characteristic deep constriction between the first and second setigers. Other oweniids described or reported from Antarctica are: *Owenia fusiformis* delle Chiaje 1842, *Myriochele heeri* Mamlgren, 1867, *M. joinvillensis* Hartmann-Schröder & Rosenfeldt, 1989, *M. longicollaris* Hartmann-Schröder & Rosenfeldt, 1989 and *Myrioglobula antarctica* Hartman, 1967. Hartman (1967) reported *Myriochele* near *pygidialis* Hartman, 1960 from the Bransfield Strait area, a species originally described from off California, but the same author (Hartman 1978) later acknowledged it to be *M. scotiae.*

The present study of oweniid material collected during three Spanish Antarctic cruises known as Bentart94, Bentart95 and

Gebrap96, and specimens from different type collections, shows that *Myriochele scotiae* Hartman, 1978, *Galathowenia wilsoni* Blake, 1984 and *Myriochele terranovensis* Cantone & Di Pietro, 1998 represent the same species. The original description of *M. scotiae* is emended, and this species is reassigned to the genus *Galathowenia* Kirkegaard, 1959. *Galathowenia wilsoni* and *M. terranovensis* are qualified as junior synonyms of *G. scotiae,* while *M. joinvillensis* and *M. longicollaris* are recognized as valid species.

The Spanish Antarctic cruises Bentart94 and Bentart95 were carried out for the purpose of acquiring knowledge of the composition and dynamics of the benthic communities around the South Shetland Islands, while Gebrap96 was mainly geared towards obtaining information on marine geophysics in the Bransfield Strait (Antarctica). Field sampling methods, geographical location of the stations sampled and sediment parameters are described in Olaso (1994), Ramos (1995) and Sáiz-Salinas et al. (1997).

Data concerning general polychaete taxonomy and ecology of Bentart cruises are published in San Martín & Parapar (1997), Parapar & San Martín (1997) and San Martín et al. (2000); data concerning polychaetes collected in the Gebrap cruise are unpublished.

Materials and Methods

Samples from Bentart and Gebrap cruises were mostly collected in soft substrata (mud and muddy sand) by means of Van Veen grab, Anchor dredge and Rocky dredge in Feb 1994, Jan to Feb 1995 and Dec 1996 to Jan 1997. Specimens were fixed in formalin, preserved in 70% ethanol and deposited at the Museo Nacional de Ciencias Naturales de Madrid, Spain (MNCNM) and the Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía of the Universidade da Coruña, Spain (DBA). For comparative purposes, type material of *Myriochele scotiae* and *Galathowenia wilsoni,* loaned by the National Museum of Natural History, Washington DC, U.S.A. (USNM), *Myriochele terranovensis,* loaned by the Università di Catania (Italy) (UDC) and *Myriochele longicollaris* and *Myriochele joinvillensis,* loaned by the Zoologisches Museum der Universität Hamburg, Germany (ZMH), were also examined. Specimens used for scanning electron microscopy (SEM) were prepared by critical point drying, coated with gold in a BAL-TEC SCD 004 evaporator and examined and photographed in a JEOL JSM-6400 scanning electron microscope.

Family Oweniidae Rioja, 1917
Genus *Galathowenia* Kirkegaard, 1959
Galathowenia scotiae (Hartman, 1978) emended

Figs. 1, 2, Table 1

Myriochele near *pygidialis* Hartman, 1967: 148–149. Not Hartman, 1960. fide Hartman, 1978.

Myriochele scotiae Hartman, 1978:188–190, figs 32a–d. Blake, 1984:112–114, figs 1a–f.

Galathowenia wilsoni Blake, 1984:114–116, figs 2a–d. Imajima & Morita, 1987: 98, figs 7a–k and 8e–f.

Myriochele wilsoni Hartmann-Schröder & Rosenfeldt, 1989:81, fig. 36. Hartmann-Schröder & Rosenfeldt, 1991:81.

Myriochele terranovensis Cantone & Di Pietro, 1998:421–423, fig. 1a–f.

Material examined.—Type material of *Myriochele scotiae*: USNM 46969, 27 Feb 1969, 77°19.8′S, 36°41.3′W, 1079 m, 1 specimen, holotype; USNM 47049, 26/02/69, 77°05.5′S, 35°04′W, 743 m, 100 spec.

Type material of *Galathowenia wilsoni*: USNM 96113, 29 Jan 1968, 76°23′S, 163°28′W, 509–510 m, 1 specimen, holotype; USNM 96114, 29 Jan 1968, 76°23′S, 163°28′W, 509–510 m, 3 spec., paratypes.

Type material of *Myriochele terranovensis*: UDC: D1D, 1 specimen, holotype; D126, 7 spec., paratypes and syntypes, rocky and sandy bottoms, South "Faraglione" transect (Terra Nova Bay, Ross Sea).

Type material of *Myriochele longicollaris*: ZMH: P-19614, 1 specimen, holotype; St. 207, 68 m, 12 Mar 1984, Bransfield Strait (62°59′S, 57°05′W).

Type material of *Myriochele joinvillensis*: ZMH: P-23059, 1 specimen: ANT XV-3, MG 48-356.

Material from Bentart94: Sta. 1, 6 Feb 1994, 62°39′S, 60°23′W, 48 m, 3 specimens; Sta. 9, 7 Feb 1994, 62°39′S, 60°27′W, 240 m, 2 spec.; Sta. 20, 8 Feb 1994, 62°40′S, 60°27′W, 245 m, 1 spec.; Sta. 36, 10 Feb 1994, 62°41′S, 60°32′W, 250 m, 1 spec.; Sta. 40, 10 Feb 1994, 62°42′S, 60°35′W, 122 m, 1 spec.; Sta. 47, 11 Feb 1994, 62°46′S, 60°24′W, 123 m, 1 spec.; Sta. 54, 12 Feb 1994, 62°45′S, 60°27′W, 231 m, 2 spec.; Sta. 58, 13 Feb 1994, 62°43′S, 60°22′W, 194 m, 1 spec.; Sta. 59, 13 Feb 1994, 62°44′S, 60°21′W, 85 m, 1 spec.; Sta. 70, 15 Feb 1994, 62°44′S, 60°24′W, 191 m, 1 spec.; Sta. 80, 17 Feb 1994, 62°44′S, 60°26′W, 170 m, 1 spec.; Sta. 84, 17 Feb 1994, 62°40′S, 60°37′W, 164 m, 1 spec.; Sta. 97, 19 Feb 1994, 62°43′S, 60°30′W, 104 m, 2 spec.

Material from Bentart95: Sta. 4, 17 Jan 1995, 62°38′S, 60°25′W, 182.5 m, 4 spec.; Sta. 7, 18 Jan 1995, 62°44′S, 60°28′W, 76.2 m, 1 spec.; Sta. 8, 18 Jan 1995, 62°44′S, 60°30′W, 114 m, 4 spec.; Sta. 12, 24 Jan 1995, 62°57′S, 60°36′W, 162.8 m, 1 spec.; Sta. 23, 30 Jan 1995, 63°57′S, 60°57′W, 103 m, 2 spec.; Sta. 24, 30 Jan 1995, 63°58′S, 60°52′W, 324 m, 1 spec.; Sta. 29, 2 Feb 1995, 62°05′S, 60°25′W, 239.5 m, 1 spec.

Material from Gebrap96:Sta. DR-1, 29 Dec 1996, 62°12′S, 57°14′W to 62°12′S, 57° 10′W, 1407 to 1288 m, 7 spec.; Sta. DR-2, 30 Dec 1996, 62°14′S, 57°20′W to 62°13′S, 57°22′W, 1592 to 1269 m, 9 spec.; Sta. DR-7, 3 Jan 1997, 62°38′S, 59°06′W to 62°39′S, 59°04′W, 1416 to 1275 m, 13 spec.; Sta. DR-8, 3 Jan 1997, 62°42′S, 40°00′W to 62°41′S, 59°00′W, 1379 to 1192, 100+ spec.; Sta. DR-9, 3 Jan 1997, 62°41′S, 59°10′W to 62°42′S, 59°09′W, 1400 to 1182 m, 50+ spec.

Description.—Body cylindrical, long and thin, measuring from about 32 mm in length and 1.0 mm in width for 25 setigers in smaller entire specimens to 64 mm in length and 1.5 mm in width for 28 setigers in largest entire specimens. Body pale orange to dark brown pigmented with mid-ventral Y-line beginning just posterior to peristomium as two lines which converge and merge in setiger 2.

Anterior end truncated (Fig. 1A, D) with head region (prostomium and peristomium) with terminal ciliated mouth provided with two lips marking longitudinal mid-ventral slit on peristomium when closed (Fig. 1F). Surface of head region and buccal cavity densely covered with cilia (Fig. 1G, H). Eyespots absent. Thorax consisting of three setigers with notosetae only (Fig. 1A–C). On occasion, a fine transverse slit present between first and second setigers (arrows in Figs. 1A–D), becoming narrow body constriction in larger animals (Fig. 1D), which, in most, represents line of breakage, leaving anterior portion (comprising prostomium, peristomium and first setiger; Fig. 1F, G) completely separated from remainder of body (Fig. 1E). Fourth to eighth setigers greatly elongated, successively shorter. All setigers with notopodial capillary setae coated with minute spinules in distal half (Fig. 2C) and no acicular setae. Ventrolateral neuropodial uncinigerous tori starting from fourth setiger and comprising several transverse rows of hooked setae. Hooked setae bidentate, with curved teeth nearly equal in length and located one above the other or slightly offset from one another in anterior neuropodia (Fig. 2D, E) and progressively located more side by side in mid-body (Fig. 2F, G) and in oblique position in posterior neuropodia (Fig. 2H). On occasion, a double upper tooth present (Fig. 2F, arrow).

Posterior end of body more or less tapered with segments occasionally much compressed, splaying out large notopodial

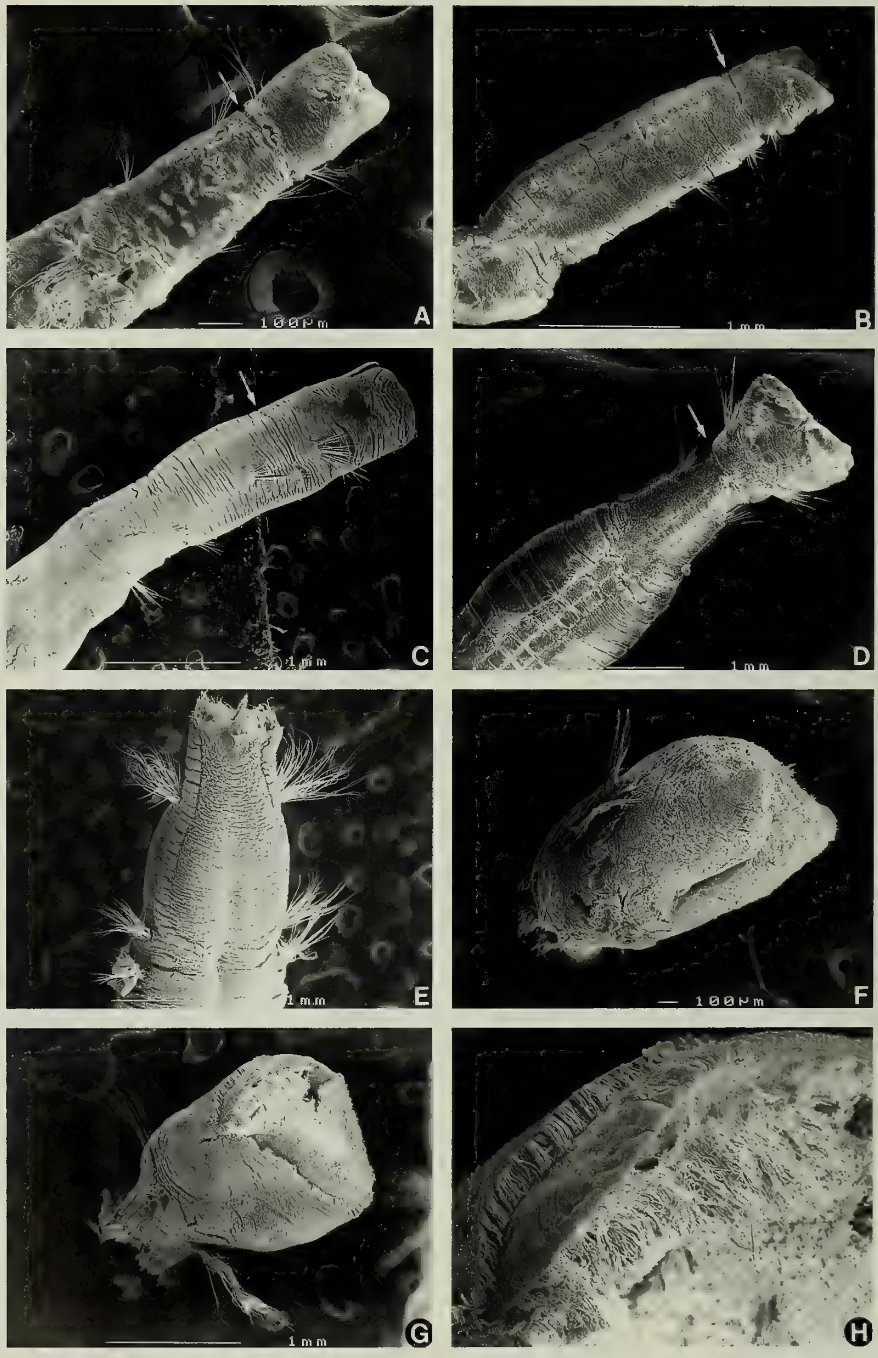

Fig. 1. *Galathowenia scotiae* new combination. A, anterior end from paratype of *M. terranovensis* (D 126), ventral view; B, anterior end from paratype of *G. scotiae* (USNM 47049), ventral view; C, anterior end from Bentart, lateral view; D, anterior end from Gebrap, ventral view; E, anterior end without head region (Gebrap), ventral view; F, G, released head regions with closed and open mouth lips respectively (Gebrap), ventral view; H, Detail of prostomial lip ciliature (Gebrap). Arrows indicate position of transverse slit between first and second setigers.

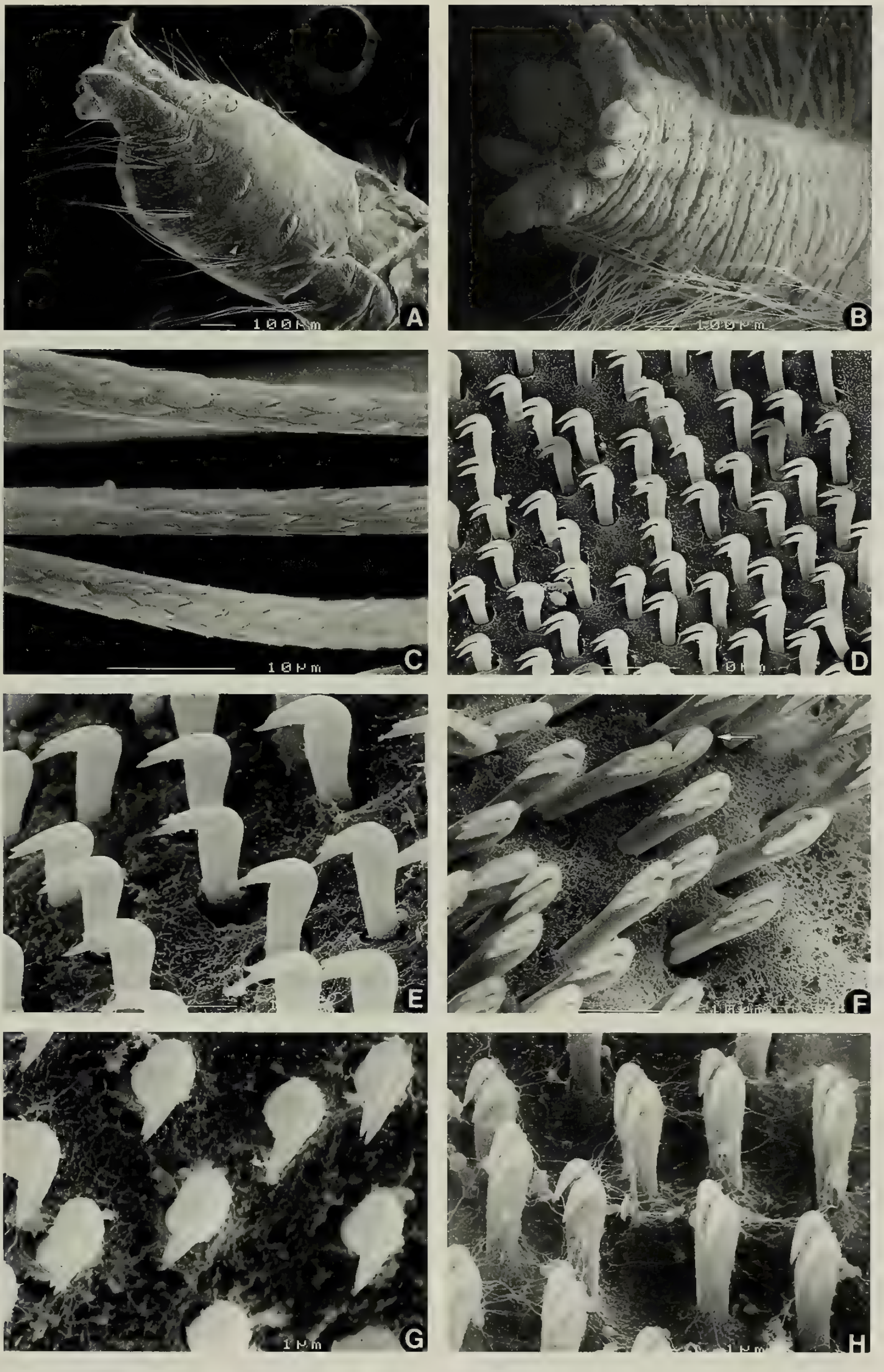

Fig. 2. *Galathowenia scotiae* new combination. A, posterior region and pygidium from Bentart95, ventral view; B, posterior region and pygidium from Gebrap, dorsal view; C, detail of spinules covering of first setiger capillary notosetae; D, E, hooked setae from first abdominal setiger from Bentart95 and Gebrap respectively in lateral view; F, G, hooked setae from midbody, frontal and upper view respectively, arrow indicate double upper tooth; H, hooked setae from posterior setiger, frontal view.

setae. Pygidium with about 5–11 irregular cirri, slightly petaloid, arranged around anus (Fig. 2A, B).

Tube long, cylindrical and rigid; with membranous inner lining, externally coated with black volcanic sand grains and occasional sponge spicules and foraminiferans.

Distribution.—*Galathowenia scotiae* new combination, seems to be widespread in Antarctic seas but mainly recorded from the Ross Sea, Weddell Sea and Bransfield Strait (see Table 1). The only record beyond Antarctic waters is from Japan by Imajima & Morita (1987) as *Galathowenia wilsoni.*

Remarks.—As stated by Nilsen & Holthe (1985), of all the polychaetes, the Oweniidae are possibly the most difficult family to remove undamaged from their tubes. This characteristic, together with their fragility and the existence of mobile, and shape variable body structures as the head region, has sometimes given rise to erroneous observations that result in false species descriptions. In the original description of *Galathowenia scotiae,* Hartman (1978) did not take into account the existence of specimens in their tubes with the anterior end still unbroken (USNM 47049, Fig. 1B) and interpreted the anterior end of the broken specimens as a characteristic reduced prostomium (Hartman, 1978:188, fig. 32a–b). This confusion was later continued by Blake (1984) in a study on Antarctic oweniids in which the author described a new species, *G. wilsoni.* The study of the type material of the two species shows no fundamental anatomical difference between them and, accordingly, both taxa represent the same species. Unlike most specimens of the *G. scotiae* type material, most of the type material belonging to *G. wilsoni* are complete animals, with no signs of anterior constriction or breakage (Blake, 1984:114–116, fig. 2a), although one of the paratypes (USNM 96114) was similarly broken between the first and second setigers.

The material of *Galathowenia wilsoni* from Japan (Imajima & Morita 1987) was not examined by the author, but the description and good illustrations as well as SEM micrographs do not appear to shed any doubt on their correct identification. Blake (1984), following Hartman (1978), synonymized *Myriochele* near *pygidialis* Hartman, 1967, recorded from the Weddell Sea, with *M. scotiae.* I also agree with this opinion, although I did not examine the material.

Hartmann-Schröder & Rosenfeldt (1989) described two new species from the South Shetland Islands: *Myriochele joinvillensis* and *M. longicollaris.* After examining only one specimen of the type series of both species, I consider that they are likely valid species, in spite of the fact that they exhibit close similarities to *Galathowenia scotiae.* Examination of a specimen of *M. joinvillensis* confirms the existence of two thoracic setigers and a short collar in this species, as the truncated anterior end shows no signs of breakage. However, in this specimen I did not observe the secondary annulation that the authors describe and illustrate in the collar and thoracic region of the holotype (Hartmann-Schröder & Rosenfeldt 1989, fig. 37). The uncini, which the authors compare with those of *M. oculata* Zachs, bear a strong resemblance to those of *G. scotiae.* It was not possible to observe the shape of the posterior region and pygidium, although judging from the description and the illustration, they would appear to be similar to *G. scotiae.* An analysis of the holotype seems to confirm the presence of an extremely long collar in the head region of *M. longicollaris,* consisting of two large anterior lateral lobes, which are much longer than in *G. scotiae.* This aspect can be observed in the original illustration (Hartmann-Schröder & Rosenfeldt 1989, figs. 40–41), in which there is, however, an error, as the deep transverse slit that is described as being between the second and third thoracic setigers is, in reality, located between the first and second as in *G. scotiae.* The hooks are again very similar to those in *G. scotiae.* The pygidium is unknown.

Cantone & Di Pietro (1998) recently described a new Antarctic species, *Myriochele terranovensis,* characterising it by the combination of four features: a deep constriction between first and second setigers, the prostomium anteriorly enlarged, short collar and the presence in the pygidium of two dorsal lobes smaller than the others (5 in total). From the study of the type material, I did not find any significant differences with *Galathowenia scotiae,* which also has in common with this species the shape of the unicini, with the two teeth in a more or less variable slanted arrangement. This variable shape of the unicini led the authors to suggest an "apparently contemporary presence in the same chaetiger of uncini of two types."

The presence of a transverse slit between the first and second setigers posteriorly transformed into a body wall constriction in a large number of the specimens studied is a common trait in *Galathowenia scotiae*: type material of *Myriochele terranovensis* (Fig. 1A), *M. longicollaris, G. wilsoni, G. scotiae* (Fig. 1B), and Bentart and Gebrap material (Fig. 1C). Its biological role could be interpreted as simply a particularly fragile spot in the body or as a breakage point closely related to seasonal body fragmentation during asexual reproduction—a biological strategy previously reported by Curtis (1977) for *Owenia fusiformis* in Greenland and Oliver (1984) for *Myriochele oculata* Zaks, 1922 in Alaskan waters and *M.* cf. *heeri* in Antarctica. That this fragmentation always occurs between the same setigers in my opinion makes this fact probably more related to a reproductive role than to accidental breakage during sample processing. In relation to this, Oliver (1984) reported that the breakage during asexual reproduction in *M. oculata* always occurs between setigers 6 to 8. In any case, only specific research on the biology of this species will reveal the true role of this structure.

Nielsen & Holthe (1985) described *Myriochele fragilis* from the Norwegian and Arctic seas. This species is superficially very close to *Galathowenia scotiae,* especially in the presence of a pronounced constriction between the first and second setiger, which, in Eliason's manuscript, makes it " . . . impossible to secure an intact animal, although I have tried to open almost 100 tubes." Nielsen & Holthe (1985) admit the similarity between *M. fragilis* and *M. scotiae* sensu Hartman (1978), but qualifying it as superficial due to differences in the number of segments, anal lobes and particularly owing to the shape of hooked setae (with both teeth consistently in a vertical row in *M. fragilis*). Nevertheless, and despite of their very different geographical distribution, I consider both species as probably very closely related.

Due to the limited number of characteristics with taxonomic relevancy in oweniids, the possibility of intraspecific variability must be given special consideration. As a result of this study, and as shown in the above description, three of the most relevant structures in oweniid taxonomy demonstrated substantial variability between specimens in *Galathowenia scotiae*: the shape of the anterior and posterior body regions and relative position of the teeth in the neuropodial bidentate hooked setae. Depending on the degree of mouth opening, the shape of the anterior region could vary from truncate (with the mouth open) to almost rounded (closed mouth). Likewise, the number of pygidial cirri and the state of contraction of the segments of the hind part of the body could vary depending on the size of the animal and the fixation. In the case of the hooked setae, a slight antero-posterior variation in the relative position of the teeth could be observed, from one upper and one lower disposition in the anteriormost neuropodia to an oblique disposition in the remainder of the body. Some variation within a single neuropodium was also reported (see Fig. 2F). With regard to the hooks, the occasional occurrence of a second uppermost tooth, which could be interpreted following Meyer & Bartolomaeus

Table 1.—Comparison of some morphological characters, bathymetry and geographical distribution of *Myriochele scotiae* Hartman, 1978, *M. wilsoni* Blake, 1984 and *M. terranovensis* Cantone & Di Pietro, 1998. ES = Elongated setigers; TS = Transverse slit between thoracic setigers 1 and 2; TAHS = Teeth arrangement on hooked setae; MVYL = Mid-ventral Y-line; PC = Number of cirri on pygidium. Size (mm) in length/width. "—" means no data. Some bibliographic data have been slightly modified or completed by personal observations from type material.

Species	Reference	Size	Setigers	ES	TS	TAHS	MVYL	PC	Tube covering	Bathymetry	Area
Myriochele near *pygidialis*	Hartman (1967)	25/0.75	32	4–6	—	Bifid claw	—	7	Fine cindery gravel	311–1153	South Shetlands and South Orkney Islands, Barnsfield Strait (Antarctica)
Myriochele scotiae	Hartman (1978)	40/2.0	24+	4–8	Yes	Slightly offset from one another?	Yes	7	Small sand grains	40–1153	Weddell Sea (Antarctica)
Myriochele scotiae	Blake (1984)	20/0.75	24	4–6	Yes	One above the other	—	6–7	—	411–923	Ross Sea and N of Amundsen Sea (Antarctica)
Galathowenia wilsoni	Blake (1984)	35/1.0	21	4–7	Yes	Slightly offset from one another	Yes	8	Fine silt and sand particles	411–608	Ross Sea and N of Amundsen Sea (Antarctica)
Galathowenia wilsoni	Imajima & Morita (1987)	32/0.9	20–30	5–7	Yes	Side by side at different levels or one above the other	Yes	8	Fine silt and sand grains, foraminiferans	56–1050	Japan
Myriochele wilsoni	Hartmann-Schröder & Rosenfeldt (1989)	32	27	—	—	Side by side at different levels	—	—	Sand grains	120–510	Bransfield Strait, King George and Elephant Islands (Antarctica)
Myriochele wilsoni	Hartmann-Schröeder & Rosenfeldt (1991)	27	24	—	—	—	Yes	—	Black and white sand grains and sponge spicules	134–370	Elephant Island (Antarctica)
Myriochele terranovensis	Cantone & Di Pietro (1998)	10/0.3	17	5–6	Yes	Two types: upper and lower and side by side	Yes	5	Sand grains and sponge spicules	120–332	Terra Nova Bay (Antarctica)

Table 1.—Continued.

Species	Reference	Size	Setigers	ES	TS	TAHS	MVYL	PC	Tube covering	Bathymetry	Area
Galathowenia scotiae	This study	32/1.0 to 64/1.5	25	4–8	Yes	Variable, but mainly obliquely arranged	Yes	5–11	Black sand grains	48–1592	South Shetlands Islands and Barnsfield Strait (Antarctica)

(1996) as the third spine of a capitium of a hook in which the rostrum was reduced, was not previously documented in any other oweniid species. For the above reasons, in my opinion and as mentioned previously by other authors such as Martín (1989) with *Galathowenia oculata* (Zaks, 1922), the anatomical variability in the hooked setae, the different position of the lips of the mouth and the different degree of body contraction, must be included in every oweniid description and taken into account in every dichotomous key to avoid, as much as possible, multispecific descriptions and/or unclear species determinations.

Nilsen & Holthe (1985) included a key of Arctic and Scandinavian oweniid species in which the different species of *Myriochele* are distinguished only on the basis of the shape of the uncini and tube. In addition to the uncini, Imajima & Morita (1987) also used the presence or absence of eyes and the number of pygidial lobes. Lastly, Cantone & Di Pietro (1998) provided a key of the Antarctic oweniids based on structures, which the authors believe are easy to detect, such as the shape of the different structures related to the anterior end—the collar and prostomium—and posterior end, while ignoring other features such as the shape of the ventral hooks. Because body shape and certain meristic characteristics have shown, in this study, to exhibit some degree of variability, I believe that these characteristics should be avoided, where possible, in a dichotomous key, or at the very least, used with caution. In contrast, I consider the inclusion of the shape of the ventral hooks in the keys to be valid, and I agree with Nilsen & Holthe (1989) who consider them to be a crucial characteristic in the classification and identification of oweniids, although it is always necessary to take their slight intraspecific variability into account.

Authors such as Fauchald (1977), Kirkegaard (1983, 1996), Blake (1984) and Imajima & Morita (1987) regard the genus *Galathowenia* as valid and have used it to name this species. Nevertheless, as Mackie

& Pleijel (1990) have pointed out, there is no consensus on this matter, so other authors including Nilsen & Holthe (1985, 1989), Hartmann-Schröder & Rosenfeldt (1989, 1991), Hartmann-Schröder (1996) and Cantone & Di Pietro (1998) regard it as a junior synonym of *Myriochele.* In my opinion, this genus seems to be well defined by the truncated anterior end of the head region, terminal mouth and notopodial fascicle with capillary setae only. Nevertheless, the aim of this paper is to put forth the synonymy between *M. scotiae, G. wilsoni* and *M. terranovensis.* A review of the genus *Myriochele* Malmgren, 1867 and *Galathowenia* Kirkegard, 1959 is beyond the scope of this paper.

The presence of abundant ciliature in the head region and anterior lips as the feeding apparatus of this species, an aspect previously emphasised by Imajima & Morita (1987), would appear to confirm the high level of sediment selectivity in oweniids as suggested by Fauchald & Jumars (1979). However, the animal feeding position is still unclear—whether it projects the anterior end to the water in an upright position like *Owenia fusiformis* or downwards like the maldanids, as proposed by those authors.

Key to Antarctic species of Oweniidae

1a. Cephalic region with tentacular crown .... *Owenia fusiformis*
1b. Cephalic region without tentacular crown 2
2a. One thoracic setiger .... *Myrioglobula antarctica*
2b. Two or three thoracic setigers 3
3a. Head region anteriorly rounded, abdominal notopodia with capillary and acicular setae, teeth of uncini arranged one above the other .... *Myriochele heeri*
3b. Head region anteriorly truncated, abdominal notopodia with capillary setae only, teeth of uncini more or less arranged in an oblique row 4
4a. Two thoracic setigers .... *Galathowenia joinvillensis*
4b. Three thoracic setigers 5
5a. Collar about four times longer than wide .... *Galathowenia longicollaris*
5b. Collar about the same length than width .... *Galathowenia scotiae*

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Interstitial acoels (Platyhelminthes: Acoela) from Bermuda

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Abstract.—One new genus, *Antrosagittifera,* and four new species of interstitial acoel flatworms from Bermuda are described, bringing the total number of known acoels from Bermuda to eight. The new species are *Haploposthia vandula, Parahaploposthia velvetum, Antrosagittifera corallina,* and *Proporus bermudensis.* A previously described species, *Pseudaphanostoma opisthorchis,* is reassigned to the genus *Haploposthia.*

Hyman (1939) provided the first taxonomic report of acoels from Bermuda with her descriptions of *Amphiscolops bermudensis* and *A. sargassi,* which were collected from rooted seaweeds and floating Sargassum, respectively. She also reported the presence of *A. langerhansi* which was not found in nature in Bermuda, but was present in aquaria at the Bermuda Biological Station.

A fourth seaweed-dwelling species of Acoela, *Convoluta sutcliffei* (Hanson, 1961) has since been transferred the genus *Pseudohaplogonaria* by Dörjes (1968).

During a 5-day stay at the Bermuda Biological Station in June 1999, we collected and examined interstitial fauna from two locations, North Rock and Castle Roads. We report here our findings of one new genus and four new species of interstitial acoels. Photographs and sketches of some of these species collected by J. P. S. Smith, III and S. Tyler in March 1985 were compared with these new findings.

Methods

Animals were extracted from sediment using magnesium-chloride anesthetization (Sterrer 1971). Squeeze preparations for light microscopic observation were made by placing live specimens on a slide along with a drop of magnesium chloride isotonic to seawater.

For histological study, specimens were relaxed in isotonic magnesium chloride, fixed in phosphate-buffered 2.5% (v/v) glutaraldehyde, washed in phosphate buffer (Millonig's buffer, 0.1 M), fixed in phosphate-buffered 1% (v/v) osmium tetroxide, dehydrated in acetone, and embedded in EMBed/Araldite epoxy resin. For some specimens, steps from aldehyde fixation through dehydration were enhanced by microwave radiation (Samsung oven, two 7-sec irradiations at 650 W separated by a 20-sec hiatus, with specimen-vial on ice and with water ballast of two filled 300-ml beakers; Giberson & Demaree 1995). Serial thick sections (1.25–2 μm) were prepared according to Smith & Tyler (1984) and stained without deresination in toluidine blue. Thin sections for electron microscopy were stained with uranyl acetate and lead citrate.

Whole mounts of individual worms were processed to reveal musculature through staining of their F-actin with fluorescently labeled phalloidin (BODIPY 558/668 or Alexa 488; Molecular Probes, Eugene, OR). The specimens were first relaxed in a magnesium-chloride solution isotonic to sea water, fixed for 1 hr in 4% (w/v) formaldehyde in PBS, rinsed in PBS (phosphate-buffered saline), attached with poly-L-lysine to a coverslip, permeabilized for 1 hr with 0.2% (v/v) Triton X-100 in PBS, stained 40 min with phalloidin-Alexa or

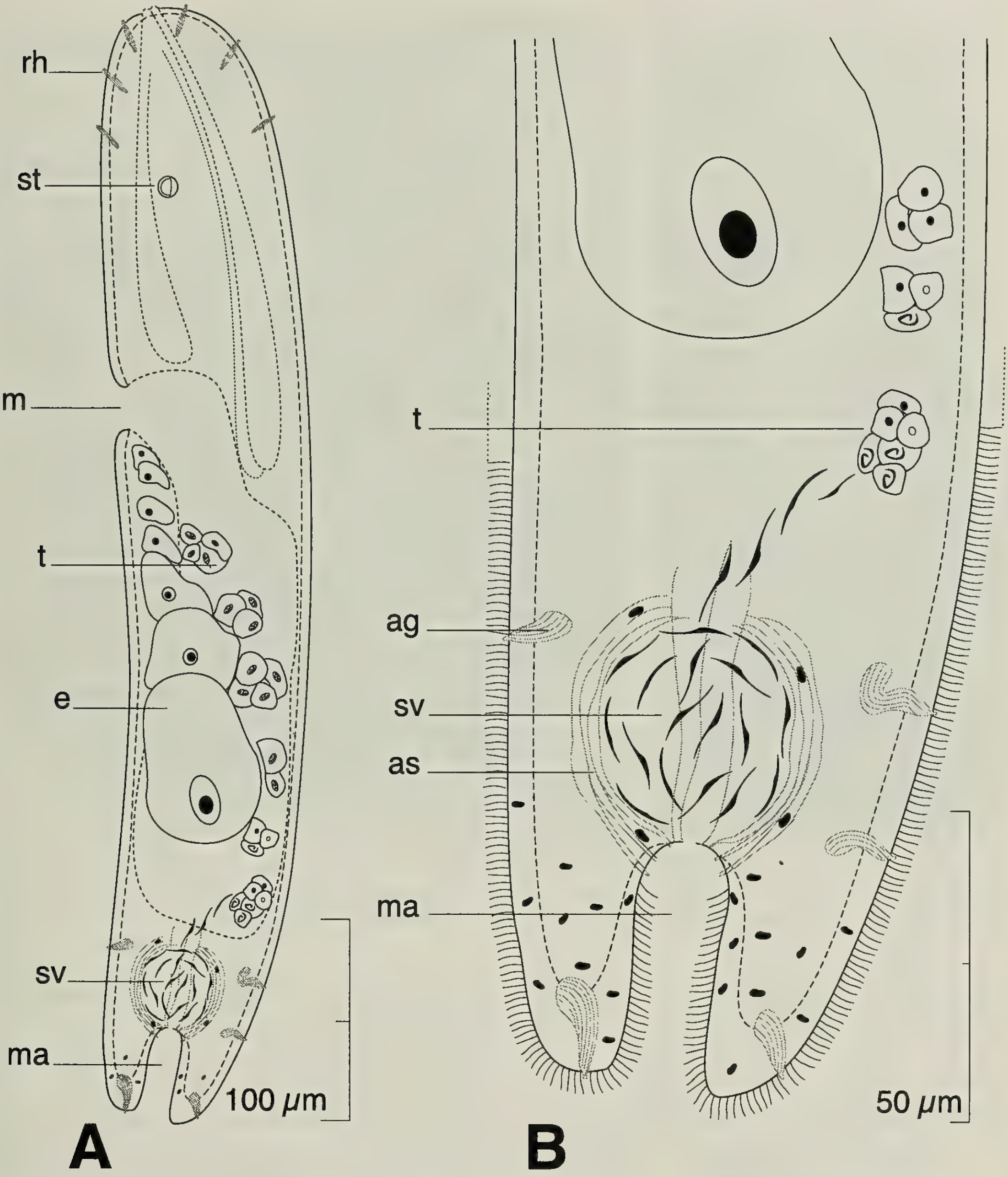

Fig. 1. *Haploposthia vandula,* new species. Sagittal reconstruction to show arrangement of organs. A, Whole organism; B, Reproductive structures in posterior portion of animal. Abbreviations: ag, accessory gland; as, accessory secretions; e, egg; m, mouth; ma, male antrum; rh, rhabdoid; st, statocyst; sv, seminal vesicle; t, testes.

phalloidin-BODIPY, and mounted under a second coverslip with Fluoromount-G. Epifluorescence images of the preparations from both dorsal and ventral aspects were viewed on a Leitz Ortholux microscope, and digital images were recorded using a Cohu 4915 CCD camera and a Scion LG3 frame grabber card on a Macintosh G3 computer. A brief summary of the body-wall musculature is given for each newly described species. A more detailed description of the body-wall musculature of these

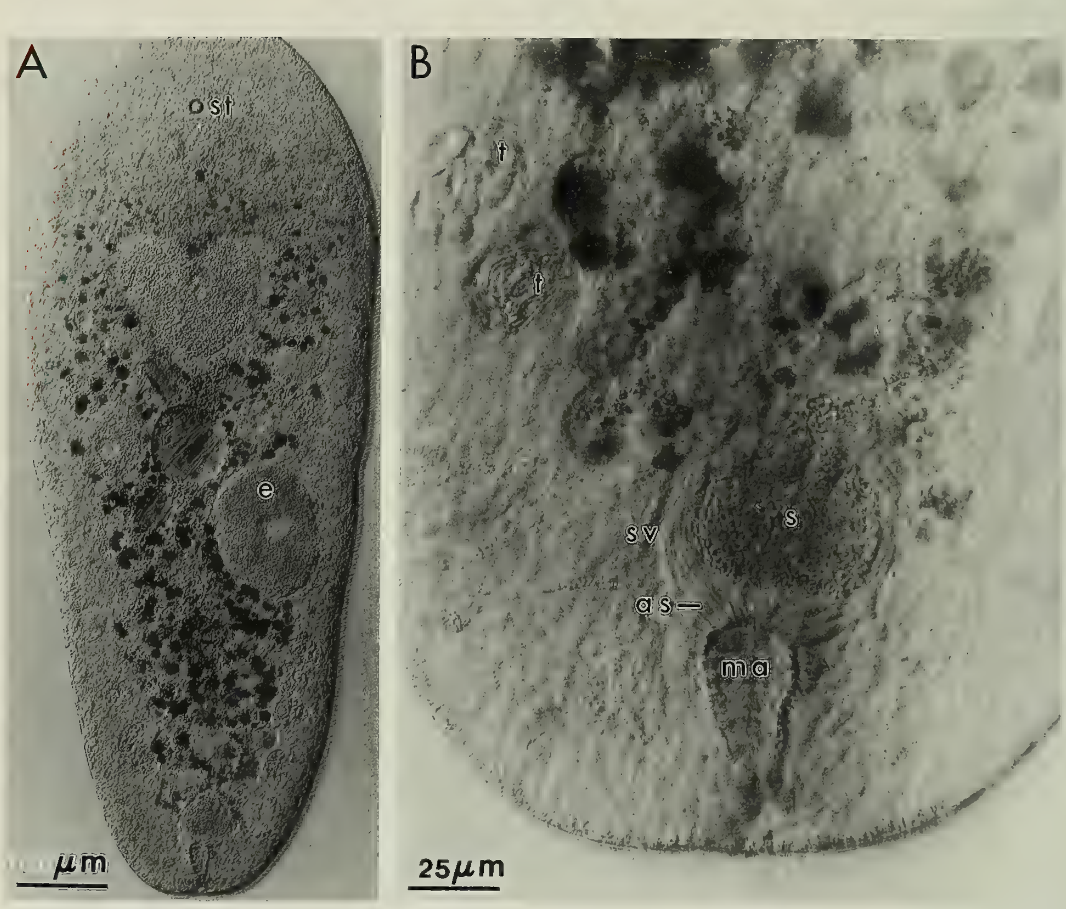

Fig. 2. *Haploposthia vandula,* new species. Photomicrographs. A, Whole-mount of living specimen, slightly flattened. B, Male reproductive structures in posterior portion of living specimen. Abbreviations: as, accessory secretions; e, egg; ma, male antrum; s, sperm; st, statocyst; sv, seminal vesicle; t, testes.

and other acoels is provided by Hooge (2001).

Family Haploposthiidae Westblad, 1948
Genus Haploposthia An der Lan, 1936
Haploposthia vandula, new species
Figs. 1, 2

Holotype.—AMNH 1601, 1.5-µm-thick serial sagittal sections of epoxy-embedded specimen stained with toluidine blue, collected June 1999.

Type locality.—Castle Roads, Bermuda. Subtidal coarse coral sand.

Paratype.—AMNH 1602, epoxy-embedded whole mount, Castle Roads, Bermuda.

Other material examined.—Living specimens in squeeze preparations; sets of 2-µm-thick serial sections of four epoxy-embedded specimens (two sagittal, one oblique-frontal) stained with toluidine blue; 60-nm-thick serial sections for transmission electron microscopy (one specimen); whole mounts for fluorescence imaging of musculature (three specimens). Specimens collected from Castle Roads and North Rock. Nomarski photographs of two specimens collected from Whalebone Bay March 1985 by J. P. S. Smith, III, and S. Tyler.

Description.—Largest adult specimens ca. 1 mm long (Fig. 1A) and ca. 250 µm wide (Fig. 2A). Anterior and posterior ends of body rounded bluntly, anterior more blunt. Body color green. Ocelli absent.

Epidermis completely ciliated. Rhabdoid

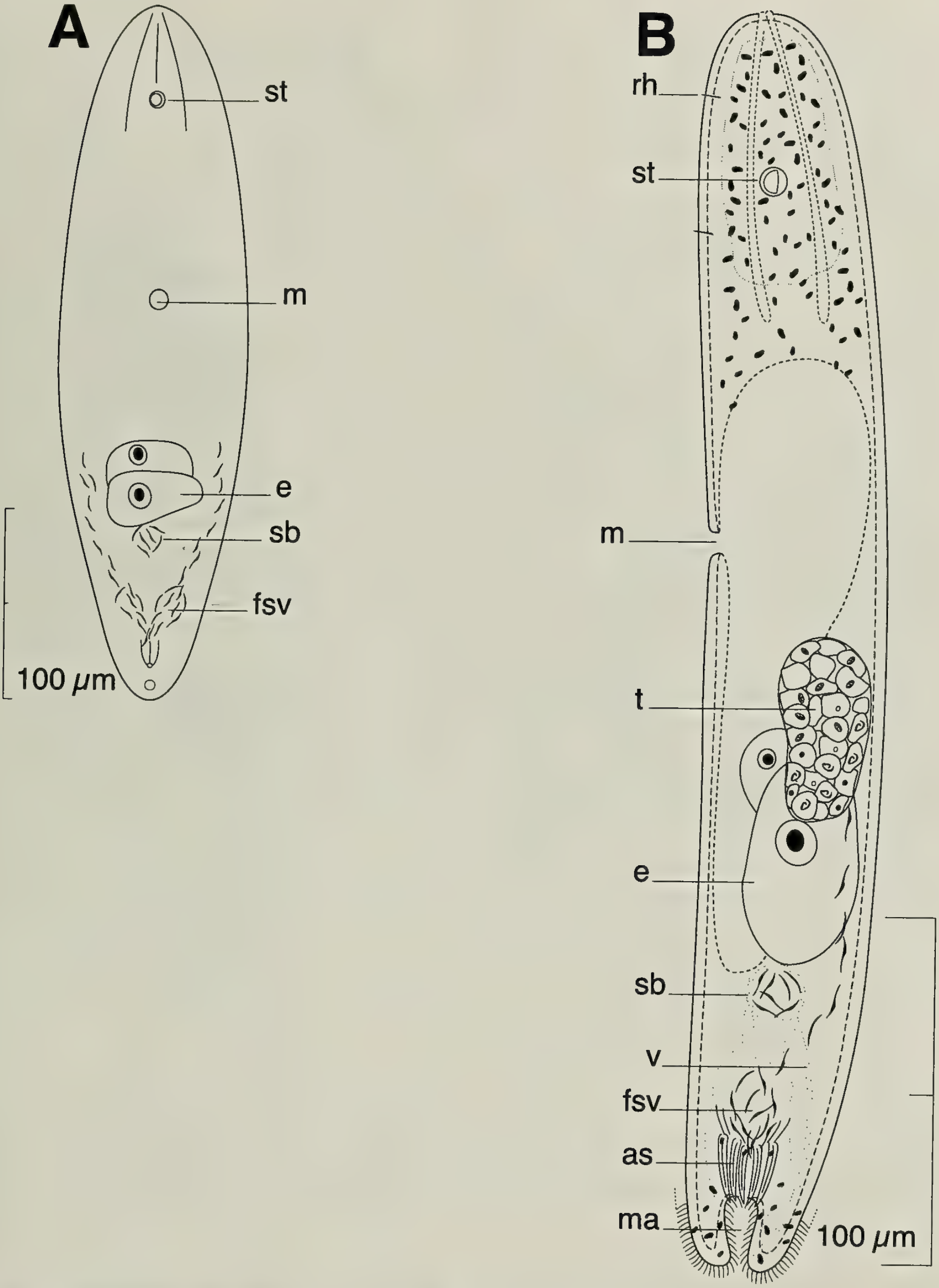

Fig. 3. *Parahaploposthia velvetum,* new species. Reconstructions to show arrangement of organs. A, Frontal view of whole organism. B, Sagittal view of whole organism. Abbreviations: as, accessory secretions; e, egg; fsv, false seminal vesicle; m, mouth; ma, male antrum; rh, rhabdoid; sb, seminal bursa; st, statocyst; t, testes; v, vagina.

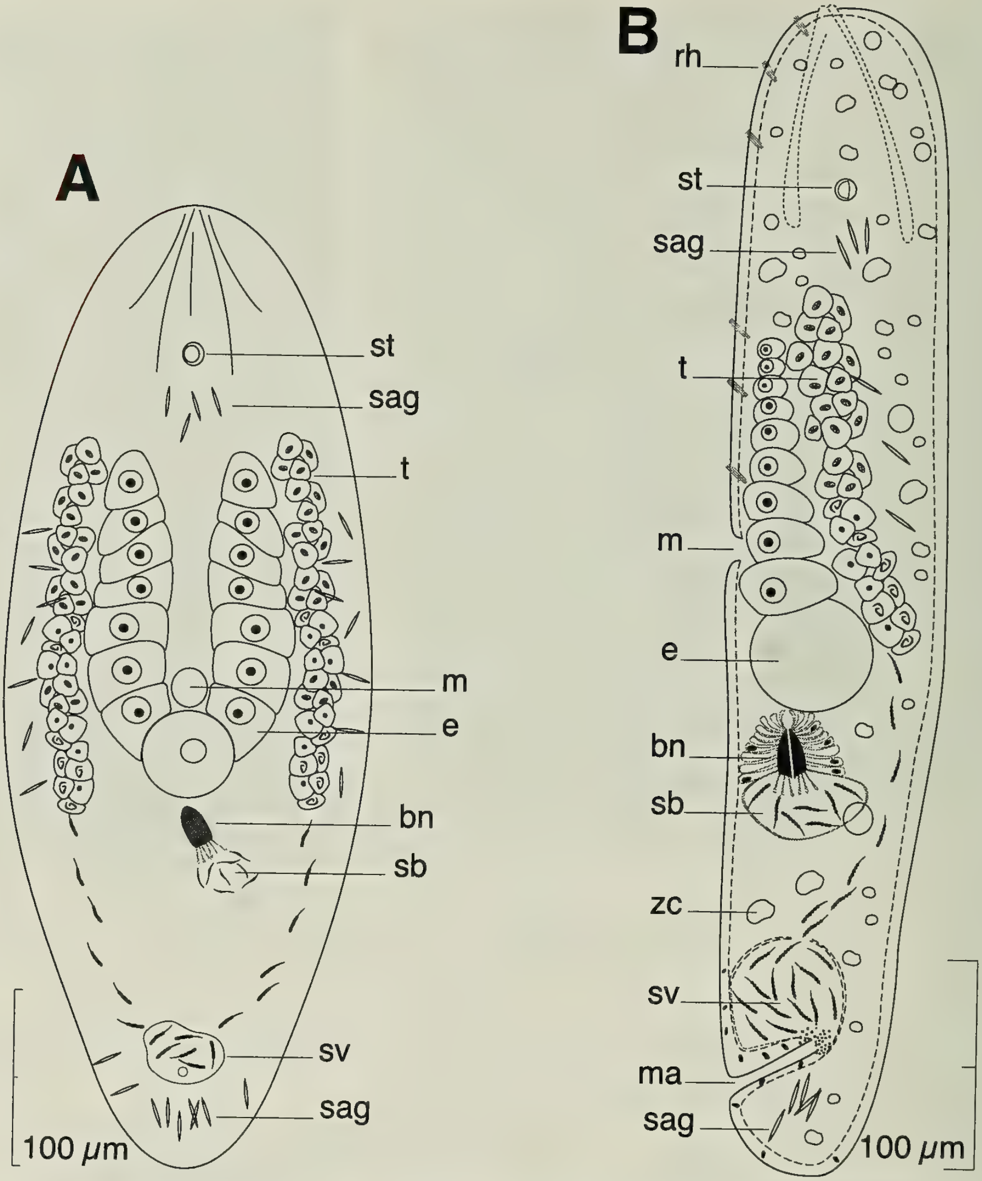

Fig. 4. *Antrosagittifera corallina,* new species. Reconstructions to show arrangement of organs. A, Frontal view of whole organism. B, Sagittal view of whole organism. Abbreviations: bn, bursal nozzle; e, egg; m, mouth; ma, male antrum; rh, rhabdoid; sag, sagittocyst; sb, seminal bursa; st, statocyst; sv, seminal vesicle; t, testes; zc, zooxanthellae.

glands few (Fig. 1A), concentrated at the anterior tip. Accessory glands present in region around male copulatory apparatus (Fig. 1B).

Musculature with circular fibers that encircle the body along entire length of animal; straight longitudinal muscles present between frontal organ and anterior edge of mouth; longitudinal muscles that have a longitudinal orientation anteriorly, but bend medially to cross diagonally over the body (longitudinal-cross-over fibers), present in both dorsal and ventral body wall; anterior with ventral diagonal muscles positioned

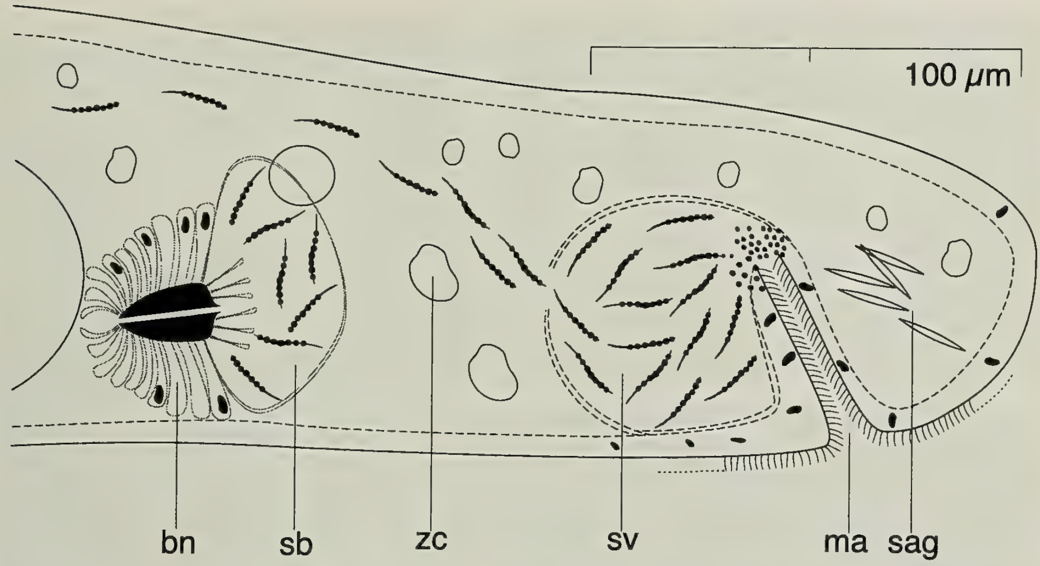

Fig. 5. *Antrosagittifera corallina,* new species. Reconstruction showing sagittal view of reproductive structures in posterior portion of animal. Abbreviations: bn, bursal nozzle; ma, male antrum; sag, sagittocyst; sb, seminal bursa; sv, seminal vesicle; zc, zooxanthellae.

between outer circular and inner longitudinal muscles.

Frontal organ strongly developed; frontal glands projecting to frontal pore from position posterior of mouth (Fig. 1A).

Mouth anterior to middle of body on ventral surface. Digestive central syncytium extends posteriorly from level of mouth to level of seminal vesicle.

Indistinct common germinal center producing strings of eggs and testes follicles (Fig. 1).

Male genital pore terminal at posterior end of body (Figs. 1, 2). Male antrum ciliated, short and tubular; proximal portion without cilia; antrum opening directly to seminal vesicle. Seminal vesicle surrounded by gland necks that pass through epithelium of antrum (Figs. 1B, 2B). By electron microscopy, these elongate gland necks are seen to contain thin rhabdiform granules that stain metachromatically (pink) with toluidine blue. Thin parenchymal muscles extend anteriorly from proximal end of male antrum, terminating slightly anterior to seminal vesicle.

Seminal bursa, vagina, and female pore absent.

Etymology.—The specific epithet is a combination from the Latin *viridis,* meaning green, referring to the body color, and the Latin *glandula,* referring to the gland secretions that surround the seminal vesicle.

Taxonomic remarks.—At least three of the five known species of *Haploposthia,* i.e., *H. rubra* (An der Lan, 1936), *H. rubropunctata* Westblad, 1945, *H. erythrocephala* Kozloff, 2000, have gland cells present either at the location where the male antrum meets the seminal vesicle or at the anterior tip of the seminal vesicle. *Haploposthia vandula* differs from these species in having elongate gland necks compose the wall of the seminal vesicle, enwrapping it entirely. The glands producing the glandular secretions are not evident in our epoxy serial sections; however, the secretions appeared similar in color of staining and in density to the secretions contained within the epidermal accessory glands (Fig. 1B) in the posterior end of the animal.

Haploposthia vandula was the most

common acoel in our sediment collections from North Rock and Castle Roads. Even after we had extracted most of the adult specimens of *H. vandula* from our buckets of sediment, we could continue to extract numerous immature specimens.

Genus *Parahaploposthia* Dörjes, 1968

Parahaploposthia velvetum, new species

Fig. 3

Holotype.—AMNH 1603, 1.5-μm-thick serial sagittal sections of epoxy-embedded specimen stained with toluidine blue, collected June 1999.

Type locality.—North Rock, Bermuda. Subtidal coarse coral sand.

Paratype.—AMNH 1604, epoxy-embedded whole mount, North Rock.

Other material examined.—Living specimens in squeeze preparations; two sets of 1.5–2-μm-thick serial sagittal sections of epoxy-embedded specimens stained with toluidine blue (one sagittal, one frontal); whole mounts for fluorescence imaging of musculature (14 specimens). Specimens collected from North Rock.

Description.—Adult specimens ca. 350 μm long and 100 μm wide (Fig. 3); maximum width at middle of body and narrower at the posterior and anterior ends. Pale-yellow body color.

Epidermis completely ciliated. Rhabdoid glands absent, or only two or three present on ventral side of anterior end (Fig. 3B).

Musculature with circular fibers that encircle the body along entire length of animal; straight longitudinal muscles present between frontal organ and anterior edge of mouth; longitudinal muscles that have a longitudinal orientation anteriorly, but bend medially to cross diagonally over the body (longitudinal-cross-over fibers), present in both dorsal and ventral body wall.

Frontal organ weakly developed; frontal glands projecting to frontal pore through brain from position just posterior to it.

Mouth opening anterior to middle of body. Digestive central syncytium extends from brain posteriorly to seminal bursa.

Ovary unpaired; only one or two eggs visible in specimens; largest egg extends posteriorly past level of seminal bursa.

Seminal bursa surrounded by tissue wall (Fig. 3B). Sectioned material appears to reveal a vagina as an indistinct tissue connection from the seminal bursa to the terminal gonopore.

Paired testes compact, ca. 60 μm long, positioned behind level of mouth. Sperm aggregate as paired false seminal vesicles, uniting slightly anterior to proximal end of male antrum. A ring of secretions (Fig. 3B) surround the distal end of false seminal vesicles; glands extend posteriorly to proximal end of male antrum.

Ciliated male antrum ca. 20 μm long, tubular, with weak musculature; opens terminally at common gonopore.

Etymology.—The specific epithet is from the Latin *velvetum,* meaning velvet, referring to "softness" of the epidermis due to the sparseness of obvious rhabdoids and accessory glands.

Taxonomic remarks.—The four known species of *Parahaploposthia* share weakly developed frontal glands, unpaired ovaries, paired testes, ciliated male antrum bearing proximal glands, and the lack of a seminal vesicle or penis. The addition of *P. thiophilus* Fegley et al., 1984, to this genus expanded the diagnosis to include haploposthiids having a seminal bursa and a vagina that is a "tissue connection indistinct in sectioned material." Due to this expanded diagnosis, *P. velvetum* seems to fit well within the genus; although the presence of a vagina may be more questionable in *P. velvetum* than in *P. thiophilus. Parahaploposthia velvetum* also resembles *P. thiophilus* in having compact testes, but differs in having fewer rhabdoids and a less muscular male antrum without accessory glands associated with the gonopore. The male antrum of *P. velvetum* appears to more resemble that of *P. avesicola* Dörjes, 1968, and *P. cerebroepitheliata* Dörjes, 1968.

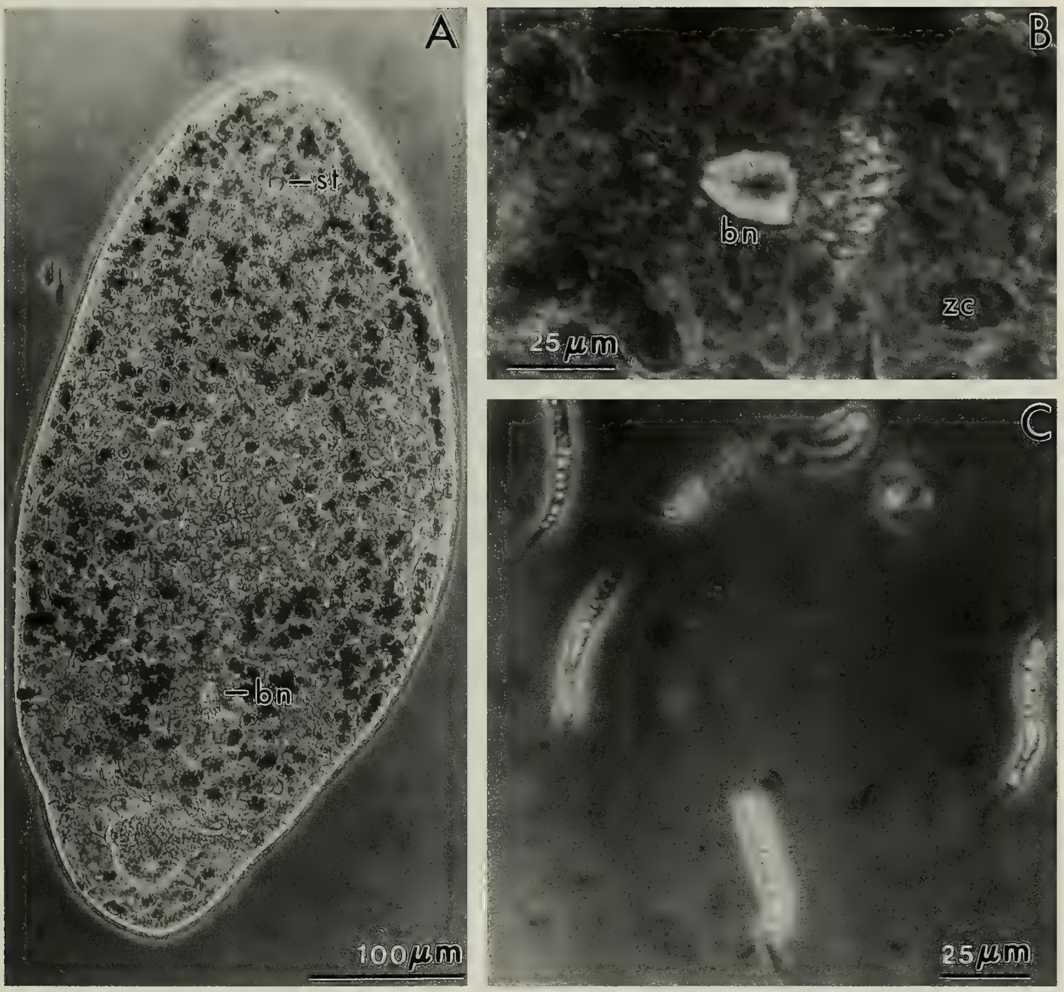

Fig. 6. *Antrosagittifera corallina,* new species. Photomicrographs. A, Whole-mount of living specimen, moderately flattened. B, Bursal nozzle. C, Sperm. Abbreviations: bn, bursal nozzle; st, statocyst; zc, zooxanthellae.

Family Sagittiferidae Kostenko & Mamkaev, 1990

Subfamily Sagittiferinae Gschwentner et al., 1999

Antrosagittifera, new genus

Diagnosis.—Sagittiferidae with long, narrow ciliated antrum, the wall of which does not contain sagittocysts. Seminal vesicle surrounded by tissue wall. Sagittocysts and symbionts are present. Does not reproduce asexually by fission.

Etymology.—*Antrosagittifera* (Latin, f.); prefix derived from the Latin *antrum.*

Type species.—*Antrosagittifera corallina,* new species

Antrosagittifera corallina, new species

Figs. 4–6

Holotype.—AMNH 1605, 2-µm-thick serial sagittal sections of epoxy-embedded specimen stained with toluidine blue, collected June 1999.

Type locality.—North Rock, Bermuda. Subtidal coarse coral sand.

Other material examined.—Living specimens in squeeze preparations; one

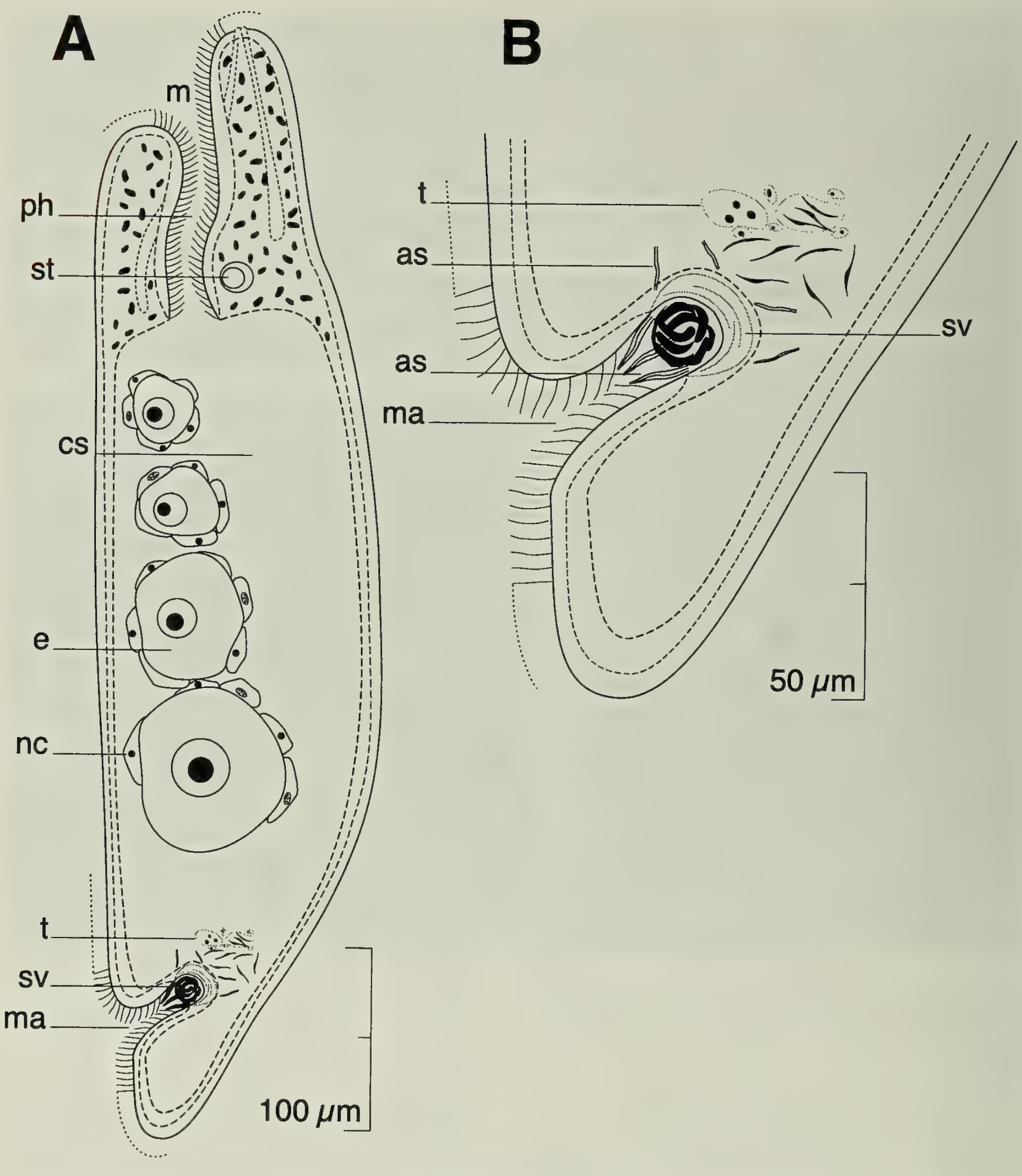

Fig. 7. *Proporus bermudensis,* new species. Sagittal reconstruction to show arrangement of organs. A, Whole animal; B, Male reproductive structures in posterior portion of animal. Abbreviations: as, accessory secretions; cs, central digestive syncytium; e, egg; m, mouth; ma, male antrum; nc, nurse cell; ph, pharynx; st, statocyst; sv, seminal vesicle; t, testes.

set of 2-μm-thick sagittal serial sections of epoxy-embedded specimens stained with toluidine blue; whole mounts for fluorescence imaging of musculature (12 specimens). Specimens collected from North Rock.

Description.—Adult specimens ca. 600 μm long and 200 μm wide (Figs. 4A, 6A). Anterior and posterior ends rounded, posterior less blunt. Greenish-brown color conferred by conspicuous zooxanthellae.

Epidermis completely ciliated. Rhabdoid

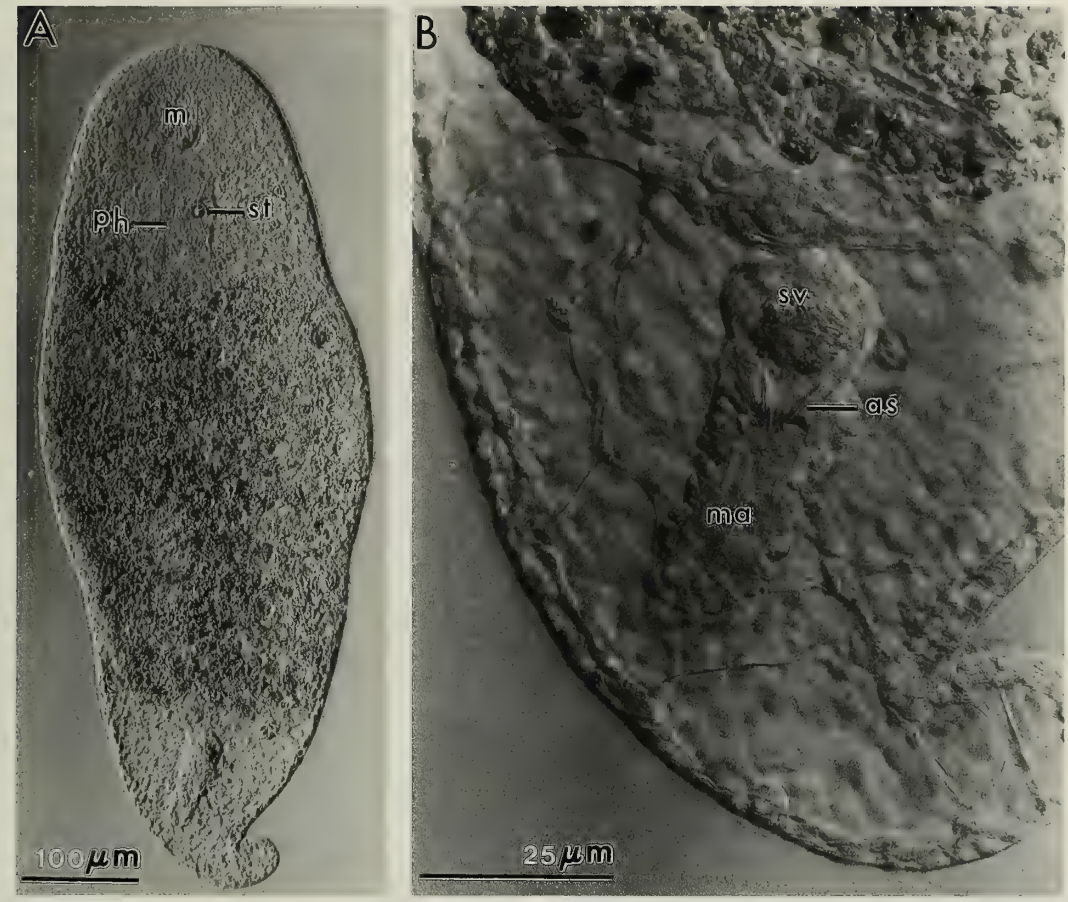

Fig. 8. *Proporus bermudensis,* new species. Photomicrographs. A, Whole-mount of living specimen, slightly flattened, ventral view. B, Male reproductive structures in posterior portion of living specimen. Abbreviations: as, accessory secretions; m, mouth; ma, male antrum; ph, pharynx; st, statocyst; sv, seminal vesicle.

glands (Fig. 4B) few and concentrated at the anterior end on the ventral side.

Musculature with circular fibers that encircle the body along entire length of animal; straight longitudinal muscles present between frontal organ and anterior edge of mouth; longitudinal muscles that have a longitudinal orientation anteriorly, but bend medially to cross diagonally over the body (longitudinal-cross-over fibers), present in both dorsal and ventral body wall; anterior with ventral diagonal muscles positioned between outer circular and inner longitudinal muscles.

Frontal organ weakly developed; frontal glands projecting to frontal pore through brain from position just posterior to statocyst.

Mouth opening at middle of body. Digestive central syncytium extends from brain, past reproductive organs, to posterior tip of body.

Germinal cells in paired strings behind statocyst (Fig. 4B); ovary ventral, testes dorsal. Mature sperm present posteriorly from level of largest egg. Mature sperm like a "string of beads" (Fig. 6C). Paired strings of developing eggs lead to a single large egg located slightly behind mouth.

Male genital pore subterminal at posterior end (Fig. 5). Male antrum long (ca. 40 μm long), with cluster of granules present

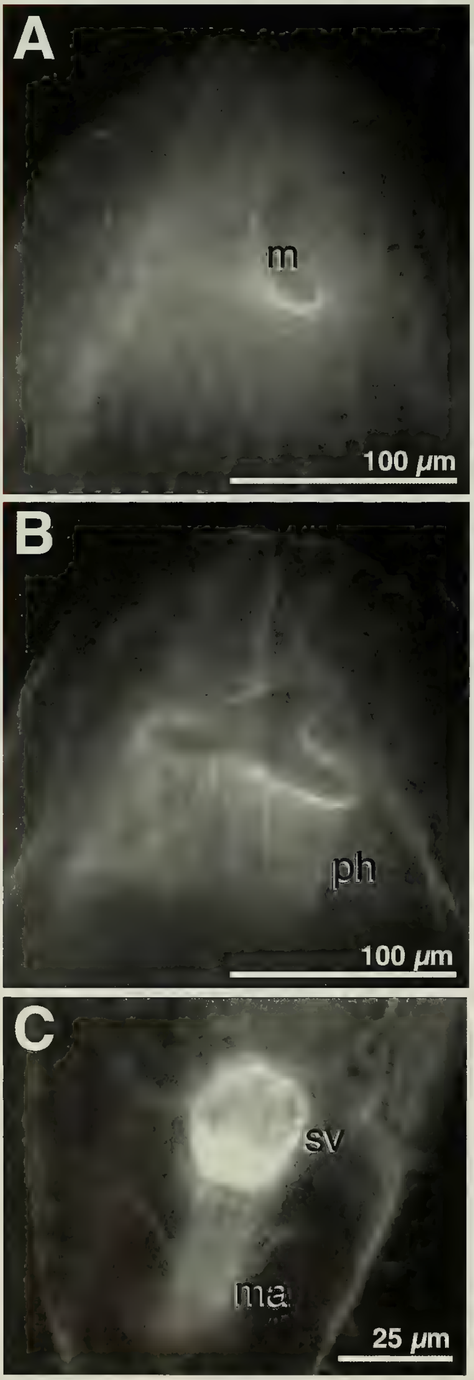

Fig. 9. *Proporus bermudensis,* new species. Whole mounts stained with Alexa-488-labeled phalloidin and viewed with epifluorescence microscopy. A, Ventral view of mouth pore. B, Inner-body musculature of anterior portion of animal, focus on pharynx. C, Inner-body musculature of posterior portion of animal, focus on male copulatory apparatus. Abbreviations: m, mouth; ma, male antrum; ph, pharynx; sv, seminal vesicle.

at its proximal end where it opens into a walled seminal vesicle.

Female pore absent. Weakly walled seminal bursa (Fig. 5), with a large (25 μm long) bursal nozzle (Figs. 5, 6B).

Sagittocysts (Figs. 4, 5) typically less than 20 μm long, scattered infrequently along lateral edges of the body and behind statocyst; largest concentration behind male copulatory organ.

Etymology.—The specific epithet is based on Latin *corallium,* referring to the coral-sand habitat in which this acoel was found.

Taxonomic remarks.—*Antrosagittifera corallina* is united with the genera *Sagittifera* Kostenko & Mamkaev, 1990, and *Symsagittifera* Kostenko & Mamkaev, 1990, in the subfamily Sagittiferinae by the presence of sagittocysts and the lack of fission as a means of reproduction. *Antrosagittifera corallina* has a long ciliated antrum that is unlike the weakly pronounced ciliated antrum of *Symsagittifera* and the complicated sagittocyst-bearing antrum of *Sagittifera.* This acoel has a walled seminal vesicle, a feature not found in the other two genera.

The sole occupant of the genus *Sagittifera, S. sagittifera* Ivanov, 1952, lacks symbionts but has a robust bursal nozzle similar to that of *Antrosagittifera corallina. Antrosagittifera corallina* lacks a female pore and vagina; although this condition is not uncommon among acoel taxa, it is possible that the pore and vagina are present in earlier developmental stages of *A. corallina* but are lost once the seminal bursa is filled with donor-sperm.

Family Proporidae Graff L v, 1882
Proporus bermudensis, new species
Figs. 7–9

Holotype.—AMNH 1606, 1.5-μm-thick serial frontal sections of epoxy-embedded specimen stained with toluidine blue, collected June 1999.

Type locality.—North Rock, Bermuda. Subtidal coarse coral sand.

Other material examined.—Living specimens in squeeze preparations; three sets of 2-μm-thick serial sections of epoxy-embedded specimens stained with toluidine blue (one sagittal, two oblique-sagittal); whole mounts for fluorescence imaging of musculature (seven specimens). Specimens collected from North Rock, Bermuda. Nomarski photographs of single specimen collected from Castle Roads, March 1985.

Description.—Adult specimens 430–800 μm long and ca. 150 μm wide (Figs. 7A, 8A). Anterior and posterior ends rounded; posterior much narrower. Body without distinct coloration. Ocelli absent.

Epidermis completely ciliated and of the same thickness throughout body. Without epidermal rhabdoid glands.

Musculature with circular fibers that encircle the body along entire length of animal; straight longitudinal muscles present in dorsal and ventral body wall; longitudinal muscles that have a longitudinal orientation anteriorly, but bend medially to cross diagonally over the body (longitudinal-cross-over fibers), present in ventral body wall; dorsal body wall with diagonal muscles interior to circular muscles.

Frontal organ weakly developed; frontal glands projecting to frontal pore from position slightly anterior to statocyst.

Mouth opening sub-terminal at anterior end of body (Figs. 7A, 8A, 9A). Long ciliated pharynx (Fig. 7A), a direct infolding of body wall, with longitudinal and circular muscle fibers (Fig. 9B). Digestive central syncytium extends posteriorly from mouth opening to position behind male copulatory apparatus.

Female and male reproductive structures contained within the digestive central syncytium (Fig. 7A).

Ovaries unpaired. Single string of eggs, each surrounded by nurse cells (Fig. 7A). Without female accessory organs.

Testes unpaired, follicular, restricted to small region immediately anterior to seminal vesicle. Sperm form a small false seminal vesicle immediately outside of the seminal vesicle. Male antrum ciliated (Figs. 7, 8B), a direct infolding of body wall including longitudinal and circular muscle fibers (Fig. 9C). Male antrum capped with a muscular seminal vesicle (Figs. 7, 8B, 9C) with unordered sperm. Rhabdoid-like accessory secretions (Figs. 7B, 8B) that surrounded the posterior portion of seminal vesicle sperm and extended into the male antrum. Additional rhabdoid secretions were present outside of the seminal vesicle in the region of the testes (Fig. 7B).

Taxonomic remarks.—As detailed in Dörjes (1971), Proporidae is composed of a single genus, *Proporus,* and four species. Our animal most resembles *P. venenosus,* which is composed of three subspecies, differing primarily in their body color. The morphology of the male antrum, seminal vesicle, and accessory secretions is very similar in *P. venenosus* and *P. bermudensis.* However, *P. venenosus* has distinct eyespots at the anterior end of its body, as well as paired testes and ovaries. Eyespots are absent in *P. bermudensis,* and its ovary and testis are unpaired.

Reassignment of *Pseudaphanostoma opisthorchis* (Mamkaev, 1967) to the genus *Haploposthia*

The male copulatory apparatus of *Pseudaphanostoma opisthorchis* (Mamkaev, 1967) bears a striking resemblance to that of *Haploposthia vandula* in the way the seminal vesicle is surrounded by gland necks. Although Mamkaev (1967) originally classified *P. opisthorchis* in the genus *Haploposthia,* Dörjes (1968) moved it to *Pseudaphanostoma,* an assignment that seems questionable given the fact that *P. opisthorchis* lacks the muscular seminal vesicle that is diagnostic of the genus *Pseudaphanostoma.* We therefore return this species to its original placement as *Haploposthia opisthorchis,* n. comb.

Acknowledgments

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Antarctodius rauscherti, a new species (Crustacea: Amphipoda: Ochlesidae) from the Antarctic Ocean

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Abstract.—The Antarctic amphipod crustacean *Antarctodius rauscherti*, new species, is described. This species can be distinguished from its hypothetical sister taxon, *Antarctodius antarcticus*, by its elongate peduncles of the antenna 1 and 2, pointed apical processes on peduncle articles 1 and 2 of antenna 1, the shortened and strongly flexed rostrum and the truncate apices of coxa 2 and 3, and the lack of a dorsal hump on pleonite 3.

During cruise 48 (ANT XV/3) of R/V Polarstern to the Weddell Sea in 1998, large numbers of crustaceans were collected by Dr. Martin Rauschert. In one of these samples was an interesting amphipod that had not appeared in previous benthic collections from this region. It proved to be new to science and is described in detail herein. It was placed in the genus *Antarctodius*, erected only recently by Berge et al. (1999). They provided a cladistic analysis of the Ochlesidae Stebbing, 1910 and Odiidae Coleman & Barnard, 1991a. They concluded the Odiidae was paraphyletic and placed this family within the Ochlesidae. In addition, they considered the genus *Antarctodius* to be plesiomorphic within the family.

Materials and Methods

The animals were fixed in 70% ethanol, transferred into glycerol for the study and drawn with a camera lucida on a Leica Wild M8 dissecting microscope. The holotype was dissected. Appendages and mouthparts were transferred onto slides and mounted in Euparal (Roth). Details were drawn under a Leica DMLB light microscope using a camera lucida.

The type material of the new species is deposited in the Museum für Naturkunde in Berlin.

Antarctodius Berge et al., 1999

Antarctodius rauscherti, new species

Figs. 1–5

Material examined.—Holotype ovigerous female, 5.7 mm; 2 paratypes, sex unknown, 3.9 and 4.7 mm; ZMB 27 309, Präp. No. 4607.

Type locality.—Polarstern station 48/115, 73°37.0′S 22°24.9′W, 6 Feb 1998, depth 756 m, dredge, 1 mm mesh size, donor M. Rauschert.

Description of holotype.—Cuticle relatively soft, pitted. Head slightly telescoped into pereonite 1; eyes apparently not present or if so pigments washed out in alcohol; rostrum strongly flexed and shortened, not surpassing half length of peduncular article 1 of antenna 1.

Pereonite 1 and 3 subequal in length (Fig. 1a); pereonite 2 shortest and pereonites 6 and 7 longest; pleonites subequal in length to pereonite 7. Pereon and pleon with keel, on pleon segment 3 shallow keel only anteriorly, posterior dorsal surface rounded. Epimera 1–3 posteroventral corner pointed, posterolateral margin lobate and rounded on pleonites 1 and 2, pointed on 3 (Fig. 1a). Posterodorsal hump on pleonite 3 absent. Urosomite 1 smooth, subequal in length to urosomites 2 and 3 combined; urosomite 2 shortest, dorsally round-

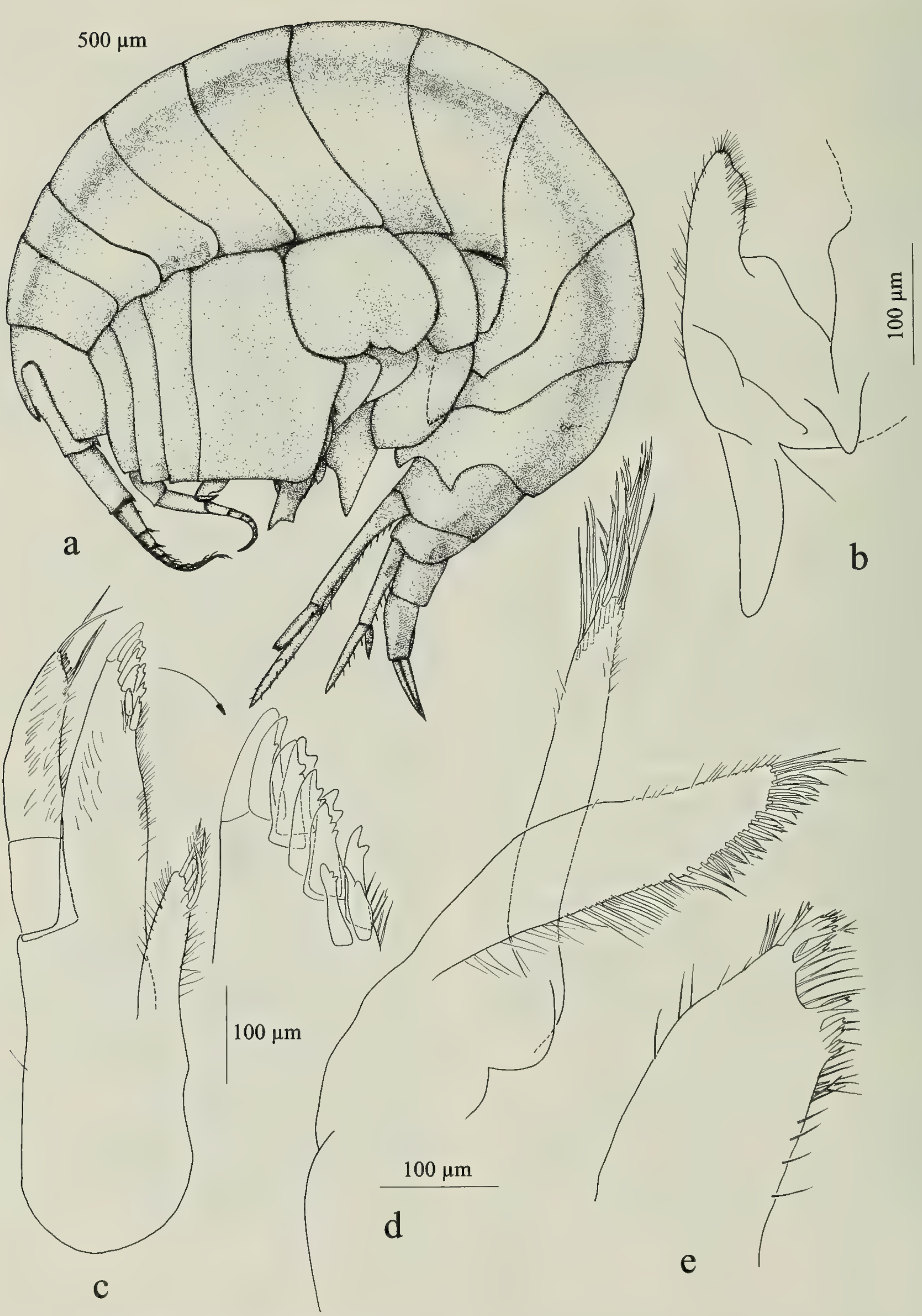

Fig. 1. *Antarctodius rauscherti,* new species, holotype ovigerous female, 5.7 mm. A, habitus, left side; b, lower lip, slightly damaged; c, maxilla 1; d, maxilla 2, plates twisted; e, apex of lower lip (hypopharynx).

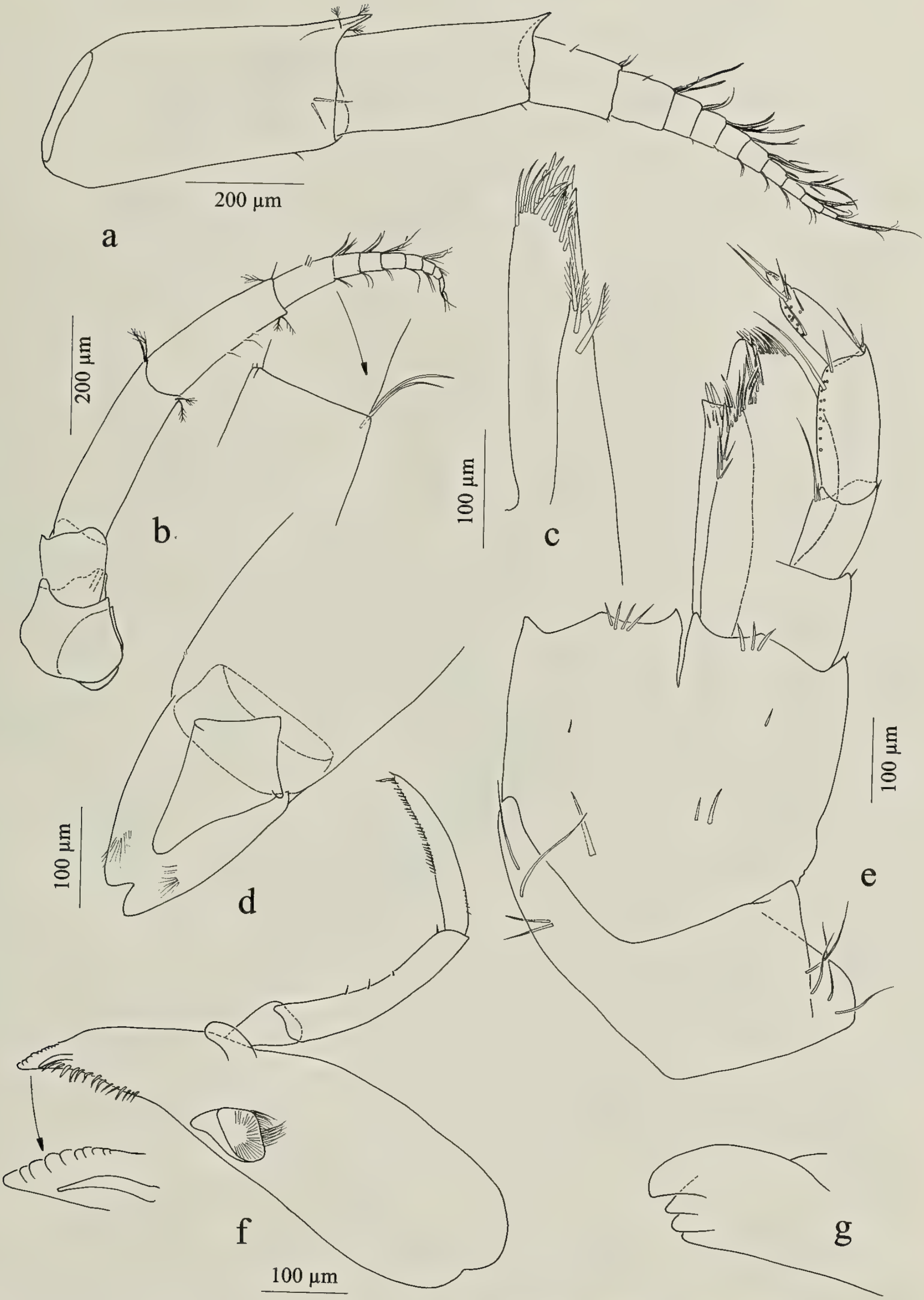

Fig. 2. *Antarctodius rauscherti,* new species, holotype ovigerous female, 5.7 mm. A, antenna 1; b, antenna 2; c, inner and outer plate of maxilliped; d, upper lip (labrum); e, maxillipeds, posterior aspect, right side plates and palp omitted; f, left mandible; g, right lacinia mobilis.

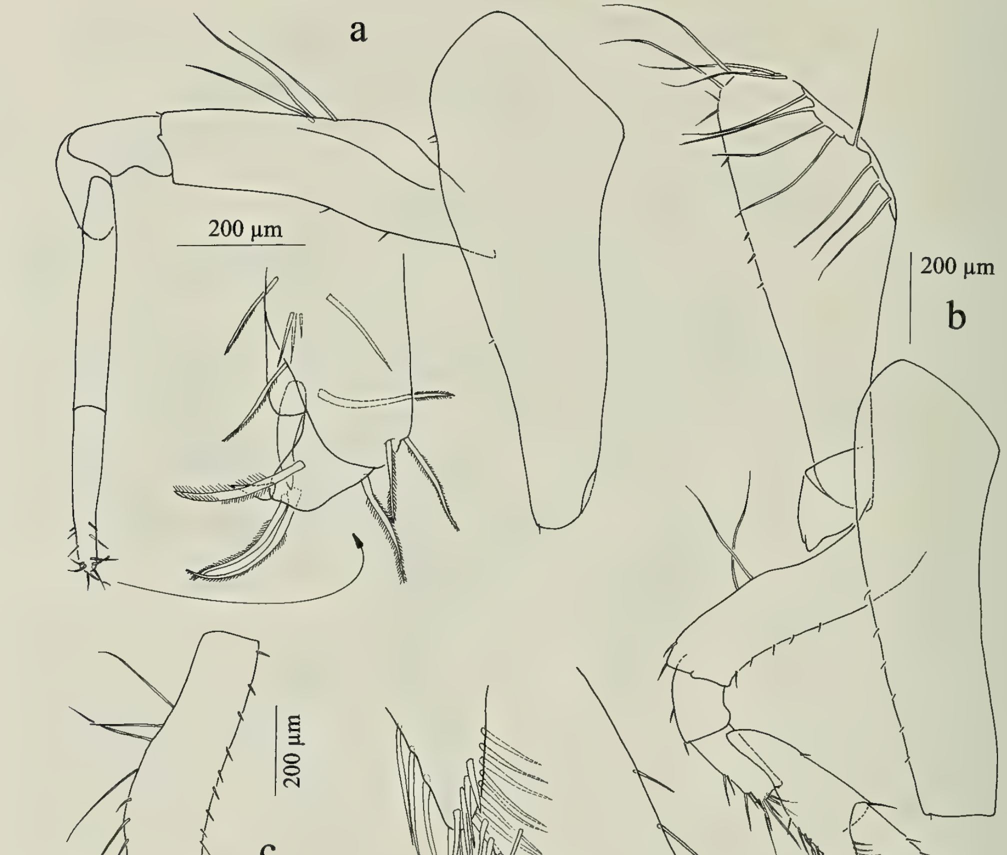

Fig. 3. *Antarctodius rauscherti*, new species, holotype ovigerous female, 5.7 mm. A, pereopod (gnathopod) 1, detail shows chela; b, pereopod (gnathopod) 2, detail shows chela; c, basis, ischium and merus of pereopod 3; d, coxa of pereopod 3; e, oostegite of pereopod 3.

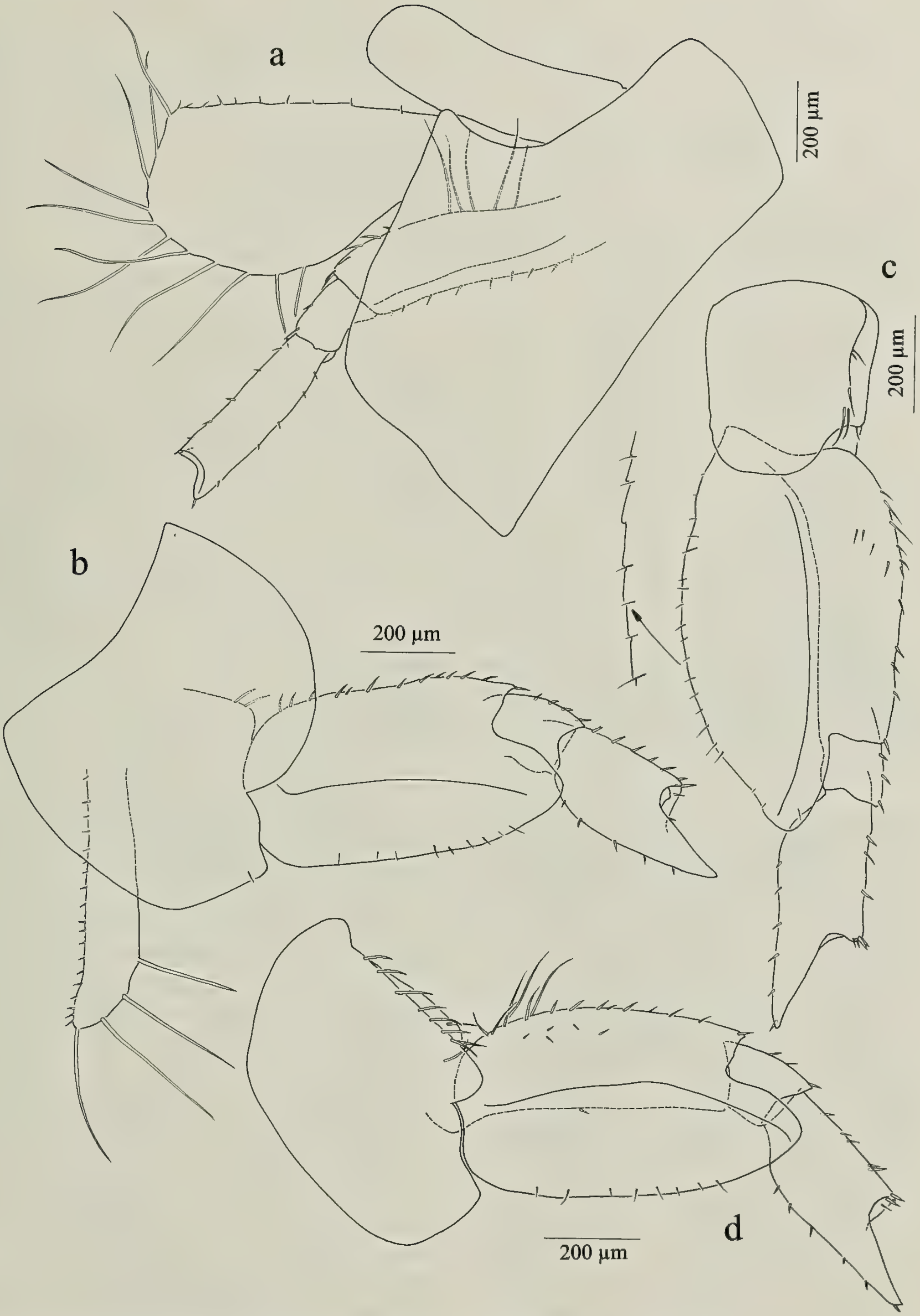

Fig. 4. *Antarctodius rauscherti,* new species, holotype ovigerous female, 5.7 mm, appendages, carpus, propodus and dactylus missing. a, pereopod 4; b, pereopod 5; c, pereopod 7; d, pereopod 6.

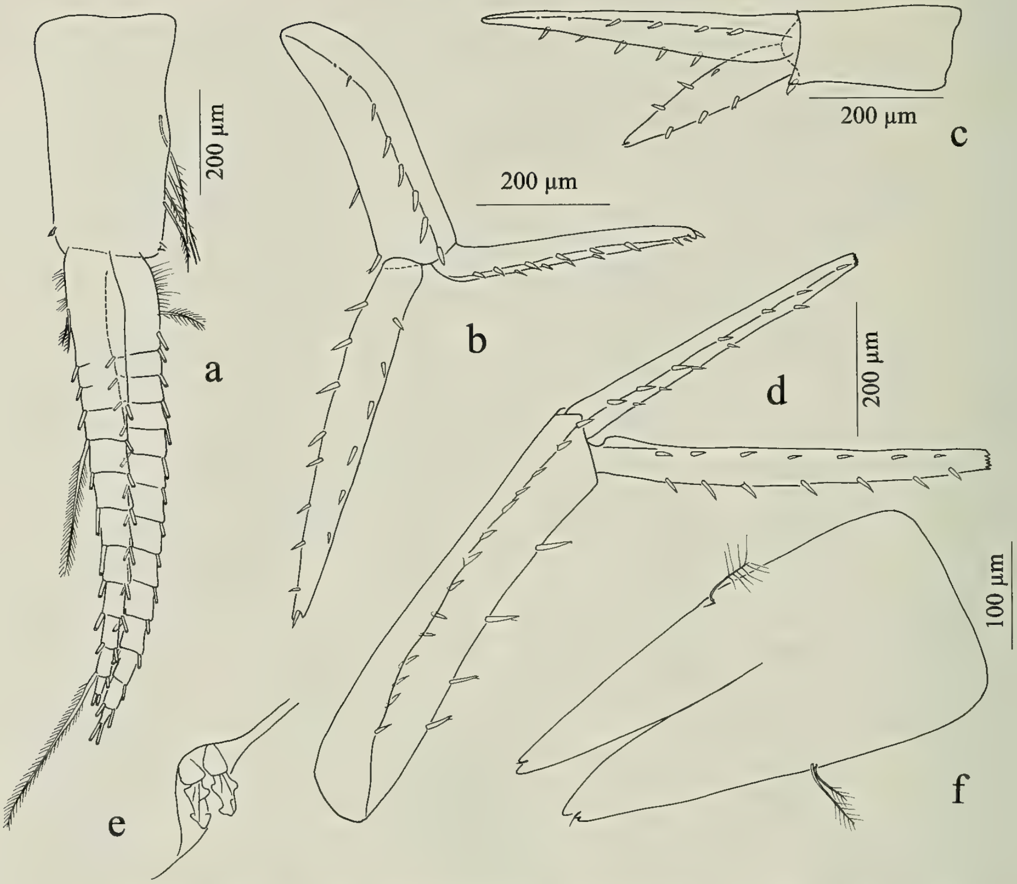

Fig. 5. *Antarctodius rauscherti*, new species, holotype ovigerous female, 5.7 mm. a, pleopod 1, setae partly omitted; b, uropod 2; c, uropod 3; d, uropod 1, apices of rami damaged; e, coupling hooks of pleopod; f, telson.

ed; urosomite 3 with laterodorsal ridge-like elevations.

Antenna 1 (Fig. 1a, 2a): peduncle article 1 slightly surpassing ventral margin of head, subequal to 2 and 3 combined, posteroventromedial angle acutely produced, article 3 with inconspicuous indication of point, flagellum 9-articulate, each equipped with long aesthetascs.

Antenna 2 (Fig. 2b): peduncle articles 1–3 about the length of article 4, article 5 subequal in length to article 4; flagellum 8-articulate.

Upper lip (labrum) (Fig. 2d) longer than wide, strongly tapering distally and clearly notched apically, apex of right side slightly shortened.

Mandible (Fig. 2f): mandibular body slender with pointed apex; incisor with denticles; lacinia mobilis on left side slender, spine-like, strongly developed and dentate on right side (Fig. 2g); spine row present; pars molaris produced; palp 3-articulate, inserted at molar level, article 3 with row of short setae and slightly longer apical setae.

Lower lip (hypopharynx) (Fig. 1b, e): lobes narrow, oblique apically and with shallow depression apicomedially and deep excavations medially; mandibular processes narrow, long and rounded.

Maxilla 1 (Fig. 1c): outer plate elongate, pointed, with oblique margin bearing stout serrate, spine-like setae on medial margin; palp 2-articulate, reaching to distal end of outer plate; inner plate short,

Table 1.—Comparison of *Antarctodius antarcticus* and *Antarctodius rauscherti,* new species.

Characters	*A. antarcticus,* female 5 mm	*A. rauscherti,* new species, holotype female 5.7 mm
Cuticle	strongly sclerotized, not transparent	soft and transparent
Rostrum	surpassing ventral margin of head, rather straight and stout	strongly shortened and flexed
Peduncle of antenna 1	bulky, article 3 not surpassing apex of coxa 1; stout with straight apical margins	elongate, article 2 surpassing apex of coxa 1; pointed postero-distomedial acute processes on articles 1–2
Peduncle article 4 of antenna 2	length 1.6 × breadth	length 3 × breadth
Peduncle article 5 of antenna 2	length 1.5 × breadth	length 3.5 × breadth
Apex of coxa 2 and 3	truncate with anterior and posterior angles rounded	truncate with anterior and poster angles angular
Coxa 5	strongly produced laterally	not strongly produced laterally
Pleonite 3	with dorsal hump posteriorly	smooth
Dorsal surface of urosomite 2	with lateral ridge-like elevations	smooth

extending beyond insertion of palp on outer plate, with 3 apical setae.

Maxilla 2 (Fig. 1d): outer plate tapering distally, about same length as inner plate, but wider, with long setae on oblique medioapical margin; inner plate with rounded apex and shorter setae apicomedially.

Maxilliped (Fig. 2c, e): basis and outer plate about subequal in length; inner plate narrow with distomedial angle produced; outer plate relatively wide, rounded apically, longer than distal margin of article 2 of palp; palp 4-articulate, somewhat longer than outer plate; article 1 short; article 2 subrectangular with long setae on medial margin; article 3 narrow, about half the width of article 2 with long slender setae medioapically.

Pereopod (gnathopod) 1 (Fig. 3a): coxa shorter than that of pereopod 2, tapering distally, anterior margin concave, posterior margin rather straight; basis expanded proximoposteriorly, with some long setae on posterior margin; ischium subequal in length to merus; carpus elongate; propodus 73% of carpus length; propodus process of chela substituted by stout spine, dactylus bulky, with spine apically (detail of Fig. 3a).

Pereopod (gnathopod) 2 (Fig. 3b): coxa concave anteromarginally, truncate apically; basis weakly sinuous in shape; ischium shortest; merus angular posterodistally; carpus lobe less than half the length of propodus; propodus weakly expanded distally, with serrate palm; dactylus stout with pointed process on inner margin (detail of Fig. 3b).

Pereopod 3 (Fig. 3c, d, e): coxa excavate anteromarginally, with truncate angular apex, subequal to that of pereopod 2; basis strongly expanded posteromarginally; ischium anteromarginally slightly excavate; merus anterodistally acutely prolonged; carpus, propodus and dactylus missing.

Pereopod 4 (Fig. 4a): coxa straight anteromarginally, slightly angularly produced anterodistally, ventral margin truncate, posteroventral angle rounded, posterior margin drawn out into a long pointed process; ischium with anteromarginal excavation; merus not much expanded, anterodistal angle drawn out a little subacutely, carpus, propodus and dactylus missing.

Pereopod 5 (Fig. 4b): coxa not strongly produced laterally, wider than long, posteriorly angular and subacute, anterior lobe rounded; basis both margins weakly convex, produced into rounded lobe posteroventrally; ischium pointed anterodistally;

merus expanded distally with long acute extension posterodistally; carpus to dactylus missing.

Pereopod 6 (Fig. 4d): coxa longer than wide, anteriorly oblique with row of setae, posteriorly rather rounded; basis longer than wide, both margins convex, posteroventral margin lobe-like; ischium pointed anterodistally; merus expanded distally with long lobe-like acute extension posterodistally; carpus to dactylus missing.

Pereopod 7 (Fig. 4c): coxa smallest; basis wide, posterior margin clearly convex, posteroventral margin lobe-like; ischium shortest, less than ⅓ of basis width; merus expanded distally with long lobe-like acute extension posterodistally; carpus, propodus and dactylus missing.

Pleopod 1 (Fig. 5a): as in the family; inner ramus slightly shortened; coupling hooks harpoon-like (Fig. 5e).

Uropod 1 (Fig. 5d): rami subequal in length, tips broken.

Uropod 2 (Fig. 5b): peduncle shorter than inner ramus; outer ramus shorter than inner, rami each with a terminal spine, both margins spinose.

Uropod 3 (Fig. 5c): peduncle short; outer ramus shorter than inner, both rami spinose.

Telson (Fig. 5f) elongate, longer than distal margin of peduncle of uropod 3, tapering distally, cleft 55% of length, with 2 pairs of long slender dorsal facial setae.

Etymology.—The species is dedicated to our dear colleague Dr. Martin Rauschert, who collected these animals.

Discussion.—The new species is similar to *Antarctodius antarcticus* (Watling & Holman, 1981), the only other ochlesid species from the high Antarctic. Only one other southern cold water species of the family Ochlesidae, *Curidea magellanica* Coleman & Barnard, 1991b, is known from the Magellanic region.

In the original description of *A. antarcticus* the palp of maxilla 1 is described as 1-articulate. In *A. rauscherti,* new species it has the same length, but without doubt is 2-articulate. The authors checked this character on *A. antarcticus* specimens from the collection of the Museum für Naturkunde Berlin and found out that also this species has a 2-articulate maxillulary palp.

Table 1 compares the two species of the genus *Antarctodius.*

Acknowledgements

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New species and records of pseudothelphusid crabs (Crustacea: Brachyura) from Central America in the Museum of Natural History of Tulane University

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Abstract.—Two new species of freshwater crabs are described. *Potamocarcinus vulcanensis,* new species, from El Salvador, resembles *P. zilchi* (Bott, 1956) in the sickle-shaped appearance of its first gonopods, but lacks the elongated and spinulous cephalic process of this species. *Ptychophallus osaensis,* new species, from Costa Rica, is characterized within the genus by the long geniculated apex and the small knob-like lobe of the lateral expansion of the first gonopods. *Phrygiopilus ibarrai* (Pretzmann, 1980) is redescribed and new records for six other species of Pseudothelphusidae are also given.

The somatic morphology of the Pseudothelphusidae offers few reliable characters for the discrimination of the different taxa. In most cases, it is only possible to establish generic and specific differences by the examination of the first male gonopods. Failure to recognize this fact made the systematics of these Neotropical freshwater crabs extremely complex (Schmitt 1969), until the standardization of the nomenclature for the description of this appendage by Smalley (1964a) who then subdivided the old genus *Pseudothelphusa* Saussure, 1857, into more rational taxonomic units (Rodríguez & Fitzpatrick 1996). Most of the material used to accomplish this task (Smalley 1964a) came from his field trips to Costa Rica, Guatemala, Nicaragua and Mexico.

After the decease of this distinguished carcinologist in 1994 (Rodríguez & Fitzpatrick 1996), the rich collection of freshwater crabs deposited by him at the Museum of Natural History of Tulane University was entrusted to the author for curation. Some of the species from Ecuador and Colombia in that collection have already been dealt with in publications by Rodríguez & von Sternberg (1998). The present contribution focusses on several species that were not recorded by Smalley in his Central American papers (Smalley 1964b, 1965, 1970), including two new species.

Abbreviations used are cl. for carapace length and cb. for carapace breadth. The materials recorded are deposited in the Museum of Natural History of Tulane University, New Orleans (TU). Smalley field numbers are abbreviated as AES.

Systematics

Family Pseudothelphusidae Rathbun, 1893

Genus *Potamocarcinus* H. Milne Edwards, 1853

Potamocarcinus aspoekorum (Pretzmann, 1968)

Material.—Belize: Oak Burn Creek, Mountains Pine Ridge, 20 Apr 1973, leg. Ding, 1 young male, cl. 10.4 mm, cb. 15.4 mm (TU 6314); Mollejon Creek, Mountains Pine Ridge, Cayo County, 7 Jul 1973, 1 juvenile male, cl. 9.3 mm, cb. 13.5 mm (TU 6329 ex Southern Illinois University Edwardsville Collections); Little Vaqueros Creek, Mountains Pine Ridge, 20 Apr 1973, 1 juvenile female, cl. 9.5 mm, cb. 14.5 mm (TU 6328).

Potamocarcinus magnus (Rathbun, 1896)

Material.—Costa Rica: Tabarcia, San José Province, 16 Feb 1960, leg. R. D. Suttkus & S. Jiménez-Canossa, 1 male juvenile, cl. 9.6 mm, cb. 13.8 mm (TU 4709); Rio Parrita, San José Province, 1 mile NW Tabarcia, tributary of Rio Candelaria, 17 Jul 1962, leg. A. E. Smalley & I. Smalley AES-298, 2 male juveniles, cl. 13.3 and 13.8 mm, cb. 18.9 and 19.6 mm (TU 4452); Rio Grande de Tárcoles, 3 miles E Atenas, small tributary on east bank of Tárcoles, 0.5 miles from Atenas-Alajuela highway, 7 Jul 1962, leg. A. E. Smalley & I. Smalley AES-282, 2 males, cl. 18.2 and 14.6 mm, cb. 27.2 and 21.3 mm, 1 female 21.9 mm, cb. 33.0 mm (TU 4437).

Potamocarcinus richmondi (Rathbun, 1893)

Material.—Costa Rica: 16.3 miles east of Turrialba, walking on road, 28 Jun 1973, leg. R. D. Suttkus & S. Jiménez-Canossa, 1 male, cl. 52.3 mm, cb. 78.7 mm (TU 98-101).

Potamocarcinus vulcanensis, new species

Fig. 1

Material.—El Salvador: Volcán Monte Cristo, 25 km N of Metapán, 2300 m alt., 10 May 1971, leg. S. Peck, 1 male holotype, cl. 12.8 mm, cb. 19.4 mm, 16 male paratypes, the 10 largest cl. 9.8–11.8 mm, cb. 15.2–17.8 mm, 4 ripe female paratypes, cl. 14.8–16.0 mm, cb. 22.8–24.8 mm, 15 immature females (TU 6273).

Type locality.—El Salvador: Volcán Monte Cristo, 25 km N of Metapan, 2300 m alt.

Diagnosis.—First gonopods with margin forming distally rounded subapical projection bent cephallically, with elongated basal swelling; caudal distal border cup-shaped, applied against cephalic apical border, leaving slit-like aperture between them; strong beak-like mesial process, with stout spine at base on cephalic surface.

Description of holotype.—Carapace 1.50 times as wide as long, surface smooth and polished; cervical grooves shallow, straight, forming wide depression on proximal half, not reaching margins of carapace; anterolateral margins between postorbital angle and level of cervical grooves straight, without postorbital notch, with about 10 depressed papillae; rest of border with flattened or squamiform, closely-set papillae (Fig. 1E). Postfrontal lobes absent, except for two shallow depressions on postfrontal area; middle groove faintly indicated. Surface of carapace between postfrontal lobes and front flat, slightly inclined forward and towards middle line. Upper margin of front in dorsal view slightly bilobed, rounded, ill defined, devoid of conspicuous papillae; lower margin strongly sinuous, advanced in front of upper margin; front low, of unequal height throughout.

Exognath of third maxilliped 0.86 length of ischium of endognath. Palm of largest cheliped (right) moderately swollen, with lower margins sinuous; fingers gaping (Fig. 1D).

First gonopods wide in latero-mesial direction, narrow in caudo-cephalic direction; margin forming distally rounded subapical process bent cephallically, with elongated basal swelling (Fig. 1A); strong beak-like mesial process, with stout spine at base on cephalic surface (Fig. 1B); caudal apical border cup-shaped, deflected cephallically and applied against cephalic apical border to enclose field of spines, leaving slit-like aperture between them (Fig. 1C).

Etymology.—The specific epithet *vulcanensis* alludes to the location of the species on the slopes of the Monte Cristo Volcano.

Remarks.—This species, together with *Potamocarcinus aspoekorum* (Pretzmann, 1968) and *P. zilchi* (Bott, 1956), forms a natural

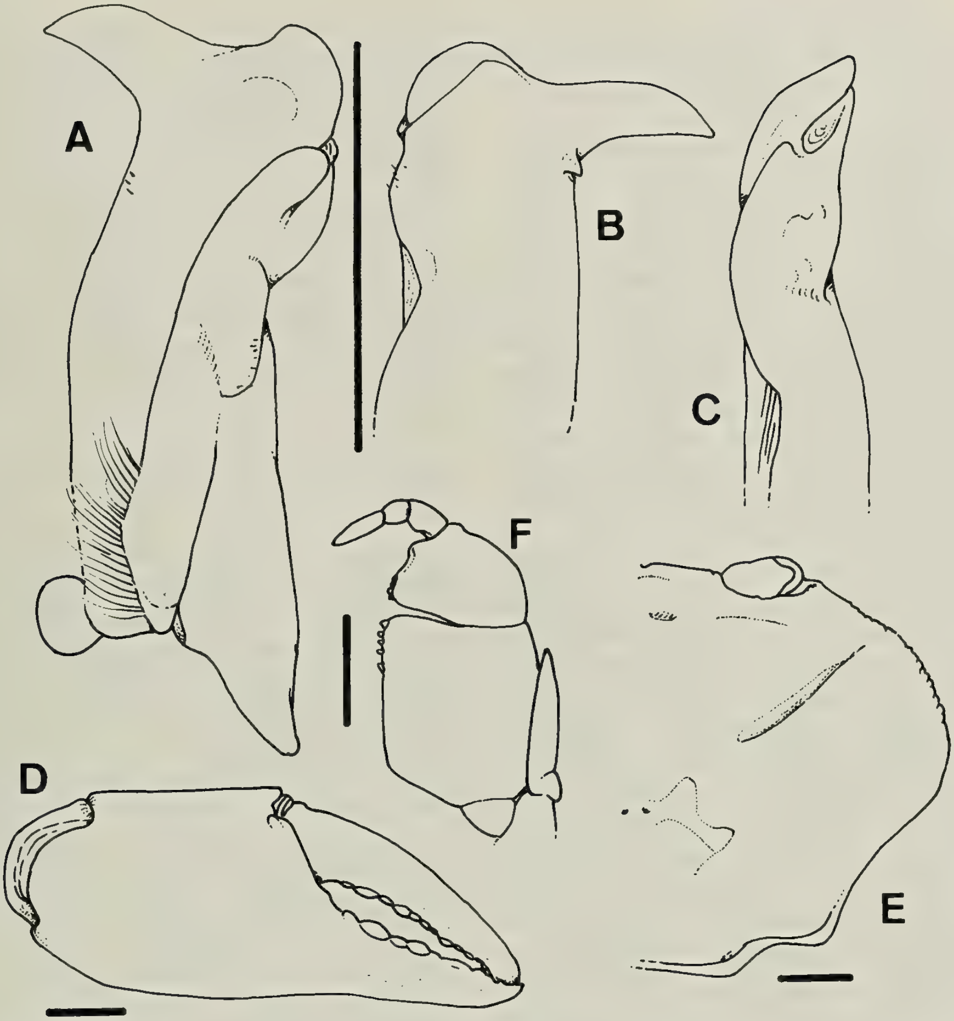

Fig. 1. *Potamocarcinus vulcanensis,* new species, holotype male from Volcán Monte Cristo, 25 km N of Metapán, Santa Ana Department, El Salvador (TU 6273): A–C, first left gonopod; A, caudal; B, apex, cephalic; C, apex, lateral; D, chela of largest cheliped, external view; E, dorsal view of right side of carapace; F, third maxilliped. Scale bars = 2 mm.

group within *Potamocarcinus,* characterized by a first gonopod with a marginal projection (Fig. 1A), a strong mesial process with a spine on the base on the cephalic surface (Fig. 1B), and a caudal apical border bent over the apex (Fig. 1C). Pretzmann (1968) grouped *P. aspeokorum* and *P. zilchi* in the subgenus *Zilchia* Pretzmann, 1968. However, Rodríguez (1982) did not recognize this subgenus because all the characters used to separate *Zilchia* are already present, although not fully developed, in other species of *Potamocarcinus. Potamocarcinus zilchi* closely resembles the new species in the sickle-shaped appearance of the first gonopods, but can be distinguished by a cephalic process that is strongly elongated and spinulous, covering the field of spines like a lid.

Phrygiopilus Smalley, 1970
Phrygiopilus ibarrai (Pretzmann, 1980)
Fig. 2

Material.—Guatemala: km 30 on road from José Pinula to Mataquesquintla, Guatemala Department, 10 Aug 1967, leg. A. E. Smalley, AES 406, 3 males, cl. 6.5–9.9 mm, cb. 9.6–14.8 mm, 1 female, cl. 8.9 mm, cb. 14.1 mm (TU 6208).

Diagnosis.—First gonopods wide in latero-mesial direction, flat in caudo-cephalic direction; margin curved strongly laterally, ending in rounded, hollow process; sperm channel opens on cephalic surface; caudal surface produced into very long and flat oval supra-apical process covered with spinules near edges; supra-apical process as long as, and broader than proximal part of gonopod; field of spines concealed between supra-apical process and cephalic border of gonopod; bifid process on mesial side at base of supra-apical process.

Redescription.—Carapace with surface smooth and polished, except for few granules on posterior branchial regions, near margins; cervical grooves shallow, slightly recurved, forming wide depressions proximally, not reaching margins of carapace; anterolateral margins lack postorbital notch, with few small dentiform papillae on distal half, rest of border without defined papillae (Fig. 2F). Postfrontal lobes only indicated by shallow anterior depressions; median groove absent, marked only by shallow depression on upper margin of front. Upper margin of front bilobed in dorsal view, well defined but devoid of conspicuous papillae; lower margin thin, moderately sinuous, advanced in front of upper margin; both frontal margins subparallel; front high, of equal height throughout.

Exognath of third maxilliped 0.85 length of ischium of endognath. Palm of largest cheliped (right) not swollen, with lower margin slightly sinuous, fingers gaping (Fig. 2G).

First gonopods wide in latero-mesial direction, flat in caudo-cephalic direction; margin curves strongly laterally, ends in rounded, hollow process (Fig. 2B, s); sperm channel opens on cephalic suface; caudal surface of gonopod produced into very long and flat oval supra-apical process covered with spinules near edges; supra-apical process as long as, and broader than proximal part of gonopod; field of spines concealed between supra-apical process and cephalic border of gonopod (Fig. 2C); bifid process on mesial side at base of supra-apical process.

Remarks.—The species was known only from the male holotype collected 14 km South of Guatemala City, near San José Pinula (Naturhistorische Museum, Vienna, N° 4065). Our specimens come from a locality about 15 km to the west of the type locality.

Phrygiopilus yoshibensis Alvarez & Villalobos, 1998

Material examined.—Mexico: Bacgularugum, stream near city of Simojovel (17°12′N, 92°38′W), District of Simojovel, State of Chiapas, drainage of Río Tlacotalpa, and ultimately, Río Grijalva, leg. R. Pineda-López, 25 May 1981, 1 male, cl. 14.1 mm, cb. 24.2 mm, 1 female, cl. 17.4 mm, cb. 29.0 mm, (TU 6286); 3 km N Tapilula on highway to Pichucalco (17°14′N, 93°00′W), leg. R. Pineda-López, 25 May 1981, 1 male, cb. 23.2 mm, posterior edge of carapace broken, 1 female, cl. 19.0 mm, cb. 25.2 mm (TU 6292).

Remarks.—The present records extend the range of the species 80 km to the west of the type locality.

Phrygiopilus montebelloensis Alvarez & Villalobos, 1998

Material examined.—Mexico: Laguna Tzizcao (16°09′N, 91°40′W), Lagos de Montebello, State of Chiapas, leg. R. Pineda-López, 22 May 1951, 1 male, cl. 13.5 mm, cb. 22.9 mm, 2 females, cl. 10.3 and 10.0 mm, cb. 16.2 and 15.7 mm (TU-6257).

Remarks.—These specimens come from a locality almost identical to the type locality, whose coordinates are given by Alvarez & Villalobos (1998) as 16°09′N, 91°39′W.

The species of *Phrygiopilus* occupy two disjunct areas in Central America: (1) Wa-

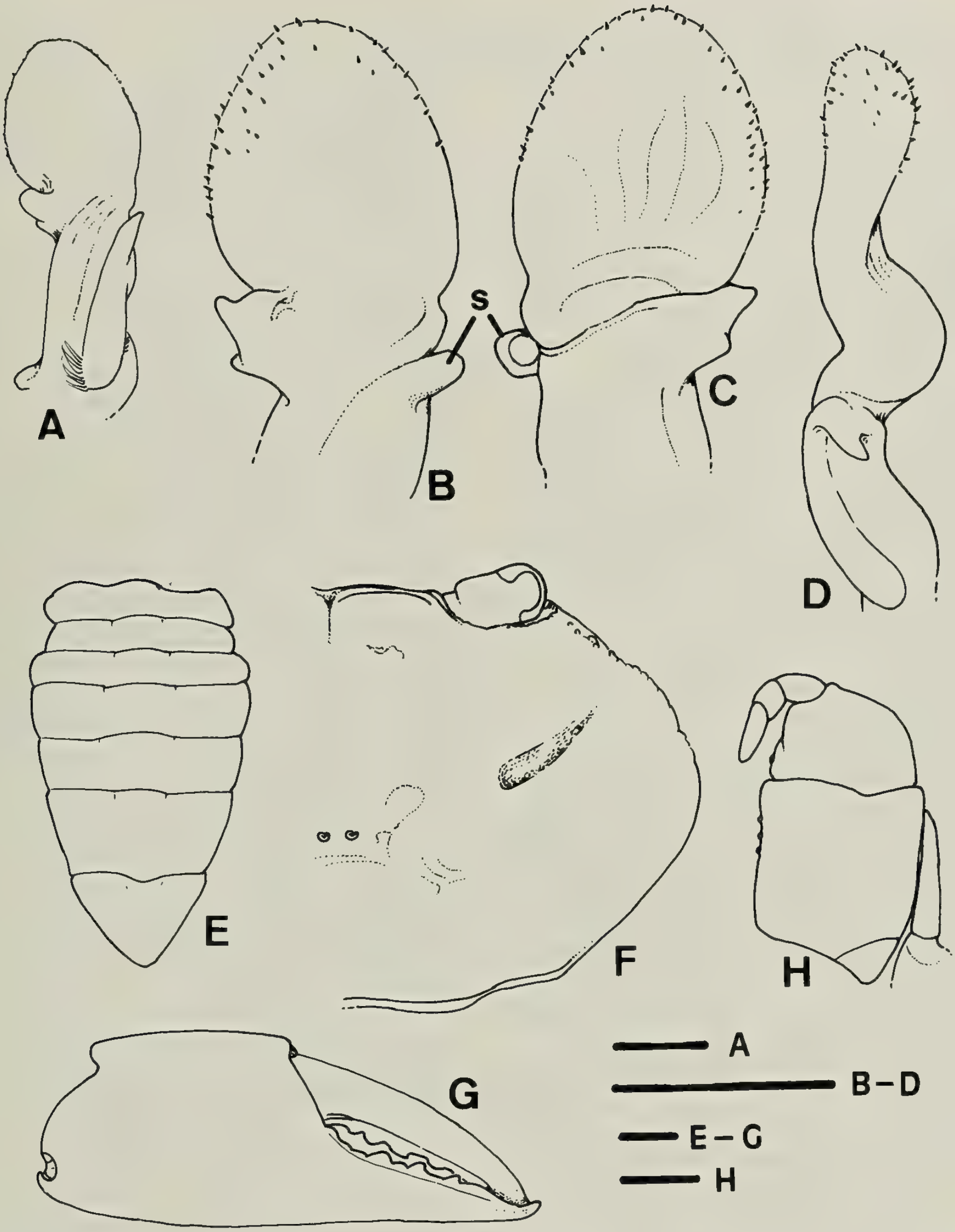

Fig. 2. *Phrygiopilus ibarrai* (Pretzmann, 1980), male from km 30 on road from José Pinula to Mataquesquintla, Guatemala Department, Guatemala (TU 6208): A–D, first left gonopod; A, caudal; B, apex, mesocaudal; C, apex, laterocephalic; D, apex, lateral; E, abdomen; F, dorsal view of right side of carapace; G, chela of largest cheliped, external view; H, third maxilliped; s, end of marginal process. Scale bars = 1 mm.

tercourses in Guatemala that drain into the Caribbean Sea (*Phrygiopilus chuacusensis* Smalley, 1970, *P. acanthophallus* Smalley, 1970, and *P. ibarrai*). *Phrygiopilus chuacusensis* is from a locality in karstic areas drained by the Motagua river, while the other two species are from the headwaters of the Polochic river. The type locality of *P. strengerae* (Pretzmann, 1965), stated to be "Trace Aguas, Caco", Guatemala, could not be located. According to Reddell (1981) the cave at Trece Aguas, Cacao, probably is in the karstic system Seamay-Sejul, where the holotype of *P. acanthophallus* was also collected (Smalley 1970). (2) Watercourses in the State of Chiapas, Mexico, flowing into the Gulf of Mexico (*Phrygiopilus yoshibensis* and *P. montebelloensis*). The first species is from the basin of the Grijalva river, the seond from the Usumacinta river.

The six species of *Phrygiopilus* can be distinguished by characters of the first male gonopods, as follows.

1. Lateral lobe present; supra-apical process implanted on a sinuous peduncle . . . . *P. strengerae*
–. Lateral lobe absent; supra-apical process sessile 2
2. Stout spines only on the supra-apical process 3
–. Stout spines not confined to supra-apical process 5
3. Mesial process bifid . . . . *P. ibarrai*
–. Mesial process conical 4
4. Supra-apical process rounded . . . . *P. acanthophallus*
–. Supra-apical process subtriangular . . . . *P. chuacusensis*
5. Lateral process without stout spines; supra-apical process off main axis of gonopod, giving L-shaped appearance to apex . . . . *P. montebelloensis*
–. Lateral process with stout spines; supra-apical process in line with main axis of gonopod . . . . *P. yoshibensis*

Genus *Ptychophallus* Smalley, 1964b

Ptychophallus osaensis, new species

Fig. 3

Material.—Costa Rica: Rincón de Osa, Puntarenas Province, 1971, 1 male holotype, cl. 28.5, cb. 47.9, 1 male paratype, cl. 19.9 mm, cb. 31.9 mm (TU 6271); Rincón de Osa, Puntarenas Province, Jul 1972, leg. R. Zeledón, 8 males, cl. 14.6–27.1 mm, cb. 22.6–43.7 mm, 1 mature female, cl. 32.4 mm, cb. 53.6 mm, 4 juvenile females, cl. 15.9–20.3 mm, cb. 24.5–32.4 mm (TU 6251).

Type locality.—Costa Rica: Rincón de Osa, Puntarenas Province.

Diagnosis.—First gonopods wide in caudal view, narrow in lateral view, strongly arched in caudo-cephalic direction, with lateral expansion divided into larger proximal rounded lobe, transversely directed toward caudal side, and distal knob-like lobe, transversely directed toward cephalic side and parallel to disto-caudal ridge in caudal view; disto-caudal ridge narrow, reaching level of median notch of lateral projection; apex of gonopods pedunculated, strongly bent toward latero-cephalic side, oval-oblong in distal view, lateral and mesial borders rounded and expanded, conspicuous notch on caudal border and semicircular thin ridge over spermatic channel; border of apical mesial process rounded, projected; mesial subapical process wide, rounded.

Description of holotype.—Carapace 1.70 times as wide as long, surface smooth, polished, except for scattered flat brown papillae over gastric and anterior branchial regions, near margins; cardiac and intestinal regions only faintly delimited by shallow, indistinct depressions; cervical grooves forming wide depression curving backwards, not reaching margins of carapace; anterolateral margins between external orbital angles and level of cervical grooves with shallow postorbital notch and faintly indicated papillae; rest of carapace margins with approximately 20 papilliform teeth, which are rounded at beginning of series and widely triangular posteriorly (Fig. 3F). Postfrontol lobes wide, transverse, delimited anteriorly by thin groove; median groove wide and deep, making V-shaped incision on upper margin of front. Surface of carapace between postfrontal lobes and front flat, slightly inclined forward and towards middle line. Upper margin of front in dorsal view slightly bilobed, divided into 2 halves by median notch, margin thin, well marked by small tubercles; lower margin of front thin, moderately sinuous, not conspicuously advanced in front of upper margin; both frontal margins subparallel.

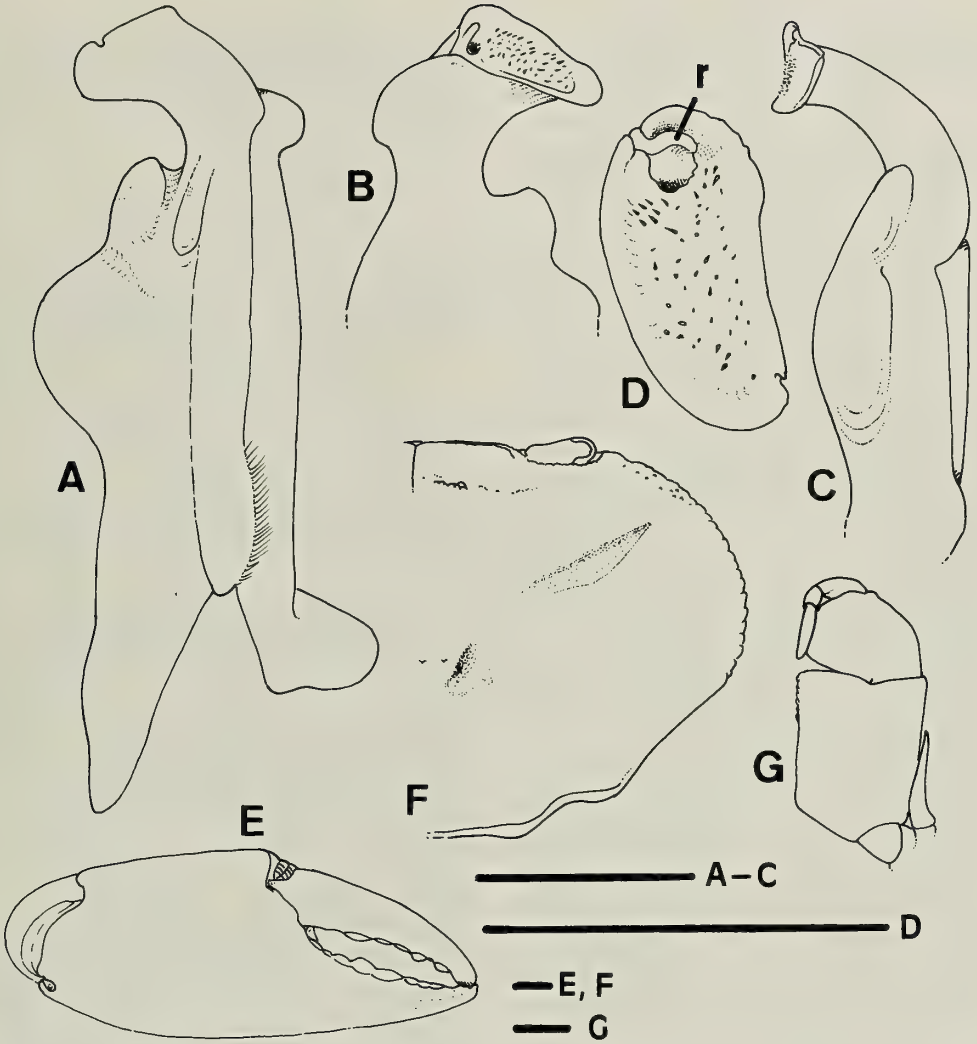

Fig. 3. *Ptychophallus osaensis,* new species, holotype male from Rincón de Osa, Puntarenas Department, Costa Rica (TU 6251): A–D, first right gonopod; A, caudal; B, apex, cephalic; C, apex, lateral; D, apex, distal; E, chela of largest cheliped, external view; F, dorsal view of right side of carapace; G, third maxilliped; r, ridge over spermatic channel. Scale bars = 2 mm.

Exognath of third maxilliped 0.66 length of ischium of endognath. Palm of largest cheliped (right) moderately swollen, upper margin convex, lower margin slightly sinuous, fingers gaping, rows of small black-brown points on external surface, teeth completely eroded (Fig. 3E).

First gonopods wide in caudal view, narrow in lateral view, strongly arched in caudo-cephalic direction. Lateral projection large (Fig. 3A), divided in 2 lobes by shallow median notch; proximal lobe larger, rounded, transversely directed toward caudal side; distal lobe knob-like, transversely directed toward cephalic side, parallel to disto-caudal ridge in caudal view. Disto-caudal ridge narrow, reaching level of median notch of lateral projection (Fig. 3A). Subapical mesial process wide, rounded (Fig. 3B). Apex of gonopods pedunculated, strongly bent toward latero-cephalic side (Fig. 3C), applied against sternites when abdomen closed; border of apical mesial process rounded, projected; profile of apex oval-oblong in distal view, lateral, mesial borders rounded and expanded, lacking conspicuous notch on caudal border; semicircular thin ridge over spermatic channel (Fig. 3D, r) lacking flat papilla.

Etymology.—The species is named for the Osa Peninsula, Costa Rica, where the species was first collected.

Remarks.—Ptychophallus osaensis can be distinguished from all other species in the genus by the first gonopods which have a small knob-like lobe on the lateral expansion (Fig. 3A), a distinctly-shaped mesial subapical process (Fig. 3B) and a long geniculated apex (Fig. 3C). *Ptychophallus osaensis* and *P. tristani* (Rathbun, 1896) are the only species of this genus with a wide mesial subapical process of gonopods; in *P. osaensis* this process is regularly rounded, whereas in *P. tristani* the process is hatchet-shaped (Smalley 1964b).

Rodríguez & Hedström (2000) have shown that the first gonopods of *Ptychophallus* shows a progressive transformation of the apex, leading to the formation of an apical receptacle, possibly for the retention of spermatophora during copulation. The present new species belongs to the most primitive group of *Ptychophallus* (together with *P. colombianus* (Rathbun, 1893), *P. tristani* and *P. kuna* Campos & Lemaitre, 1999) characterized by a first gonopod with a wide lateral expansion and a pedunculated apex. This group also includes the male specimen recorded by Smalley (1964b) as *P. exilipes* (Rathbun, 1898). The type specimen of *P. exilipes* described by Rathbun was collected at El Coronel, on the Atlantic slope of Costa Rica, and is a female, so its status is uncertain. The specimen described by Smalley (1964b) from Costa Rica was collected at a locality on the Pacific slope, 50 miles south from the type locality, and most probably is not conspecific with Rathbun's (1898) species. The five species of *Ptychophallus* discussed here can be can be distinguished from each other by characters of the first male gonopods, as follows.

1. Lateral expansion undivided 2
–. Lateral expansion divided into two unequal segments 3
2. Mesial sub apical process digitiform . . . . *P. exilipes* (sensu Smalley 1964b)
–. Mesial subapical process triangular . . . . *P. colombianus*
3. Proximal lobe of lateral expansion smaller than distal one. Mesial subapical process wide, hatchet-shaped . . . . . *P. tristani*
–. Proximal lobe of lateral expansion conspicuously larger than distal one 5
5. Mesial subapical process rounded . . . . *P. osaensis*
–. Mesial subapical process flange like . . . . *P. kuna*

Raddaus Pretzmann, 1965

Raddaus bocourti (A. Milne Edwards, 1866)

Material.—Guatemala: Lago de Atitlán, 4 miles E of Panajachel, Solola Department, 6 Aug 1967, leg. A. E. Smalley & I. Smalley AES 313, 3 immature males, 13.6–18.7 mm, cb. 20.5–27.0 mm, 2 females cl. 13.0–33.1 mm, cb. 19.0–53.4 mm (TU 4461); Rio Piscaya, 2 km N junction National RT5–RT4, small tributary of Rio Piscaya, at 40 km N from Guatemala, Guatemala Department, 12 Aug 1967, leg. A. E. Smalley AES 408, 1 immature male, cl. 15.8, cb. 23.3 mm, 3 immature females, cl. 16.5–27.5 mm, cb. 25.0–44.0 mm (TU 5801); km 56 from Guatemala city on route 5 to Salamá, small tributary of Rio Grande, Department Guatemala, 16 Aug 1967, leg. A. E. Smalley AES 413, 2 immature males, 18.6 and 18.8 mm, cb. 27.7 and 29.8 mm (TU 5799); km 71 from Guatemala City, route 5 toward Salamá, small tributary of Rio Grande, Guatemala Department, 16 Aug 1967, leg. A. E. Smalley AES 412, 2 immature males, cl. 11.0 and 12.5 mm, cb. 16.2 mm and 18.0 mm, 3 juvenile females, cl. 8.0–10.8 mm, cb. 12.0–15.9 mm (TU 5802).

Belize: Dry Colombia River at Colombia

Forest Camp, Rio Grande drainage, 7 Jul 1971, leg. Greenfield, 1 male cl. 45.2, cb. 75.9 mm, 1 female with young under the abdomen, cl. 49.2 mm, cb. 81.2 mm (TU 6385).

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Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with descriptions of new genera and species. Part VI. *Pylopagurus* A. Milne-Edwards & Bouvier, 1891, *Haigia* McLaughlin, 1981, and *Pylopaguridium*, a new genus

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Abstract.—In this final part of a six-part series, two new species of *Pylopagurus* A. Milne-Edwards & Bouvier are described, *P. macgeorgei* and *P. gorei,* and one existing species, *P. longicarpus* Walton, is placed in synonymy with *P. holmesi* Schmitt. Some species of *Pylopagurus* have been found to exhibit weak development of a male sexual tube, thus requiring emendation of the generic diagnosis. A new monotypic genus, *Pylopaguridium,* is proposed for a new species, *P. markhami,* in which males have asymmetrical coxae of the fifth pereopods. The monotypic Pacific genus *Haigia* McLaughlin, is reviewed. An amended key to all the genera of the "*Pylopagurus-Tomopagurus*" group, and a key to the species now assigned to *Pylopagurus* are included. All species of *Pylopagurus, Pylopaguridium,* and *Haigia* are diagnosed or described and illustrated, and their morphological variations discussed.

As pointed out by McLaughlin (1981a), the principal characters uniting the genera *Pylopagurus* A. Milne-Edwards & Bouvier, 1891 and *Tomopagurus* A. Milne-Edwards & Bouvier, 1893, presumably were the presence of 11 pairs of biserial gills (cf. McLaughlin & de Saint Laurent 1998), the occurrence of paired first female pleopods modified as gonopods, and the absence of secondary sexual modifications in males. In her initial revision of the "*Pylopagurus-Tomopagurus*" group, McLaughlin (1981a) subdivided *Pylopagurus* sensu lato into 11 genera, and redefined *Tomopagurus* to include species in which female gonopods might not develop. Subsequently, Lemaitre & McLaughlin (1996) described and added another genus, *Protoniopagurus* Lemaitre & McLaughlin, 1996, to the group. In this concluding study of *Pylopagurus* sensu stricto, we have found it necessary to adjust our concept of the genus again as the result of the observations of slight sexual tube development in some species and in related "*Pylopagurus-Tomopagurus*" group genera. It would appear that these genera bridge phylogenetic gaps between those genera with highly specialized male secondary sexual adaptations, other genera in which females develop modified paired first pleopods, and those more simplistic genera such as the heterogeneous genus *Pagurus* Fabricius, 1775.

Specimens included in part VI have come from the Allan Hancock Foundation, University of Southern California, now part of the collections of the Natural History Museum of Los Angeles County (LACM CR); Dauphin Island Sea Lab, University of Alabama (DISL); Florida Department of Natural Resources, St. Petersburg (DNR); Florida International University, Miami (FIU); Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá (ICN-MHN-CR); Instituto de Investigaciones Marinas y Costeras de Punta de Betín, Santa Marta (INVEMAR-CRU); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Muséum national d'Histoire naturelle, Paris (MNHN); Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden (RMNH); National Marine Fisheries Service (NMFS); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Rosenstiel School of Marine and Atmospheric Science, University of Miami (UMML, RSMAS); Swedish Museum of Natural History, Stockholm (SMNH); Texas A & M University (TAM); The Natural History Museum [formerly British Museum (Natural History)], London (NHM); and the senior author's personal collection (PMcL). Specimens have been returned to and/or deposited in these institutions.

In the "Material examined" sections, the specimens are listed from north to south. The station abbreviation D, refers to SCUBA dive stations, NR, to stations of the Bellairs Research Institute, Barbados. The following abbreviations used refer to vessels utilized by various institutions or expeditions: A, United States Fish Commission Steamer *Albatross;* AN, B/I *Ancón* (INVEMAR); BA, U.S. Coast and Geodetic Survey Steamer *Bache*; B, M/V *Bellows* (FIU); BK, U.S. Coast Survey Steamer *Blake*; DE, R/V *Delaware,* U.S. National Oceanic and Atmospheric Administartion; DO, R/V *Dolphin,* South Carolina Wildlife and Marine Resources Center; E, M/V *Explorer* (NMFS); EW, R/V *Eastward,* (VIMS); FH, United States Fish Commission Steamer *Fish Hawk;* G, R/V *Gerda* (RSMAS); JSL, research submersible *Johnson Sea Link I* (Harbor Branch Oceanographic Foundation, Fort Pierce, Florida); JSDSE, Johnson-Smithsonian Deep Sea Expedition; M, R/V *Megalopa;* O, M/V *Oregon* (NMFS); P, R/V *John Elliott Pillsbury* (RSMAS); PE, R/V *Pelican* (U.S. Fish and Wildlife Service); SB, M/V *Silver Bay* (RSMAS); SUIBE, State University of Iowa Bahamas Expedition; T, M/V *Tursiops* (NMFS). A single measurement, shield length (sl), measured in millimeters (mm) from the tip of the rostrum to the midpoint of the posterior margin of the shield provides an indication of animal size. Other abbreviations used are: juv, juvenile(s); ovig, ovigerous; sta, station.

Pylopagurus A. Milne-Edwards & Bouvier, 1891

Pylopagurus A. Milne-Edwards & Bouvier, 1891:103; 1893:74 (in part).—Faxon, 1895:61 (in part).—Alcock, 1905:189 (in part).—Schmitt, 1921:143 (in part).—Barnard, 1950:453.—Walton, 1954:140 (in part).—Forest & de Saint Laurent, 1968:145 (in part).—Scanland & Hopkins, 1969:257.—Miyake, 1978:119 (in part); 1982:227 (in part); 1991:227 (in part).—McLaughlin, 1981a:2 (in part).

Type species.—*Eupagurus discoidalis* A. Milne-Edwards, 1880, by designation by Miyake (1978). Gender: masculine.

Amended diagnosis.—Eleven pairs of biserial gills. Lateral projections widely separated from acute rostrum. Ocular acicles triangular, often acutely so, with small to moderately strong submarginal spine; usually separated basally by more than basal width of 1 acicle. Maxillule (Fig. 1a) with external lobe of endopod obsolete to moderately well developed, never recurved, internal lobe with 1 terminal bristle. Maxilla (Fig. 1b) with proximal lobe of scaphognathite moderately narrow to moderately broad. First maxilliped (Fig. 1c) with slender exopod. Third maxilliped with well developed crista dentata and prominent accessory tooth; merus frequently with spine at dorsodistal margin, carpus unarmed. Sternite of third maxillipeds unarmed or with 1 or 2 small spines on either side of midline.

Right cheliped markedly larger than left; chela subcircular to subrectangular, oper-

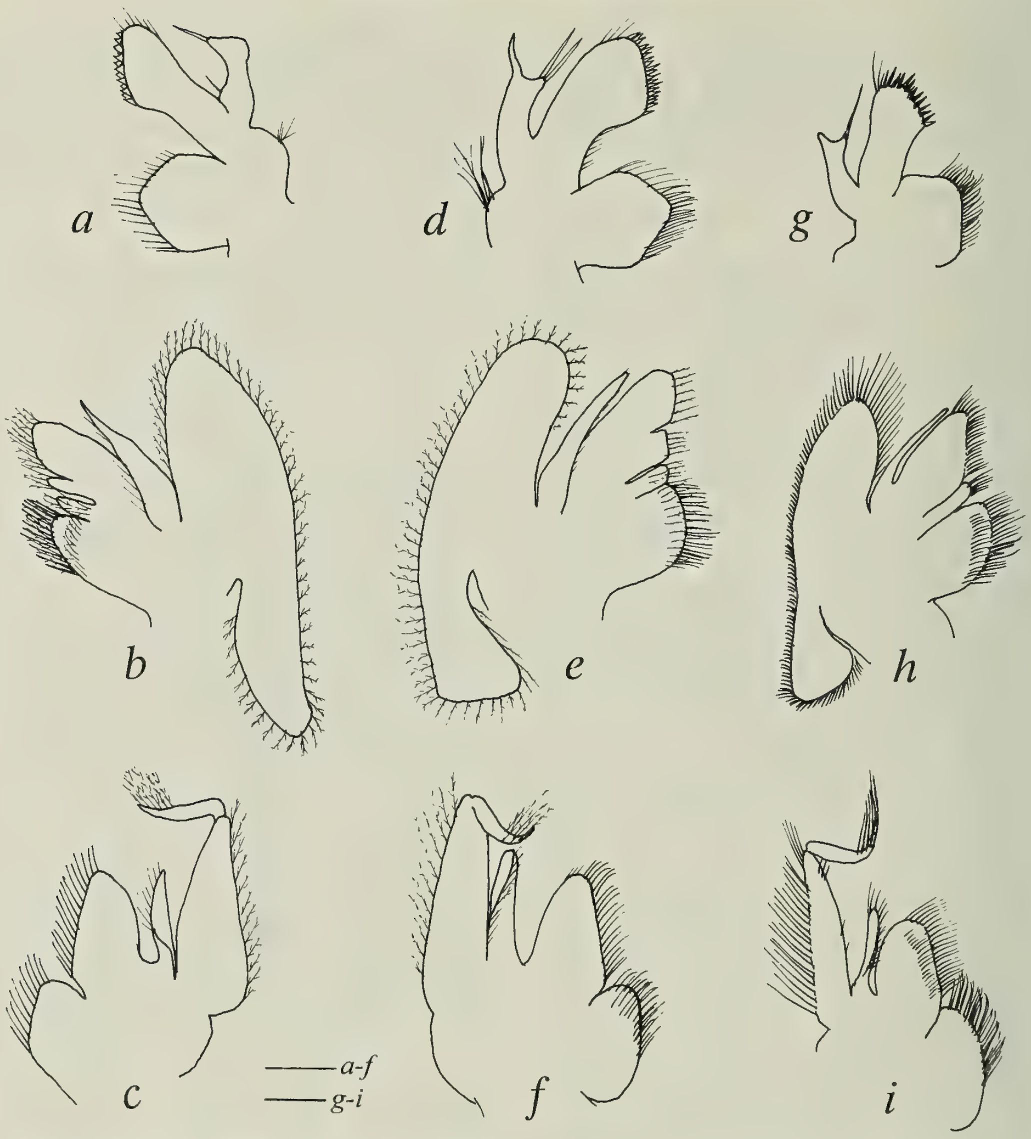

Fig. 1. Mouthparts, internal view. a–c, *Pylopagurus discoidalis* (A. Milne-Edwards, 1880), right, ♀ (sl = 4.2 mm), sta P-890, off Lesser Antilles, UMML 32:4756; d–f, *Haigia diegensis* (Scanland & Hopkins, 1969), left, ovig ♀ (sl = 5.2 mm), Los Angeles Harbor, PMcL; g–i, *Pylopaguridium markhami,* new species, left, paratype ♂ (sl = 2.0 mm), sta D68, Turks and Caicos Islands, USNM 306896. a, d, g, maxillule; b, e, h, maxilla; c, f, i, first maxilliped. Scales equal 0.5 mm (a–f), and 0.2 mm (g–i).

culate; angle of articulation of chela and carpus generally perpendicular. Left cheliped with chela small; dactyl and fixed finger dorsoventrally compressed; palm flattened, slightly concave or slightly convex; angle of articulation of chela and carpus perpendicular or only slightly twisted. Ambulatory legs with or without dorsodistal carpal spine. Fourth pereopods with well developed dactyls, elongate claw and usually small to very prominent preungual process; propodal rasp consisting of single row of corneous scales.

Sternite of third pereopods with narrow, subovate, subquadrate, or subsemicircular anterior lobe. Sternites of pereopods 4 and

5, and less frequently also third, often with capsulate setae. Males with coxae of fifth pereopods symmetrical; usually without, but occasionally with, vas deferens protruded from one or both coxal gonopores to form very short to moderately short sexual tube(s); 3 unpaired unequally biramous left pleopods (3–5). Females with paired gonopores on coxae of third pereopods; paired first pleopods (Figs. 2g, 4g) incompletely 2-segmented and modified as gonopods, and 4 unpaired biramous left pleopods, second through fourth with both rami well developed, fifth with endopod reduced or rudimentary.

Abdomen straight or rarely flexed. Uropods symmetrical or nearly so. Telson with lateral indentations suggesting division into anterior and posterior portions; posterior lobes symmetrical or only slightly asymmetrical, terminal margins concave or oblique, armed with 2 to several small to moderately large spines; posterolateral margins usually with distinct corneous or calcareous plate.

Distribution.—Western Atlantic from southeastern United States (North Carolina) to central Brazil; Caribbean and Gulf of Mexico; eastern Pacific from southern California to Baja California and the northern Gulf of California, Mexico.

Remarks.—McLaughlin (1981a) subdivided the genus *Pylopagurus* sensu lato into several genera primarily distinguished from other genera of the family by gill number and structure, and the presence of paired female gonopods. In other genera included in this "*Pylopagurus-Tomopagurus*" group, the development of any form of secondary male sexual characters had not been recognized. Thus, we were understandably surprised to notice that in one new species of the genus, males had clearly developed, albeit short, right sexual tubes. While at first we were tempted to consider this protrusion of the vas deferens as merely an artifact of preservation, the observed sexual tube was as well developed as that reported for some species of *Parapagurodes* McLaughlin & Haig, 1973 (cf. McLaughlin & Jensen 1996). The potential for development of a male sexual tube in the "*Pylopagurus-Tomopagurus*" group was unquestionably established when males of additional species of *Pylopagurus* were also found to exhibit such development. Close reexamination of the other genera and species will be necessary to determine the extent to which sexual tube development has progressed in the group.

McLaughlin (1981a) restricted *Pylopagurus* to species typified by *P. discoidalis* (A. Milne-Edwards, 1880), and additionally assigned *P. holmesi* (Schmitt, 1921), *P. longicarpus* Walton, 1954, *P. stewarti* (Filhol, 1883), and *P. serpulophilus* Miyake, 1978, to this genus. During the course of this extended study, McLaughlin & Gunn (1992) determined that both *P. stewarti* and *P. serpulophilus* correctly should have been assigned to *Australeremus* McLaughlin, 1981a. McLaughlin & Gunn (1992) also synonymized Miyake's (1978) taxon with *A. triserratus* (Ortmann, 1892). More recently, *Australeremus* has been reduced to subgeneric rank within the genus *Lophopagurus* McLaughlin, 1981a (de Saint Laurent & McLaughlin 2000). In the present study we have concluded that *P. longicarpus* is synonymous with *P. holmesi.*

Pylopagurus pattiae Lemaitre & Campos, 1993
Figs. 2, 3

Pylopagurus pattiae Lemaitre & Campos, 1993:554, figs. 1, 2 (type locality: Bahía de Chengue, Colombia).

Holotype.—♂ (sl = 2.0 mm), Bahía de Chengue, Parque Nacional Natural Tayrona, north of Santa Marta, Colombia, 20–40 m, 3 Dec 1988, coll. N. H. Campos, USNM 259412.

Paratypes.—Parque Nacional Natural Tayrona, north of Santa Marta, Colombia: 2 ♂ (sl = 1.7, 1.8 mm), Bahía de Chengue, 20–40 m, 3 Dec 1988, coll. N. H. Campos, USNM 251896.—2 ♂ (sl = 1.4, 1.7 mm), 2 ovig ♀ (sl = 1.7, 1.8 mm), Bahía de Cinto, 20–40 m, 30 Nov 1989, coll. N. H. Campos, USNM 251897.—16 ♂ (sl = 1.1–2.1 mm), 4 ♀ (sl = 1.5–1.9 mm), 10 ovig ♀ (sl = 1.6–1.9 mm), Bahía de Concha, 20–40 m, 3 Dec 1988, coll. N. H. Campos, INVEMAR-CRU-1202, ICN-MHN-CR.

Other material examined.—Caribbean Sea: 1 ♀ (sl = 1.8 mm), Chub Cay, Bahamas, sta JSL-1-3660, 25°23.08′N, 77°51.129′W, 77 m, 15 Feb 1994, colls. P. Santos, G. Goodfriend, J. Elliott, J. Harasewych, USNM 309719.—2 ♂ (sl = 1.4, 1.6 mm), sta P-775, 12°0.5′N, 72°38.50′W, 78–82 m, 29 Jul 1968, USNM 309717.—37 ♂ (sl = 1.5–3.6 mm), 6 ♀ (sl = 2.4–2.6 mm), 4 ovig ♀ (sl = 2.1–2.6 mm), 1 intersex (sl = 1.9 mm), some with rhizocephalan, sta P-718, 11°22.50′N, 64°08.60′W, 60 m, 20 Jul 1968, RMNH D48671, SNHM 31601-31605, USNM 309713.—1 ♂ (sl = 2.7 mm), (in poor condition), sta P-842, 11°10.60′N, 60°31.20′W, 68–73 m, 1 Jul 1969, USNM 309718.—10 ♂ (sl = 2.5–2.9 mm), 1 ♀ (sl = 2.6 mm), 5 ovig ♀ (sl = 1.8–2.5 mm), 1 juv sex indet. (sl = 1.1 mm), sta P-721, 11°06.50′N, 64°22.50′W, 25–27 m, 21 Jul 1968, USNM 309714.—1 ♂ (sl = 2.1 mm), sta P-727, 10°20′N, 65°02′W, 64 m, 21 Jul 1968, USNM 309715.—1 ♀ (sl = 2.3 mm), sta P-734, 11°01.80′N, 65°34.20′W, 60–67 m, 22 Jul 1968, USNM 309716.—1 ♂ (sl = 2.3 mm), Shelf Expedition sta 1, Luymes, Guyana, RMNH D48672.

Diagnosis.—Shield (Fig. 2a) distinctly longer than broad; rostrum triangular, blunt or acute, and frequently with tiny spinule; lateral projections broadly triangular, terminally rounded. Ocular peduncles moderately short and stout, corneas weakly dilated; ocular acicles triangular, with small submarginal spine; separated basally by slightly more than basal width of 1 acicle. Antennular and antennal peduncles both at most slightly overreaching distal margins of corneas. Antennal acicles short, usually not reaching to bases of corneas, rarely very slightly beyond.

Right cheliped (Figs. 2b, 3b, c) varying from moderately short and broad to appreciably elongate. Dactyl approximately as broad as fixed finger and 0.65–0.75 times length of palm, dorsal surface flattened, unarmed, dorsomesial margin raised as crenulate ridge. Palm and fixed finger circumscribed by raised crenulate ridge, dorsal surface flattened or weakly convex, unarmed; dorsoproximal surface, mesial, lateral and ventral surfaces with scattered small tubercles or granules, weakest or absent ventrally. Carpus subtriangular, moderately long; dorsodistal margin often with small spine mesially, dorsal margin often with row of small tubercles or protuberances, surfaces frequently covered with minute granules. Merus with small spine at ventrolateral distal angle, ventromesial margin serrate.

Left cheliped (Figs. 2c, 3a) with propodal-carpal articulation perpendicular to slightly twisted. Dactyl and fixed finger with few tufts of setae on dorsal and ventral surfaces distally; palm circumscribed by low, finely denticulate ridge, dorsal surface and dorsomesial margin each with several to numerous minute tubercles or granules. Carpus subtriangular or subtrapezoidal; dorsodistal margin with 4 spines, dorsal margin with row of setae. Merus with several spiniform bristles on dorsodistal margin.

Ambulatory legs (Fig. 2e, d) not markedly compressed laterally; similar from left to right. Dactyls slightly shorter to slightly longer than propodi, with long, slender corneous claws; dorsal margins each with row of long setae and bristles; ventral margins each with 5–8 corneous spines. Propodi approximately 1.20–1.40 times length of carpi; each with row of setae on dorsal margin occasionally arising from low protuberances and giving impression of minute serrations; ventral margins with row of corneous spines and corneous bristles at distal angle. Carpi each with small dorsodistal spine and dorsal row of setae and few bristles, sometimes also arising from very small protu-

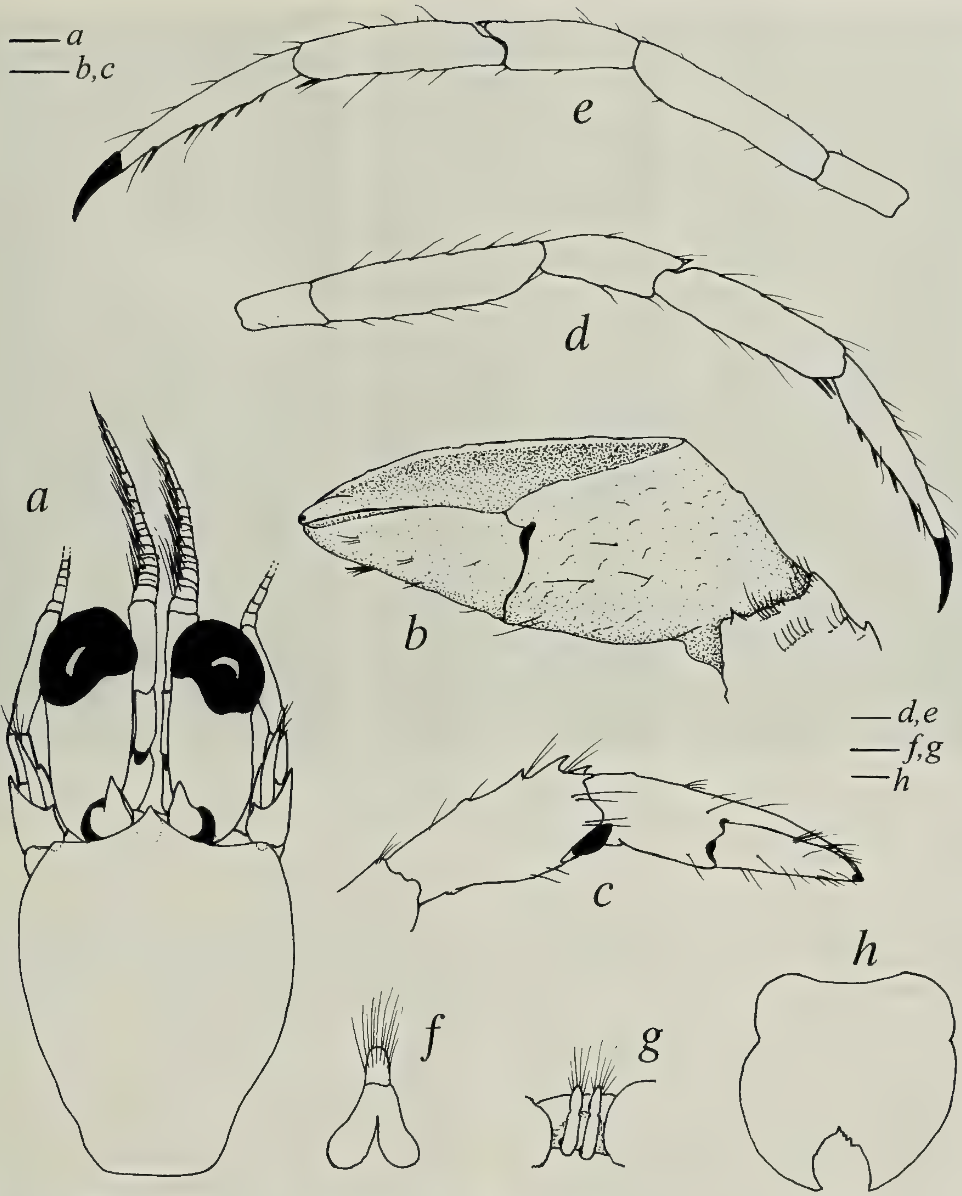

Fig. 2. *Pylopagurus pattiae* Lemaitre & Campos, 1993. a, c–h, paratype ovig ♀ (sl = 1.8 mm), Colombia, USNM 251897; b, ♀ (sl = 1.8 mm), Bahamas, USNM 309719. a, shield and cephalic appendages, dorsal; b, right chela, mesiodorsal; c, left carpus and chela, mesial; d, second right pereopod, lateral; e, third left pereopod, mesial; f, anterior and posterior lobes of sternite of third pereopods, ventral; g, part of coxae and sternite of fifth pereopods, and first pleopods, ventral; h, telson, dorsal. Scales equal 0.25 mm (a–e) and 0.1 mm (f–h).

berances, and giving a minutely serrate appearance. Meri with setae and few bristles on dorsal and ventral margins.

Sternite of third pereopods (Fig. 2f) with setose, subovate anterior lobe. Sternites of fourth and fifth pereopods each with 2 or more capsulate setae. Males without vas deferens protruded from gonopores to form short sexual tubes.

Telson (Fig. 2h) with posterior lobes separated by shallow median cleft, terminal margins oblique, each armed with 1–3 un-

Fig. 3. Chelae of *Pylopagurus pattiae* Lemaitre & Campos, 1993, dorsal. a, b, ♂ (sl = 2.8 mm), sta P-718, Caribbean Sea, USNM 309713; c, ♂ (sl = 2.1 mm), same sta, SNHM 31601-31605. a, left, (27.5×); b, right (11.9×); c, right (37.5×).

equal sharp or blunt spines; lateral margins evenly rounded, each ending posteriorly in strong spine.

Color.—General coloration orange. Ocular peduncles with light orange band near mid-length. Chelae with cutting edges of fingers orange; dorsal surface of right chela with three longitudinally ovate white spots with orange outlines, one medially on palm, one medially at base of fixed finger, and one basally on dactyl and extending slightly onto palm (after Lemaitre & Campos 1993).

Habitat.—All known specimens have been found living in semi-transparent tubes built by polychaetes of the family Onyphidae (*Hyalinoecia* sp.), except a specimen from the Bahamas which was found in a scaphopod *Dentalium* shell.

Distribution.—Caribbean Sea: Bahamas; Colombia; Guiana; and northern coast of Venezuela; 20–82 m.

Remarks.—Individuals of *Pylopagurus pattiae,* like those of the other two new species of this genus described herein, grow only to a relatively small size, with females ovigerous reaching shield lengths between 1.6 and 2.1 mm. The largest specimen seen in our material was a male with a shield length of 3.6 mm. Lemaitre & Campos (1993) considered *P. pattiae* very similar to *P. discoidalis,* a common western Atlantic and Caribbean species that reaches considerably larger size. Although the two species are usually readily distinguished by the armature of the propodi and carpi of the ambulatory legs, small specimens of *P. discoidalis* (sl ≤ 2.0 mm) occasionally do not exhibit the characteristic armature of the dorsal surfaces of these segments. For these small specimens a more reliable differentiating character is the length of the antennal acicles in relation to the corneas. In *P. pat-*

tiae, the acicles are quite short, usually not reaching as far as the bases of the corneas (Fig. 2a); only rarely have we observed specimens in which the acicles have reached beyond the bases of the corneas, and then only slightly. In contrast, the acicles in *P. discoidalis* reach at least midlength of the corneas, and usually beyond (Fig. 4a).

Pylopagurus pattiae has so far been found outside the Caribbean coast of South America only once, in the Bahamas, whereas *P. discoidalis* is broadly distributed from the southeastern coast of the United States to the northeastern coast of South America. *Pylopagurus discoidalis* most commonly occupies shells of *Dentalium* spp., with or without associated anemones, whereas *P. pattiae* has been found almost exclusively living in corneous, semi-transparent tubes built by polychaetes of the family Onyphidae. Males of *P. pattiae* often exhibit marked variation in the length of the right cheliped that does not appear to be consistently size-related. Similarly to *P. discoidalis,* the dorsal surface of the right chela in *P. pattiae* can be strongly influenced by the type of habitat utilized. The dorsal surface of the chela of the only specimen of *P. pattiae* found in a *Dentalium* shell is much more concave (Fig. 2b) than that in specimens found in polychaete tubes (Fig. 3b, c).

This species has occasionally been found infested with one or two unidentified rhizocephalan parasites. Of three individuals from sta P-718 (USNM 309713) obviously infected, one was a male (sl = 3.5 mm) with well developed paired female gonopods, but a second male (sl = 2.6 mm) similarly infected, but perhaps with a second rhizocephalan species, showed no "feminizing" effect. A parasitized female (sl = 2.6 mm) had only one unusually elongate gonopod present. A fourth specimen (sl = 1.9 mm), from this same station had female-like pleopods, but only three in number. Neither male nor female gonopores were delineated; however, one very elongate female gonopod was developed. In this specimen, there was no external indication of a parasitic infection.

Pylopagurus discoidalis (A. Milne-Edwards, 1880)
Figs. 4–6

Eupagurus discoidalis A. Milne-Edwards, 1880:41 (type locality: BK station 157, off Montserratt).—Miyake, 1978:119.

Pylopagurus discoidalis: A. Milne-Edwards & Bouvier, 1891:104; 1893:76, pl. 6, figs. 7–14.—Alcock, 1905:189.—Schmitt, 1921:145.—Barnard, 1947:377.—Provenzano, 1963:239.—Williams, 1965:134, fig. 109; 1984:226, fig. 162.—Abele & Kim, 1986:388, fig. 389d, e.—McLaughlin, 1981a:2.—Lemaitre & Campos, 1993:557.

Pylopagurus u.: Stebbing, 1910:359.

Holotype.—♂ (sl = 5.5 mm), sta BK-157, off Montserratt, 219 m, 1879, MCZ 4078.

Other material examined.—Eastern coast of United States: 1 ♂ (sl = 3.3 mm), sta EW-E-1-73, off Carolinas, (no depth), 1973, USNM 309702.—(In poor condition), sta DE-7, 36°08′N, 74°49′W, 113 m, 16 May 1970, USNM 108169.—3 ♂ (sl = 2.0–3.5 mm), 1 ♀ (sl = 2.8 mm), 2 ovig ♀ (sl = 2.5, 2.6 mm), SE Cape Hatteras, North Carolina, sta A-2600, 34°39.50′N, 75°35.50′W, 291 m, 18 Oct 1885, USNM 11287.—1 ♂ (sl = 3.3 mm), sta EW-14590, North Carolina, 33°59′N, 76°15.60′W, (no depth), 29 Jul 1970, USNM 309674.—1 ♂ (sl = 5.0 mm), 1 ovig ♀ (sl = 5.2 mm), sta SB 2539, 33°03.50′N, 77°33.50′W, 183 m, 5 Dec 1960, USNM 309730.—off South Carolina, sta PE-183-3, (no depth), 14 Feb 1940, USNM 102810.—5 ♂ (sl = 1.0–2.5 mm), 1 ♀ (sl = 1.3 mm), east of Sapelo Island, Georgia, sta 298, 31°26.32′N, 79°42.13′W, 252–291 m, 6 Aug 1963, USNM 150222, 150223.—1 ♀ (sl = 3.2 mm), sta DO-573390, 30°50′N, 79°53′W, 278 m, 3 Nov 1973, coll. E. L. Wenner, USNM 188198.—1 ♀ (sl = 2.8 mm), haul

45, off Miami Beach, 139 m, 25 Aug 1951, coll. F. M. Bayer, UMML 32:4853.—1 ovig ♀ (sl = 2.7 mm), 1.4 mi (2.6 km) off sea buoy Miami, 73 m, 24 Jan 1951, colls. G. Voss, F. M. Bayer, UMML 32:2473.—1 ♂ (sl = 3.8 mm), off Miami Beach, Florida, Marine Lab sta 46, 128 m, 25 Aug 1951, coll. F. M. Bayer, USNM 102755.—2 ♂ (sl = 2.0, 3.5 mm), 1 ovig ♀ (sl = 3.0 mm), off surfside Miami Beach, Florida, Marine Lab sta 48, 132 m, 25 Aug 1951, coll. F. M. Bayer, USNM 102754.—1 ovig ♀ (sl = 2.8 mm), off Miami, Florida, 137 m, Nov 1915, coll. J. B. Henderson, USNM 102582.—1 ♂ (sl = 3.2 mm), Miami, Florida, 55 m, coll. J. B. Henderson, USNM 102583.

Gulf of Mexico: 2 ♂ (sl = 2.9, 3.2 mm), 2 ♀ (sl = 1.7, 2.1 mm), DISL sta 22-55-VI-B-a-10, 29°32.75′N, 87°23.50′W, 91 m, 1975, USNM 309734.—1 ♀ (sl = 5.7 mm), DISL sta 22-55-VI-C-c-8, 29°32.50′N, 87°21′W, 183 m, 1975, USNM 309735.—4 ♂ (sl = 3.8–5.0 mm), 2 ♀ (sl = 3.3, 3.9 mm), 1 ovig ♀ (sl = 3.2 mm), DISL sta 13-55-V-C-c-5, 29°30.25′N, 86°25.5′W, 183 m, 20 Jul 1975, USNM 309736.—1 ♀ (sl = 3.6 mm), sta O-1447, 29°20′N, 87°30′W, 439 m, 17 Feb 1956, USNM 309691.—1 ovig ♀ (sl = 4.1 mm), sta A-2401, 28°38.5′N, 85°52.50′W, 260 m, 14 Mar 1885, USNM 9756.—1 ♂ (sl = 3.5 mm), 1 ovig ♀ (sl = 4.7 mm), sta A-2402, 28°36′N, 85°33.50′W, 203 m, 14 Mar 1885, USNM 9765.—2 ♂ (sl = 4.1, 4.6 mm), 2 ♀ (sl = 4.0–4.7 mm), 2 ovig ♀ (sl = 3.4, 4.4 mm), DISL sta 13-55-III-C-c-14, 28°22.75′N, 85°14.50′W, 1975, USNM 309737.—1 ♂ (sl = 6.5 mm), sta O-4658, 27°46′N, 93°37′W, 183 m, 30 Jan 1964, NHM 2001.368.—1 ♀ (sl = 2.4 mm), sta A-5119, 26°39′N, 83°56.50′W, 82 m, 23 Mar 1889, USNM 42556.—1 ♀ (sl = 2.6 mm), BK sta 50, 26°31′N, 85°03′W, 218 m, 1877–78, coll. A. Agassiz, MCZ 2583.—1 ♂ (sl = 1.7 mm), (in poor condition), BK (no sta number), 26°31′N, 89°03′W, 218 m, (no date), coll. A. Agassiz, MCZ 4081.—1 ovig ♀ (sl = 3.0 mm), DISL sta 22-55-II-8a-4, 26°27′N, 84°10.75′W, 183 m, 1975, USNM 309738.—1 ovig ♀ (sl = 2.4 mm), 22-51-I-B-9-3, 26°25′N, 83°50′W, USNM 309739.—1 ♂ (sl = 3.4 mm), 2 ovig ♀ (sl = 2.7, 3.0 mm), BA, off Sand Key, Florida, 137 m, 29 Mar 1872, coll. W. Stimpson, MCZ 3024, 3060, 4082.—2 ♂ (sl = 4.0, 5.0 mm), 1 ♀ (sl = 3.7 mm), sta BK-36, 23°13′N, 89°16′W, 154 m, 1877–1878; sta BK-291, 13°12′N, 59°41′W, 384 m, 9 Mar 1879, MCZ 4079 (specimens mixed in same lot).—1 ♂ (sl = 2.5 mm), 1 ♀ (sl = 2.4 mm), BA, west Florida, 21°14′N, (no longitude), 183 m, 22 Apr 1872, coll. W. Stimpson, MCZ 3023.—2 ovig ♀ (sl = 5.2, 6.1 mm), sta O-3637, 17°13′N, 87°55′W, 219–311 m, 10 Jun 1962, USNM 309692.—2 ♂ (sl = 4.8, 6.1 mm), sta 70A10-26, 15°17.80′N, 81°21.90′W, 247–256 m, 13 Jul 1970, coll. W. Pequegnat, TAM.—1 ♀ (sl = 5.7 mm), west coast of Florida, Manatee County, 61–370 m, DNR.

Straits of Florida, and Florida Keys: 1 ♀ (sl = 3.9 mm), sta P-736, 26°44′N, 79°02′W, 19 m, 1 Sep 1965, UMML 32:4761.—1 ovig ♀ (sl = 3.0 mm), sta G-413, 26°20′N, 80°00′W, 183 m, 22 Sep 1964, USNM 309681.—1 ♀ (sl = 3.5 mm), 2 molts, sta G-925, 25°58′N, 78°29′W, 240–250 m, 29 Sep 1967, UMML 32:4744.—4 ♂ (sl = 1.8–2.2 mm), 1 ♀ (sl = 1.8 mm), sta P-810, 26°04′N, 79°58′W, 810 m, 11 Oct 1968, USNM 309689.—1 ♀ (sl = 3.4 mm), + larvae, sta G-7, 25°46′N, 80°03.50′W, 137 m, 25 May 1962, UMML 32:4745.—7 ♂ (sl = 3.2–4.5 mm), 1 ♀ (sl = 3.2 mm), sta G-29, 25°41′, 80°02′W, 183–247 m, 21 Jun 1962, USNM 309678.—12 ♂ (sl = 3.4–5.0 mm), 1 ♀ (sl = 3.7 mm), 1 ovig ♀ (sl = 3.8 mm), sta G-610, 25°25′N, 80°07′W, 77–82 m, 15 Apr 1965, USNM 309705.—2 ♂ (sl = 3.5, 3.8 mm), 1 with rhizocephalan, sta G-606, 25°18′N, 80°04′W, 183 m, 15 Apr 1965, USNM 309683.—1 ♀ (sl = 2.5 mm), + molt, sta G-767, 25°13′N, 80°10′W, 108–88 m, 26 Jan 1966, UMML 32:4743.—5 ♂ (sl = 3.2–5.3 mm), 3 ♀ (sl = 3.1–4.8 mm), 2 ovig ♀ (sl = 3.3, 3.6 mm), sta G-1301, 24°57′N, 80°14′W, 274 m, 27 Mar 1971, USNM 309677.—2 ovig ♀ (sl = 3.5, 3.6 mm), sta SB-2362, 24°56′N, 80°22′W, 84 m, 25 Oct 1960, USNM 309697.—1 ♀ (sl = 4.2 mm), sta G-794, 24°54′N, 80°15′W, 212–219 m, 19 Aug 1966, USNM 309684.—1 ♀ (sl = 3.0 mm), sta M-Dredge 17, 6 mi (11.1 km) SE of Molasses Reef Light, 223 m, 9 Jul 1950, USNM 173734.—3 ♂ (sl = 3.7–4.6 mm), 3 ♀ (sl = 2.0–2.6 mm), sta G-796, 24°48.50′N, 80°20′W, 201–205 m, 19 Aug 1966, USNM 309671.—1 ♀ (sl = 2.4 mm), sta P-598, 24°47′N, 80°26′W, 183, 15 Mar 1967, UMML 32:4760.—5 ♂ (sl = 4.0–5.1 mm), 4 ♀ (sl = 3.5–4.3 mm), 5 ovig ♀ (sl = 3.6–4.4 mm), sta G-757, 24°46′N, 80°28′W, 181–183 m, 15 Sep 1965, USNM 309680.—1 ♂ (sl = 4.3 mm), sta G-589, 24°40′N, 80°48′W, 150 m, 14 Apr 1965, USNM 309682.—1 ♂ (sl = 2.4 mm), sta G-457, 24°37′N, 80°47′W, 183–174, 23 Jan 1965, USNM 309731.—4 ♂ (sl = 3.3–4.4 mm), 1 ♀ (sl = 2.3 mm), (1 in poor condition), sta G-1035, 24°34.70′N, 80°58.60′W, 253–357 m, 26 Feb 1969, USNM 309708.—2 ♂ (sl = 1.8, 2.9 mm), off Fowey Rocks, Florida, 137–183 m, May 1917, coll. J. B. Henderson, USNM 102659.—(right cheliped only), Fowey Rocks, Florida, 128 m, Aug 1916, USNM 102661.—1 ♂ (sl = 4.6 mm), 2 ♀ (sl = 4.3, 4.4 mm), 2 ovig ♀ (sl = 4.1, 4.3 mm), sta G-972, 24°24′N, 80°52′W, 221–230 m, 3 Feb 1968, USNM 309707.—1 ♂ (sl = 5.0 mm), 1 ovig ♀ (sl = 4.1 mm), sta G-1036, 24°22.50′N, 80°53′W, 417–433 m, 26 Feb 1969, USNM 309686.—10 ♂ (sl = 1.8–3.9 mm), 9 ♀ (sl = 2.0–4.2 mm), off Key West, Florida, sta FH-7279, 24°21.91′N, 81°58.41′, 179 m, 14 Feb 1902, USNM 151185.—3 ♂ (sl = 2.4–5.2 mm), 1 ♀ (sl = 3.0 mm), off Key West, Florida, sta FH-7282, 24°21.25′N, 81°52.25′W, 199 m, 19 Feb 1902, USNM 102660.—1 ♂ (sl = 2.6 mm), off Key West, Florida, 201 m, 1916, coll. J. B. Henderson, USNM 102586.—1 ♀ (sl = 4.0 mm), off Key West, Florida, 247 m, 1916, coll. J. B. Henderson, USNM 102588.—2 ♂ (sl = 3.7, 4.9 mm), off Key West, western Dry Rock, Florida, 263 m, 1916, USNM 309709.—1 ♀ (sl = 3.2 mm), off Key West, Florida, 263 m, 1916, USNM 102589.—1 ♂ (sl = 3.1 mm), 1 ♀ (sl = 2.2 mm), 2 ovig ♀ (sl = 2.9, 3.5 mm), SE of Key West, Florida, 112 m, (no depth, date), coll. J. B. Henderson, USNM 102584.—1 ♂ (sl = 3.8 mm), 2 ♀ (sl = 3.1, 4.7 mm), Sambo Key, Florida, 247 m, 1916, coll. J. B. Henderson, USNM 102581, USNM 102585, USNM 102587.—1 ♀ (sl = 2.3 mm), sta G-1085, 24°20′N, 82°24.50′W, 201–210 m, 26 Apr 1969, USNM 309732.—23 ♂ (sl = 3.2–5.1 mm), 1 with rhizocephalan, 17 ♀ (sl = 3.5–4.1 mm), 1 with rhizocephalan, 15 ovig ♀ (sl = 3.4–3.8), sta G-432, 24°19′N, 82°29′W, 188–199 m, 28 Nov 1964, USNM 309679.—1 ♀ (sl = 3.6 mm), Pourtales Plateau, SUIBE sta 56, 366 m, 27 Jun 1893, USNM 68977.—1 ♂ (sl = 3.0 mm), 1 ♀ (sl = 4.9 mm), 4 ovig ♀ (sl = 3.0–4.8 mm), sta FH-7283, 24°17′30″N, 81°53′30″W, 232 m, 19 Feb 1902, USNM 309710.—3 ♂ (sl = 2.5–5.9 mm), 7 ♀ (sl = 2.1–6.1 mm), 4 ovig ♀ (sl = 4.4–5.4 mm), sta G-1102, 24°15.50′N, 81°34′W, 247–283 m, 29 Apr 1969, USNM 309675.—3 ♂ (sl = 3.6, 6.0 mm), 2 ♀ (sl = 3.6, 4.8 mm), sta SB 2443, 24°08′N, 80°09′W, 329–366 m, 2 Nov 1960, USNM 309698, 309729.—3 ♀ (sl = 4.2–6.2 mm), sta SB 2445, 24°08′N, 80°08′W, 252 m, 3 Nov 1960, UMML 32:4862.—2 ♀ (sl = 3.7, 3.7 mm), sta SB 2454, 23°34′N, 79°04′W, 384–439 m, 5 Nov 1960, UMML 32:4863.

Caribbean Sea: 1 ovig ♀ (sl = 3.8 mm), sta A-2337, 23°10.65′N, 82°20.35′W, 364 m, 19 Jan 1885, USNM 9511.—1 ♂ (sl = 4.8 mm), sta SB 3510, 22°55′N, 78°36′W, 274 m, 7 Nov 1961, UMML 32:4865.—1 ♀ (sl = 4.6 mm), sta G-974, 21°13′N, 86°25′W, 247–283 m, 27 Jan 1968, USNM 309676.—1 ♂ (sl = 3.6 mm), sta G-947, 21°13′N, 86°25′W, 247–283 m, 27 Jan 1968, USNM 309706.—1 ovig ♀ (sl = 2.1

mm), sta P-594, 21°00.50′N, 86°23′W, 307–329 m, 15 Mar 1967, USNM 309687.—1 ♂ (sl = 3.2 mm), sta G-897, 20°59′N, 86°24′W, 210–292, 10 Sep 1967, USNM 309685.—4 ♂ (sl = 1.6–2.1 mm), 1 ♀ (sl = 1.9 mm), sta P-1143, 20°54.50′N, 73°28.20′W, 110–220 m, 13 Jan 1970, USNM 309700.—1 ♂ (sl = 3.1 mm), JSDSE sta 100, 18°40.25′15″N, 64°50.25′W, 274 m, 4 Mar 1933, USNM 309703.—1 ♂ (dry) (sl = 4.5 mm), sta O-5914, 18°13′N, 63°19′W, 201 m, 25 Feb 1966, USNM 309696.—1 ovig ♀ (sl = 3.9 mm), sta P-610, 17°02′N, 87°38.40′W, 296–329 m, 18 Mar 1967, USNM 309688.—1 ♂ (sl = 4.6 mm), sta O-4934, 16°32′N, 81°43′W, 101 m, 9 Jun 1964, USNM 309695.—1 ♂ (sl = 2.9 mm), sta O-4932, 16°06′N, 81°10.50′W, 165 m, 9 Jun 1964, PMcL.—7 ♂ (sl = 2.7–4.0 mm), 4 ♀ (sl = 2.5–3.0 mm), sta O-4837, 14°21′N, 80°15.50′W, 11 m, 12 May 1964, MNHN pg. 5946.—2 ovig ♀ (sl = 2.3, 2.5 mm), sta O-4832, 14°15.50′N, 80°27.10′W, 219–238 m, 12 May 1964, UMML 32:4776, USNM 309694.—1 ♀ (sl = 3.8 mm), sta O-4833, 14°15.50′N, 80°25.70′W, 155–82 m, 12 May 1964, UMML 32:4859.—1 ♂ (sl = 5.2 mm), sta P-776, 12°13.30′N, 72°50′W, 408–576 m, 29 Jul 1968, USNM 309699.—1 ♂ (sl = 3.7 mm), 1 ovig ♀ (sl = 5.9 mm), sta O-4398, 12°46′N, 70°41′W, 201 m, 26 Sep 1963, UMML 32:4858.—1 ♂ (sl = 3.2 mm), sta O-4423, 11°53′N, 69°28′W, 347 m, 5 Oct 1963, USNM 309693.—1 ♂ (sl = 4.3 mm), sta A-2125, 11°43′N, 69°09.50′W, 380 m, 18 Feb 1884, USNM 309701.

Western Atlantic, off Lesser Antilles: 2 ♂ (sl = 3.4, 6.5 mm), sta P-943, 16°25.90′N, 61°36.70′W, 274 m, 17 Jul 1969, UMML 32:4760.—1 ♂ (sl = 2.6 mm), 4 ♀ (sl = 3.7–4.9 mm), 2 ovig ♀ (sl = 4.0, 5.2 mm), sta P-890, 14°05.60′N, 60°51.40′W, 198–430 m, 7 Jul 1969, USNM 309728.—1 ♂ (sl = 4.8 mm), sta P-891, 14°05.20′N, 60°50.30′W, 477–1020 m, 7 Jul 1969, USNM 309733.—1 ♂ (sl = 5.5 mm), sta P-889, 14°04.40′N, 60°50.80′W, 177–219 m, 7 Jul 1969, UMML 32:4851.—1 ♂ (sl = 3.9 mm), sta BK-220, St. Lucia, 13°50.25′N, 61°03.75′W, 212 m, 16 Feb 1879, MCZ 2696.—3 ♂ (sl = 5.5–6.5 mm), 1 ♀ (sl = 4.6 mm), sta P-876, 13°13.90′N, 61°04.70′W, 241–262 m, 6 Jul 1969, USNM 309727.—1 ♂ (sl = 4.4 mm), 1 ♀ (sl = 3.8 mm), sta BK-223, St. Vincent, 13°08.40′N, 61°13.83′W, 267 m, 303 m, 18 Feb 1879, MCZ 4080.—4 ♂ (sl = 4.3–5.7 mm), 2 ♀ (sl = 5.1, 5.7 mm), 1 juv sex indet. (sl = 1.2 mm), sta O-5015, 13°02′N, 59°34′W, 201–247 m, 20 Sep 1964, RMNH D48673.—1 ♂ (sl = 5.1 mm), sta O-5017, 13°01.50′N, 59°39.50′W, 247–252 m, 20 Sep 1964, UMML 32:4855.—6 ♂ (sl = 4.8–7.1 mm), 8 ♀ (sl = 4.2–5.8), 2 ovig ♀ (sl = 4.7, 5.1 mm), sta O-5018, 13°00′N, 59°33′W, 320 m, 20 Sep 1964, USNM 309726.

Barbados: 1 ♀ (sl = 3.9 mm), sta BK-290, Barbados, 13°11.90′N, 59°38.75′W, 133 m, 9 Mar 1879, MCZ 2730.—1 ♀ (sl = 3.4 mm), sta BK-300, Barbados, 13°06.50′N, 59°39.33′W, 150 m, 10 Mar 1879, MCZ 2714.—2 ♂ (sl = 2.0, 2.2 mm), 225 m, 27 Nov 1962, colls. R. Work, J. Lewis.—10 ♂ (sl = 1.4–3.3 mm), 5 ♀ (sl = 2.2–2.8 mm), 3 ovig ♀ (sl = 1.3–2.8 mm), sta NR-12-4, (no depth, date), coll. J. Lewis, UMML 32:4781, USNM 309673.—1 ♀ (sl = 2.1 mm) sta NR-21-1, (no depth, date), coll. J. Lewis, PMcL.

Northeastern coast South America: 1 ♂ (sl = 5.0 mm), sta O-1989, 9°45′N, 59°45′W, (no depth), 4 Nov 1957, USNM 103390.—2 ♂ (sl = 5.6, 7.1 mm), 3 ♀ (sl = 5.8–6.9 mm), 1 ovig ♀ (sl = 5.8 mm), sta O-4304, 7°30′N, 55°00′W, 183 m, 24 Mar 1963, USNM 309725.—1 ♂ (sl = 4.9 mm), off Amazon River, sta O-2068, 2°35′N, 47°48′W, 219 m, 15 Nov 1957, USNM 103391.—3 ♂ (sl = 3.1–4.4 mm), 5 ♀ (sl = 3.3–4.6 mm), sta O-2068, 2°35′N, 47°48′W, 219 m, 15 Nov 1957, UMML 32:2471, MNHN pg-5947.—1 ovig ♀ (sl 4.0 mm), sta O-2080, 2°04′N, 47°00′W, 229 m, 17 Nov 1957, USNM 101664.—8 ♂ (sl = 3.0–4.6 mm), 9 ♀ (sl = 2.7–4.3 mm), 2 ovig ♀ (sl = 3.3, 3.4

mm), sta O-4226, 0°18′N, 44°17′W, 274 m, 9 Mar 1963, USNM 309724.

Diagnosis.—Shield (Fig. 4a) slightly longer than broad to slightly broader than long; rostrum usually reaching to mid-length of ocular acicles or beyond, broadly triangular, often terminating in small spinule; lateral projections obtusely triangular, terminating acutely or bluntly. Ocular peduncles short to very short, corneas dilated; ocular acicles triangular, acute, unarmed; separated basally by 1.50–2.00 times basal width of 1 acicle. Antennular peduncles overreach ocular peduncles by almost entire length of ultimate segment. Antennal peduncles overreach ocular peduncles at least one-half length of ultimate segment; antennal acicles reach mid-length of corneas or beyond.

Right cheliped (Figs. 4b, c, 5b–d) with chela subcircular to ovate. Dactyl broad, varying from only slightly narrower than palm to approximately one-half width of palm (dorsal view); with dorsal surface flattened or slightly convex, smooth, granular or minutely spinulose, dorsomesial margin raised as low, sometimes crenulate ridge. Palm and fixed finger circumscribed by low, smooth or crenulate ridge; dorsal surface somewhat concave (Figs. 4b, 5b, c), flattened or slightly convex (Figs. 4c, 5d), smooth, granular or minutely spinulose; dorsoproximal surface, mesial, lateral and ventral faces all with small tubercles and/or low, granular or weakly spinulose ridges, inner ventral surface of fixed finger with oval area of decalcification adjacent to articulation of dactyl. Carpus short, subtriangular to subtrapezoidal; dorsodistal margin crenulate or spinulose, dorsomesial distal angle usually with 1 or 2 acute spine, dorsal surface with short, transverse, spinulose or tuberculate ridges, dorsolateral distal angle with 1 or 2 minute spinules; ventral surface unarmed.

Left cheliped (Figs. 4d, 5a) with propodal-carpal articulation perpendicular. Dactyl unarmed or with serrate dorsomesial margin; palm and fixed finger circumscribed by low, crenulate or spinulose ridge, dorsal surface flattened or weakly convex, smooth, granular, or with scattered small spinules; dorsodistal surfaces of dactyl and fixed finger with few tufts of setae, ventrodistal surfaces each with several dense tufts of setae. Carpus subtriangular, dorsal surface strongly sloping mesially in distal half; distal margin with several small spines, dorsolateral margin with row of spines or spinulose, transverse ridges, dorsomesial surface with numerous spinulose tubercles or short, transverse, spinulose ridges.

Ambulatory legs (Fig. 6a, b) markedly compressed laterally; similar from left to right. Dactyls short and moderately to very broad, equal to or slightly shorter than propodi; with very long terminal claws; dorsal margins each with row of widely-spaced low protuberances, and frequently corneous spiniform bristles or spinules; ventral margins each with 4–6 corneous spines. Propodi also quite short, equal to or slightly longer than carpi; each usually with 3–5 corneous spines on ventral margin, dorsal margins each with usually double row of spinules or small spines, at least on second right, often giving a serrate or denticulate appearance, spines largest distally. Carpi each usually with 1 or 2 moderately strong spines at distal margin and row of small spines, spinules, or spinulose protuberances on dorsal surface (strongest on right second). Meri unarmed or with row of tiny spinules on ventral margins.

Sternite of third pereopods with semisubovate to narrowly subquadrate anterior lobe. Sternites of third to fifth pereopods each usually with several capsulate setae. Males occasionally with vas deferens protruded from one or both gonopores to form short, transparent sexual tube(s) (Fig. 4e, f).

Telson (Fig. 4h) with posterior lobes separated by very small, or often indistinct median cleft, terminal margins oblique or obliquely concave, each armed with 2–4 moderately strong spines interspersed with much smaller spines or spinules; lateral margins usually with narrow corneous or weakly calcified plate.

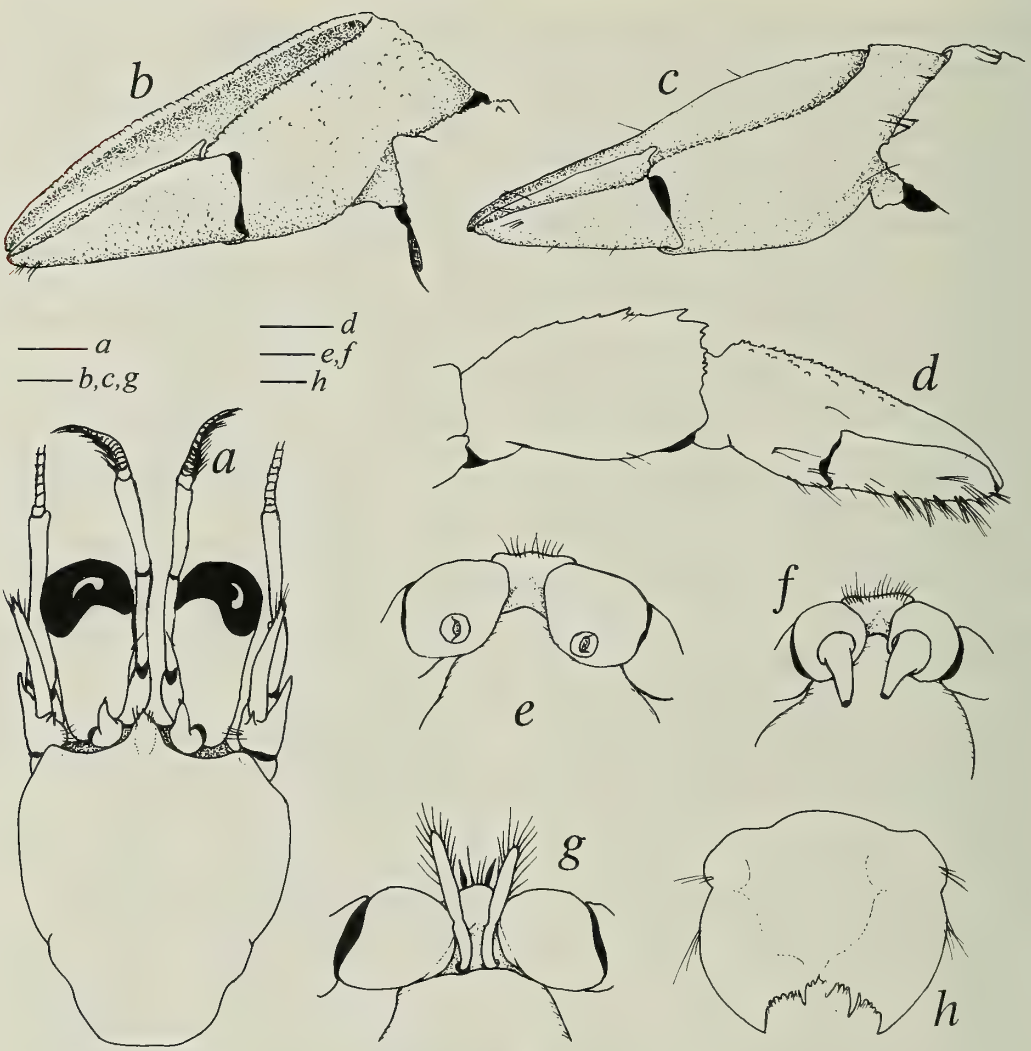

Fig. 4. *Pylopagurus discoidalis* (A. Milne-Edwards, 1880). a, b, d, h, ovig ♀ (sl = 4.9 mm), sta P-890, off Lesser Antilles, UMML 32:4756; c, ovig ♀ (sl = 3.0 mm), sta M-Dredge17, Florida Keys, USNM 173734; e, ♂ (sl = 2.1 mm), sta P-1143, Caribbean Sea, USNM 309700; f, ♂ (sl = 1.6 mm), same sta, USNM 309700; g, ovig ♀ (sl = 4.3 mm), sta G-1102, Straits of Florida, USNM 309675. a, shield and cephalic appendages, dorsal; b, c, chela, mesiodorsal; d, left carpus and chela, mesial; e, f, male coxae and sternite of fifth pereopods, sexual tubes, and part of abdomen (lower), ventral; g, female coxae and sternite of fifth pereopods, and part of abdomen (lower) showing first pleopods; h, telson, dorsal. Scales equal 1 mm (a, d), 0.5 mm (b, c, g), and 0.25 mm (e, g, h).

Color.—Variable (see Remarks).

Habitat.—Most commonly shells of scaphopod mollusks (*Dentalium* spp.), with or without an accompanying anemone.

Distribution.—Western Atlantic from North Carolina, and the Gulf of Mexico, to the northeastern coast of South America; 11–433 m, perhaps as great as 1020 m.

Remarks.—Pylopagurus discoidalis is a morphologically variably species, particularly in the shape and color of the right cheliped. Initially it was believed that two, closely allied, species were represented in the Caribbean. However, as has been demonstrated in other pagurid species, if sufficient numbers of specimens from differing

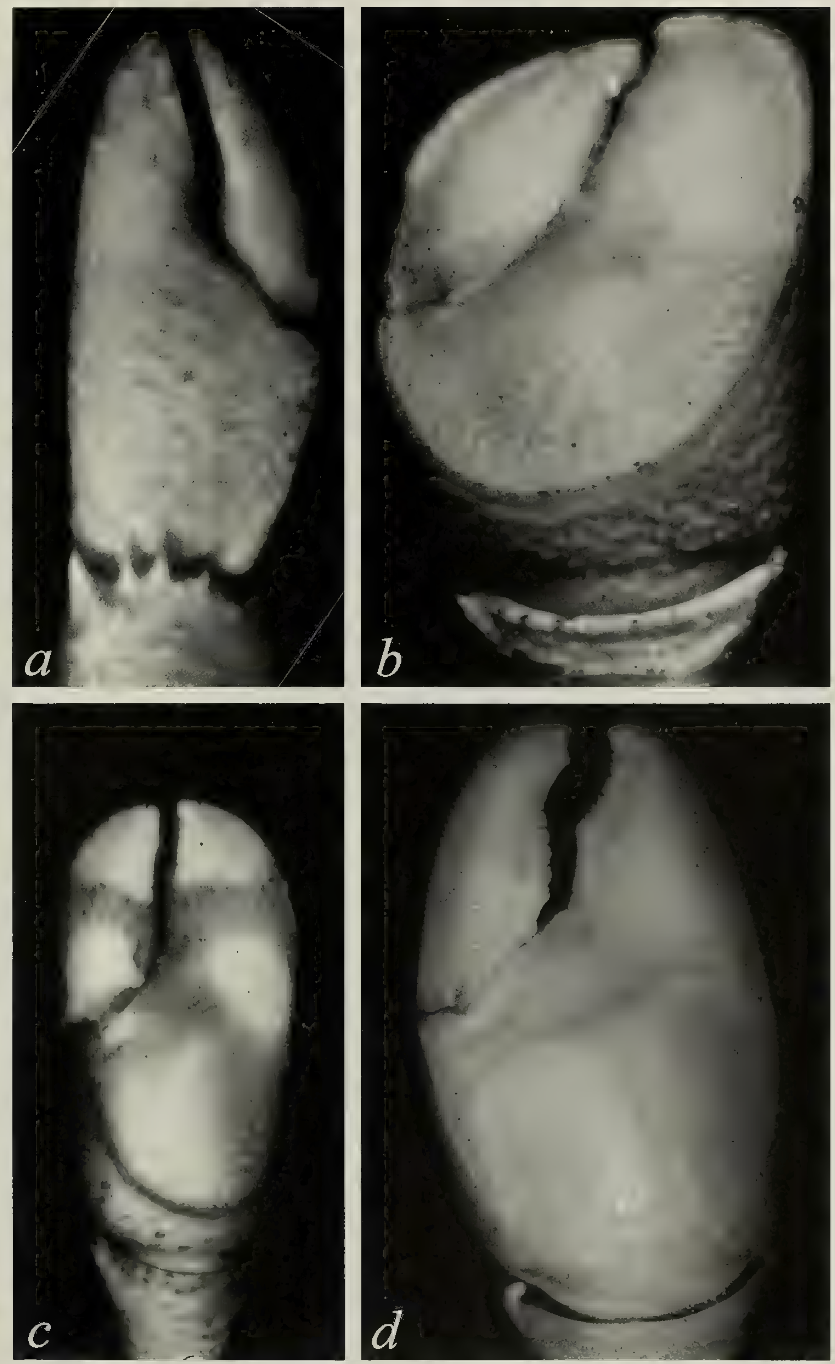

Fig. 5. Chelae of *Pylopagurus discoidalis* (A. Milne-Edwards, 1880), dorsal. a, b, holotype ♂ (sl = 5.5 mm), sta BK-157, off Montserratt, MCZ 4078; c, ♂ (sl = 6.1 mm), sta 70A10-26, Gulf of Mexico, TAM; d, ♂ (sl = 4.9 mm), sta G-610, Straits of Florida, USNM 309705. a, left (19.4×); b, right (8.1×); c, right (3.1×); d, right (8.0×).

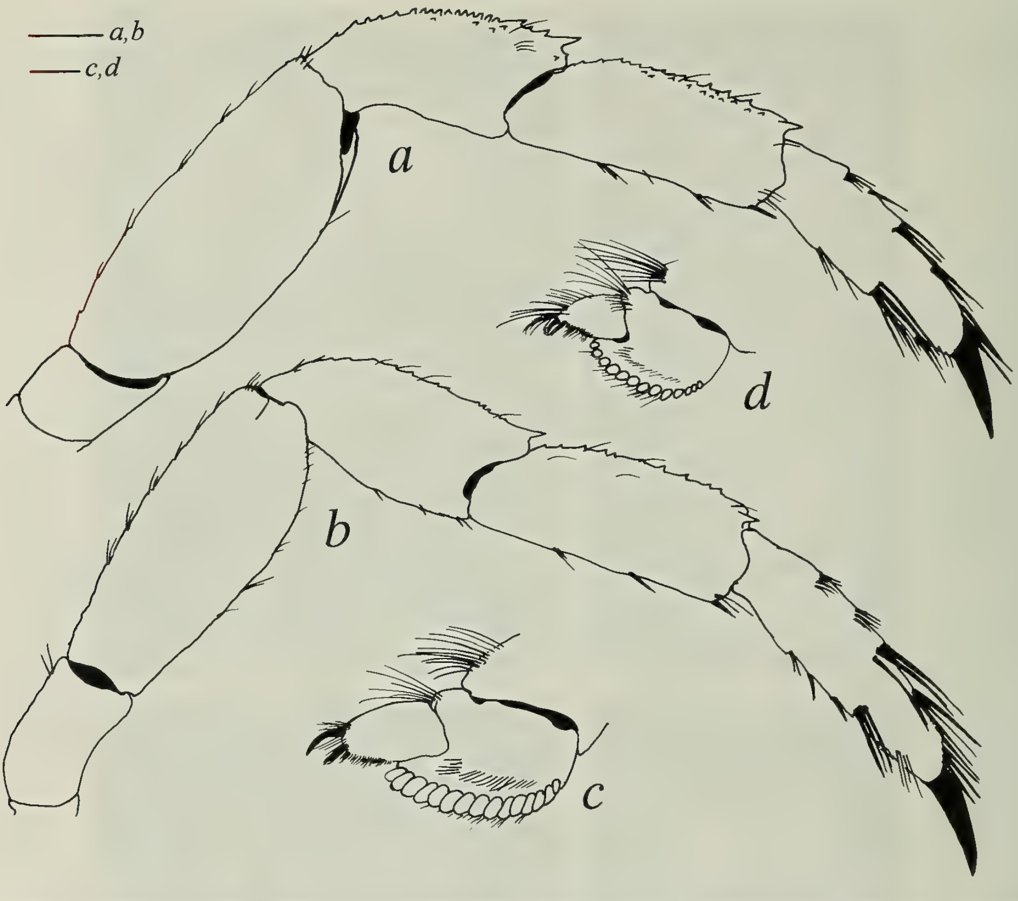

Fig. 6. *Pylopagurus discoidalis* (A. Milne-Edwards, 1880). a–c, ovig ♀ (sl = 4.9 mm), sta P-890, off Lesser Antilles, UMML 32:4756; d, ovig ♀ (sl = 3.0 mm), sta M-Dredge17, Florida Keys, USNM 173734. a, right second pereopod, lateral; b, right third pereopod, lateral; c, d, propodus and dactyl of left fourth pereopod, lateral. Scales equal 1 mm (a, b), and 0.25 mm (c, d).

localities are examined, continuums are often found. For example, variation correlated with geographic distribution was found to account for morphological differences among populations of *Pagurus lepidus* (Bouvier, 1898) (cf. Haig & McLaughlin 1991). Habitat differences in populations of *Lophopagurus* (*Australeremus*) *cookii* (Filhol, 1883) were suggested as the cause of variation in uropod symmetry observed in that species (McLaughlin & Gunn 1992), whereas sexual dimorphism contributed to the major morphological differences found in *Pagurus benedicti* (Bouvier, 1898) (cf. McLaughlin & Haig 1993).

A. Milne-Edwards & Bouvier (1893) [repeated by Williams (1984: 226) under his comments on variation] suggested that the large chela of *P. discoidalis* was initially elongate, but became more discoid with age. However, if size can be equated to advanced age, this hypothesis is not substantiated by our large sample of specimens. Rather, in *P. discoidalis* shell selection and/or association appears to greatly influence morphology. Regardless of size, virtually all the specimens that inhabited well calcified *Dentalium* sp. shells, free of epizoans, had long and relatively narrow shields and almost circular right chelae (Fig. 5b, c); the propodal rasp of the fourth pereopod consists of relatively large ovate scales (Fig.

6c). In contrast, individuals that were found occupying shells that were encrusted with, or had been decalcified or dissolved by anemones, had broader shields and more elongate chelae. In these latter specimens, the dorsal surface of the right palm was convex (Figs. 4c, 5d) rather than straight or concave and the dactyl often appreciably narrower (dorsal view) than the fixed finger; the the propodal rasp of the fourth pereopod consists of small, subcircular scales (Fig. 6d).

The color patterns of the right cheliped, although variable, appear also to be correlated with habitat. In unassociated scaphopod-dwelling *P. discoidalis* specimens, the chela is basically white with a band of red or reddish orange on dactyl and fixed finger and irregular bands on the palm (Fig. 5c). The extent of pigmentation on the palm is variable. In specimens associated with anemones, the base color of the chela is orange with ovate patches of white rimmed with orange on palm, fixed finger and dactyl. This pattern appears less variable.

Additionally, variations in ocular peduncle length and stoutness, corneal dilation, length/breadth relationships of the ambulatory dactyls and propodi, and strength of the armature of the ambulatory propodi and carpi have been observed. In contrast to size-related variations in the development of the ocular peduncles reported for juveniles (crab stages 1–10) of *Paguristes* Dana, 1851 (cf. Provenzano & Rice 1966) and *Pagurus* (cf. Carvacho 1988) in which the ocular peduncles become increasingly longer and more slender with increasing size, the opposite was found to be the case for juvenile and very young adults (sl = 2.0 mm) of *P. discoidalis.* The ocular peduncles in this size group routinely had longer, more slender ocular peduncles than were seen in larger specimens of either sex. Similarly, the younger, smaller individuals tended to have proportionately longer and more slender ambulatory dactyls than did larger individuals. Therefore, while the short, stout ocular peduncles with strongly dilated corneas are distinctive for moderate to large specimens of *P. discoidalis,* as are the short, broad ambulatory dactyls and propodi, these characters do not apply to juveniles and young adults, and will not serve to distinguish small specimens of *P. discoidalis* from other regional species. As previously indicated, small specimens of *P. discoidalis* are best distinguished from the superficially similar *P. pattiae* by the longer antennal acicles of the former species, and the stronger armature of the dorsal surface of the carpus of the left cheliped. Small specimens of *P. discoidalis* also can most easily be distinguished from *P. macgeorgei,* new species, by the armature of the carpus of left cheliped, and from *P. gorei,* new species, by the marginal or submarginal ridge that circumscribes the right chela of *P. discoidalis.*

Pylopagurus holmesi Schmitt, 1921

Figs. 7–9

Pylopagurus holmesi Schmitt, 1921:144, fig. 94 (type locality: Santa Catalina Island, California).—Walton, 1954:141, pl. 39.—Scanland & Hopkins, 1969:259.—Haig, 1977:14.—McLaughlin, 1981a: 3.

Pylopagurus longicarpus Walton, 1954: 144, pl. 40 (type locality: Puerto Refugio, Angel de la Guardia Island, Gulf of California, Mexico).—McLaughlin, 1981b: 3.

Holotype.—♂ (sl = 4.0 mm), sta T156, Santa Catalina Island, California, taken by Venice Marine Biological Station near Catalina Harbor, 23 Jun 1916, USNM 53330.

Holotype of Pylopagurus longicarpus, *Walton, 1954.*—♂ (sl = 2.0 mm), sta 1057-40, off Puerto Refugio, Angel de la Guardia Island, Gulf of California, Mexico, 51–56 fm (93.3–102.4 m), 29 Jan 1940, LACM CR19400296.

Other material examined.—Eastern Pacific: 1 ♀ (sl = 3.2 mm), near Portuguese Bend, San Pedro, California, (no depth), 23 Jun 1914, coll. A. Dohrn, USNM 50461.—1 ♂ (sl = 3.5 mm), 2 ovig ♀ (sl = 2.9, 3.6 mm), sta T155, Catalina Harbor, California, (no depth), 23 Jun 1916, USNM 309721.—1 ♂ (sl = 3.1 mm), 7 ovig ♀ (sl = 2.2–3.0 mm), sta T154, SW Catalina Harbor, California, (no depth), 23 Jun 1916, USNM 309720.—5 ovig ♀ (sl = 2.2–3.0 mm), sta D93, near Rocky Point, California, (no depth), 10 May 1924, USNM 309722.—2 ♂ (sl = 3.6, 4.0 mm), 2 ovig ♀ (sl = 3.1, 3.7 mm), Santa Catalina Island, California, near Venice Marine Biological Station, (no depth), 23 Jun 1916, USNM 53328, 53330 (paratypes).—1 ♂ (sl = 2.4 mm), 1 ovig ♀ (sl = 2.1 mm), sta 575-36, Scripps Institution of Oceanography pier, 50-7 fm (91.4–12.8 m), 15 Sep 1915, USNM 53944.—3 ♂ (sl = 2.4–2.6 mm), 1 ovig ♀ (sl = 2.7 mm), 32°38′N, 117°14′W, (no depth), 3 Nov 1907, USNM 53945.—1 ♂ (sl = 2.2 mm), 1 ♀ (sl = 2.4 mm), sta 3788, San Diego California, (no depth, date), coll. U. S. Bureau of Fisheries, USNM 52677.—2 ♂ (sl = 3.1, 4.8 mm), 1 with rhizocephalan, 1 ♀ (sl = 3.3 mm), 1 ovig ♀ (sl = 3.9 mm), sta 1010-39, off San Benito Island, Baja California, Mexico, 130–174 m, 20 Sep 1939, LACM CR193911418.—3 ♂ (sl = 3.7–4.5 mm), 3 ♀ (sl = 2.5–4.2 mm), 5 mi (9.3 km) off San Benito Island, Mexico, 159–174 m, (no date), LACM CR15000035.—3 ♂ (sl = 2.4–2.6 mm), 3 ♀ (sl = 2.3–2.5 mm), sta 1057-40, off Puerto Refugio, Angel de la Guardia Island, Gulf of California, Mexico, 93–99 m, 29 Jan 1940, coll. B. C. Walton (as *Pylopagurus longicarpus*), LACM CR19402906.—7 ♂ (sl = 2.9–4.6 mm), 3 ovig ♀ (sl = 3.2–3.4 mm), sta 575-36, N of San Pedro Nolasco Island, Baja California, Mexico, 183 m, 12 Mar 1936, USNM 309723.

Diagnosis.—Shield (Fig. 7a) longer than broad; rostrum triangular, reaching beyond midpoint of ocular acicles, with terminal spine or spinule; lateral projections bluntly triangular, unarmed. Ocular peduncles short, stout, corneas slightly dilated; ocular acicles triangular or subovate, with strong submarginal spine; separated basally by basal width to 1.75 times basal width of 1 acicle. Antennular peduncles exceeding corneas by 0.50 or less length of ultimate antennular segment. Antennal peduncles exceeding corneas by 0.30–0.50 length of fifth antennal segment.

Right cheliped (Figs. 7b, 8b, c) subovate or subcircular. Dactyl broad, with dorsal surface flattened, smooth, dorsomesial margin raised as low, crenulate ridge. Palm and fixed finger circumscribed by low, denticulate or tuberculate ridge dorsomesially and dorsolaterally, and submarginal ridge proximally, dorsal surface flattened, smooth or minutely granular; dorsoproximal surface, mesial, lateral and ventral surfaces all with small to minute tubercles or spinules. Carpus varying from short and broad to moderately elongate and subrectangular, dorsomesial and dorsolateral margins not delimited, surfaces all with closely-spaced small spinules or spinulose tubercles. Merus usually with spinulose or granular ventral surface, ventrodistal margins spinulose or serrate.

Left cheliped (Figs. 7c, 8a) with brush formed of tufts of stiff setae on ventral surface of dactyl and fixed finger; dorsomesial and dorsolateral margins of palm each with very low spinose or spinulose ridge, dorsal surface grenally flattened, minutely spinulose. Carpus subtriangular, with row of small spines on dorsolateral margin, dorsal surface spinulose, distal margin with several stronger spines extending mesially and laterally.

Ambulatory legs (Fig. 9) somewhat compressed laterally; similar from left to right. Dactyls equal or slightly longer than propodi, with moderate to long corneous claws; dorsal margins each with row of long, corneous, spiniform bristles, ventral margins each with row of 4–6 corneous spines. Propodi each with row of small spines on dorsal surface (strongest on second) and usually accompanied mesially by 1–3 irregular rows of much smaller spinules, ventral surfaces of second each with row of widely-spaced corneous bristles or spines, ventrodistal margins of third each with pair of corneous spines. Carpi each

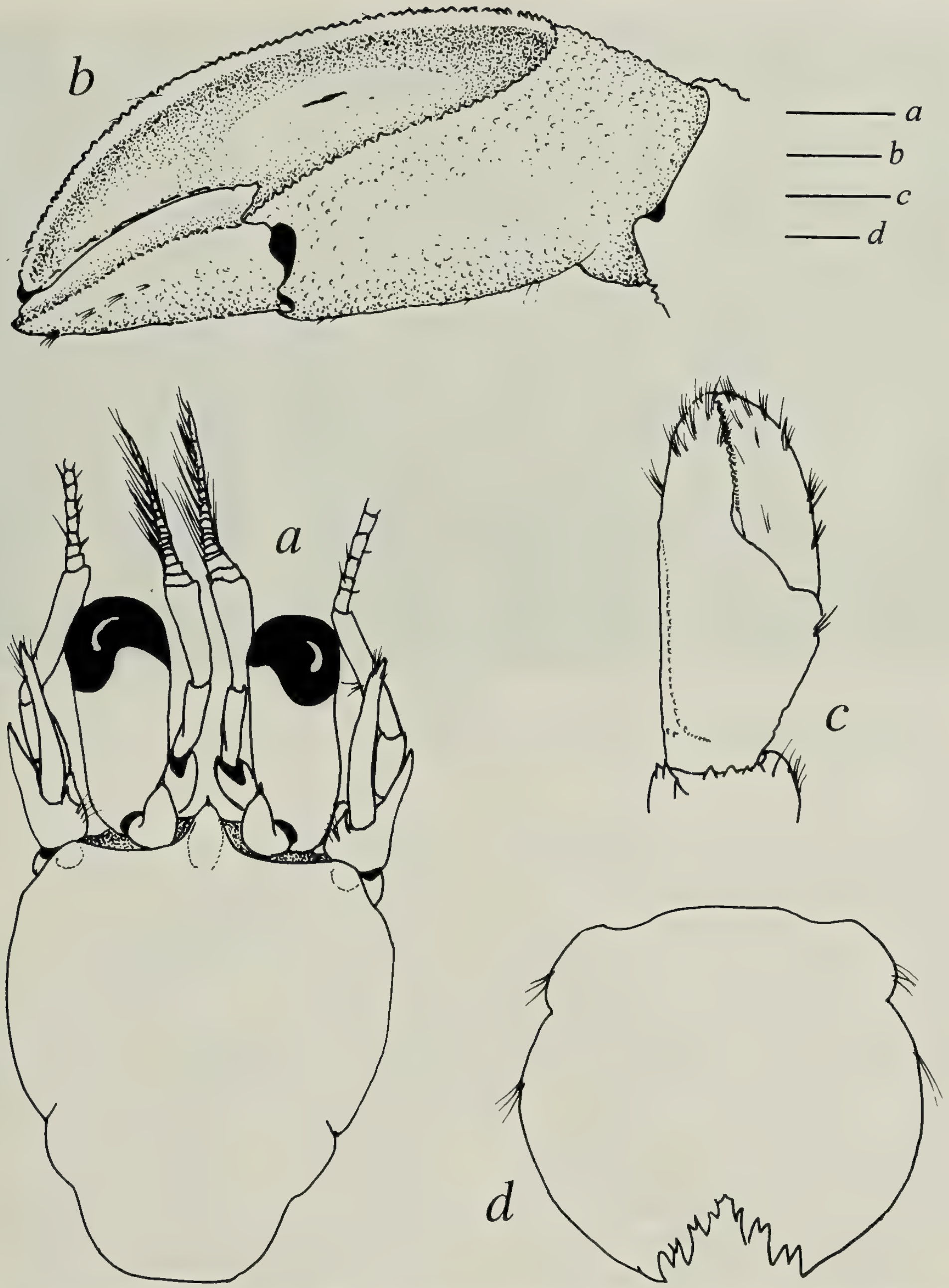

Fig. 7. *Pylopagurus holmesi* Schmitt, 1921, holotype ♂ (sl = 4.0 mm), sta T156, Santa Catalina Island, California, USNM 53330. a, shield and cephalic appendages, dorsal; b, right chela, mesiodorsal; c, left chela, dorsal; d, telson, dorsal. Scales equal 1 mm (a–c), and 0.25 mm (d).

with row of small spines on dorsal margin (largest on second), and accompanied by 1–3 irregular rows of much smaller spinules laterally. Meri with dorsal margins of second unarmed, dorsal margins of third each with row of small corneous spines.

Sternite of third pereopods with small, subovate to subquadrate anterior lobe.

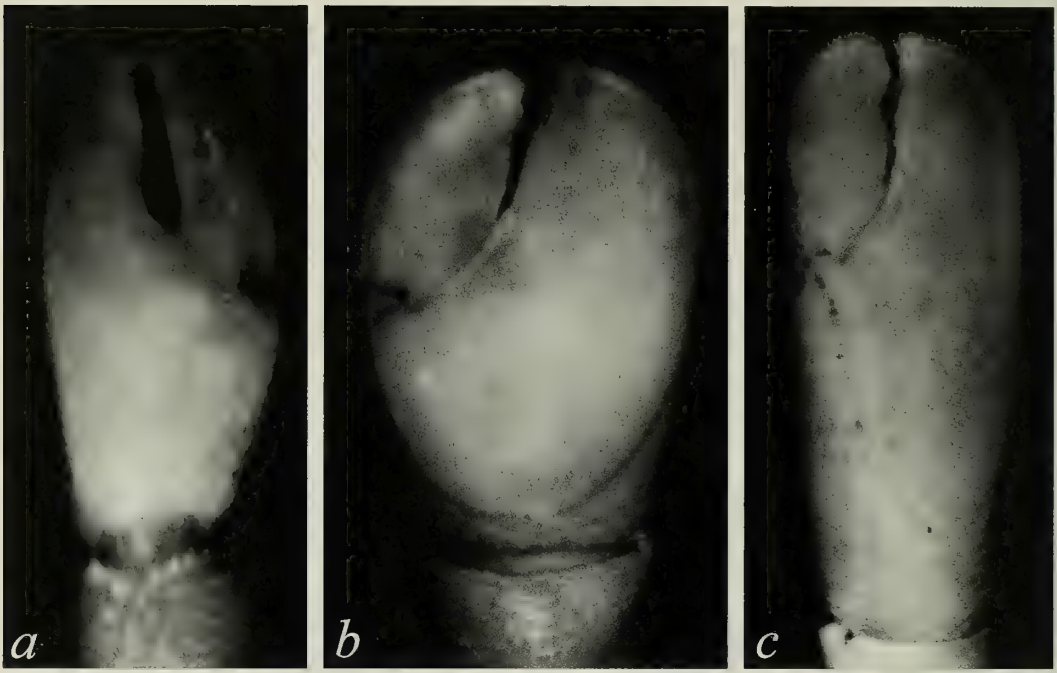

Fig. 8. Chelae of *Pylopagurus holmesi* Schmitt, 1921, dorsal. a, b, ♀ (sl = 3.3 mm), sta 1010-39, Baja California, Mexico, LACM CR193911418; c, ♂ (sl = 2.5 mm), sta 1057-40, Gulf of California, Mexico, LACM CR19402906. a, left (28.1×); b, right (14.4×); c, right (14.3×).

Males apparently without vas deferens produced as short sexual tube(s).

Telson (Fig. 7d) with posterior lobes separated by small median cleft; terminal margins oblique, each with 1–5 blunt or acute spines, strongest at outer angle, lateral margins angular or rounded, each with narrow corneous or weakly calcified plate.

Color.—Unknown.

Habitat.—Walton (1954) reported that specimens he identified as *P. holmesi* occupied *Dentalium* sp. shells and occasionally a tubular bryozoan colony [*Antropora tincta* (Hastings)], whereas specimens he considered to represent *P. longicarpus* were found predominantly in chitinous tubes of the polychaete *Hyalinoecia juvenalis* Moore. Specimens that we examined that were still accompanied by their "housing", occupied scaphopod shells encrusted with a bryozoan.

Distribution.—Eastern Pacific from Channel Islands, California to Baja California and Gulf of California, Mexico; 2–457 m (Walton 1954).

Remarks.—Schmitt (1921) related *P. holmesi* to the western Atlantic *P. discoidalis,* and the two certainly can be considered geminate species. In describing a new species, *P. longicarpus,* from the Gulf of California, Mexico, Walton (1954) separated his taxon from *P. holmesi,* as his specific epithet reflects, by the elongate right chelipeds of males. He noted that "younger forms" and females were practically indistinguishable from *P. holmesi.* Although we have examined only a relatively few specimens, other than the length/width ratio of the carpus and chela of the right cheliped (Fig. 8b, c) in the largest males of *P. longicarpus,* we could find no morphological distinctions between the two taxa. Considering the morphological variability observed in specimens of *P. discoidalis* that appear to be influenced by habitat, it is probable that a similar situation accounts

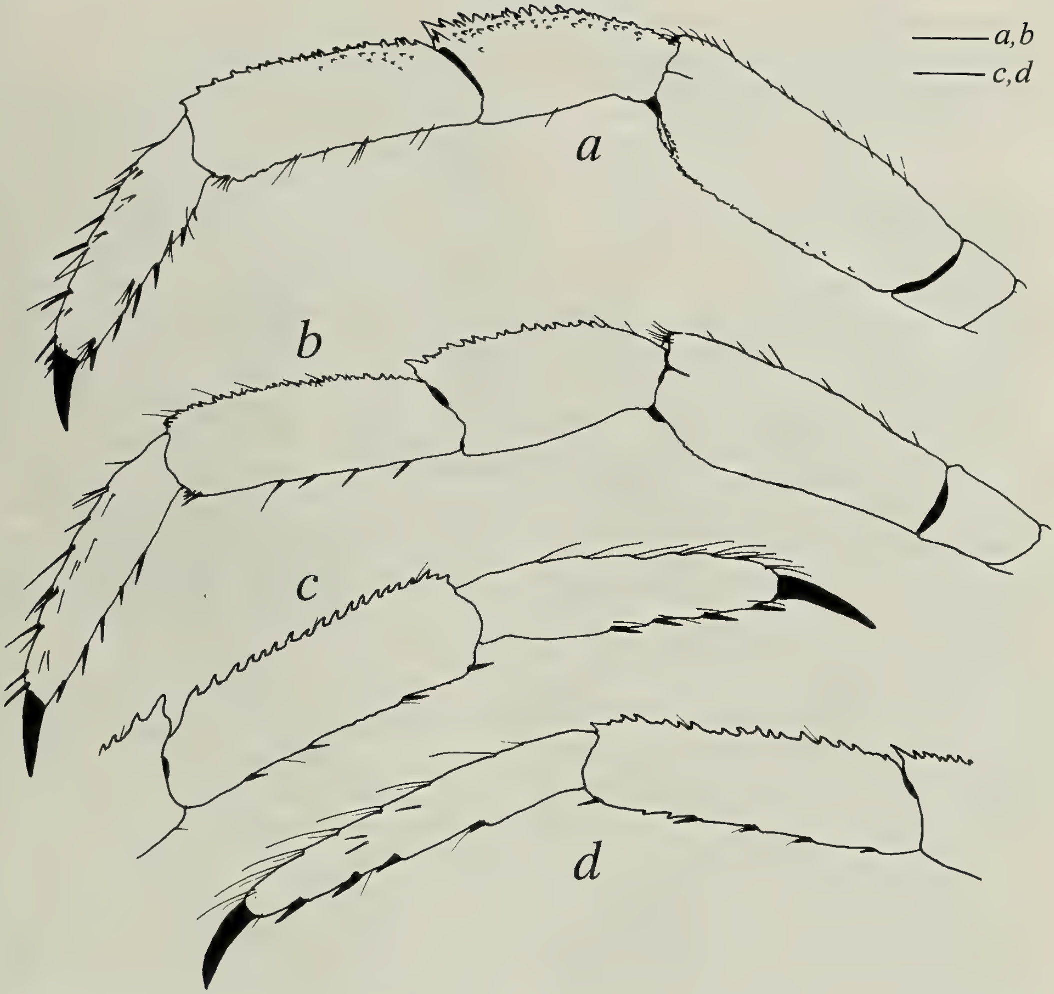

Fig. 9. *Pylopagurus holmesi* Schmitt, 1921. a, b, holotype ♂ (sl = 4.0 mm), sta T156, Santa Catalina Island, California, USNM 53330; c, d, ♂ (sl = 2.5 mm), sta 1057-40, Gulf of California, Mexico, LACM CR19402906. a, left second pereopod, lateral; b, left third pereopod, lateral; c, propodus and dactyl of left second pereopod, mesial; d, propodus and dactyl of left third pereopod, lateral. Scales equal 1 mm (a, b), and 0.5 mm (c, d).

for the cheliped variations seen in the Pacific species.

In our small sample of Walton's (1954) *P. longicarpus,* there appears to be some slight differences in the length of the ambulatory dactyls relative to that of the propodi (Fig. 9c, d) from those of Schmitt's (1921) *P. holmesi* (Fig. 9a, b). However, Walton referred to the "heterogonic" growth most apparent in the form of the right cheliped, but also occurring in the other appendages as well. Considering the small size of *P. longicarpus* (mean of 33 specimens given as 2.0 mm; Walton 1954: 145), it is probable that the observed differences are attributable to size differences, as has been discussed for *P. discoidalis.*

Walton (1954:143) remarked on the broad bathymetric range of *P. holmesi* ("from one . . . to 250 fms"), which is unusual for a subtropical species, and might give cause to believe that two taxa had been confounded. We have not reexamined all of Walton's material, but the depth distribution of his *P. longicarpus* falls well within the range of *P. holmesi* from Schmitt's (1921) original material and from subsequent collections in the San Diego area. The Atlantic geminate species, *P. discoidalis,* has an even broader bathymetric range.

Pylopagurus macgeorgei, new species

Figs. 10, 11a, b, 12

Holotype.—ovig ♀ (sl = 3.9 mm), sta B78-8, S of Cay Sal, Cay Sal Banks, Bahamas, 23°35′N, 80°22′W, 453 m, 15 May 1978, USNM 306889.

Paratypes.—Straits of Florida: 4 ♂ (sl = 2.5–2.9 mm), 3 ♀ (sl = 2.5–2.9 mm), 1 ovig ♀ (sl = 2.6 mm), sta G-524, 26°17′N, 78°41′W, 513–715 m, 3 Mar 1965, USNM 306890.—1 ♂ (sl = 3.9 mm), SB sta 3515, 24°03′N, 79°31′W, 576 m, 8 Nov 1961, SNHM 5267.

Caribbean Sea: 1 ♂ (sl = 1.9 mm), off St. Lucia, Lesser Antilles, sta P-889, 14°04.40′N, 60°50.80′W, 668–725 m, 7 Jul 1969, RMNH D48670.—1 ♀ (sl = 4.2 mm), Gulf of Morrosquillo, Colombia, sta AN-E67, 9°45.36′N, 76°15.35′W, 269–300 m, 13 Apr 1999, INVEMAR-CRU 2062.

Description.—Shield (Fig. 10a) appreciably longer than broad; anterior margin between rostrum and nearly obsolete lateral projections nearly straight; anterolateral margins sloping; posterior margin truncate; dorsal surface glabrous. Rostrum broadly triangular, with acute distinct terminal spine. Lateral projections rounded, unarmed.

Ocular peduncles (including corneas) 0.50 or slightly less than 0.50 length of shield, moderately slender proximally, broadening distally; peduncles twice to 2.50 times as long as shield (corneal diameter included). Ocular acicles very narrowly triangular, terminating acutely, with small submarginal spine; separated basally by approximately twice basal width of 1 acicle.

Antennular peduncles overreaching distal margins of corneas by 0.50–0.90 times length of ultimate segment. Ultimate and penultimate segments with sparse scattered short setae. Basal segment with very small spine on lateral face dorsally.

Antennal peduncles overreaching distal margins of corneas by 0.35–0.50 times length of ultimate segment. Fifth and fourth segments with scattered short setae. Third segment with tiny spinule at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in bifid spine; dorsomesial angle with small spine. First segment produced ventrally and with spinule at ventrolateral margin. Antennal acicles reaching or overreaching distal margins of corneas; reaching to or nearly to mid-length of fifth peduncular segment. Flagellum with 2 or 3 long and 1 or 2 short setae every article, at least in proximal half. Sternite of third maxillipeds unarmed or with tiny spinule on either side of median cleft.

Right cheliped (Figs. 10b, 11b) moderately stout. Dactyl approximately 0.75 times length of palm; dorsomesial margin developed as thin elevated ridge in proximal 0.65, horizontal distally; dorsal surface weakly convex, unarmed; cutting edge calcareous with 1 weakly developed tooth distally; terminating in small corneous claw and slightly overlapped by fixed finger; ventral surface with few tufts of short setae. Palm about as long as broad or slightly longer than broad; dorsal surface weakly convex (Fig. 10b), unarmed, dorsal surface of fixed finger weakly concave; dorsomesial and dorsolateral margins elevated to form marginal ridge, joined by similar ridge proximally on palm, adjacent proximal area with scattered very low protuberances and sparse very short setae; mesial, lateral and ventral surfaces also with few sparse tufts of short setae; cutting edge of fixed finger calcareous, with 1 broad calcareous tooth. Carpus 0.60–0.70 times length of merus, roundly subtriangular; dorsomesial and dorsolateral margins not delimited, dorsomesial distal angle with very small spine; dorsal surface with few low, sometimes spinulose protuberances laterally; other surfaces unarmed. Merus triangular; dorsodistal

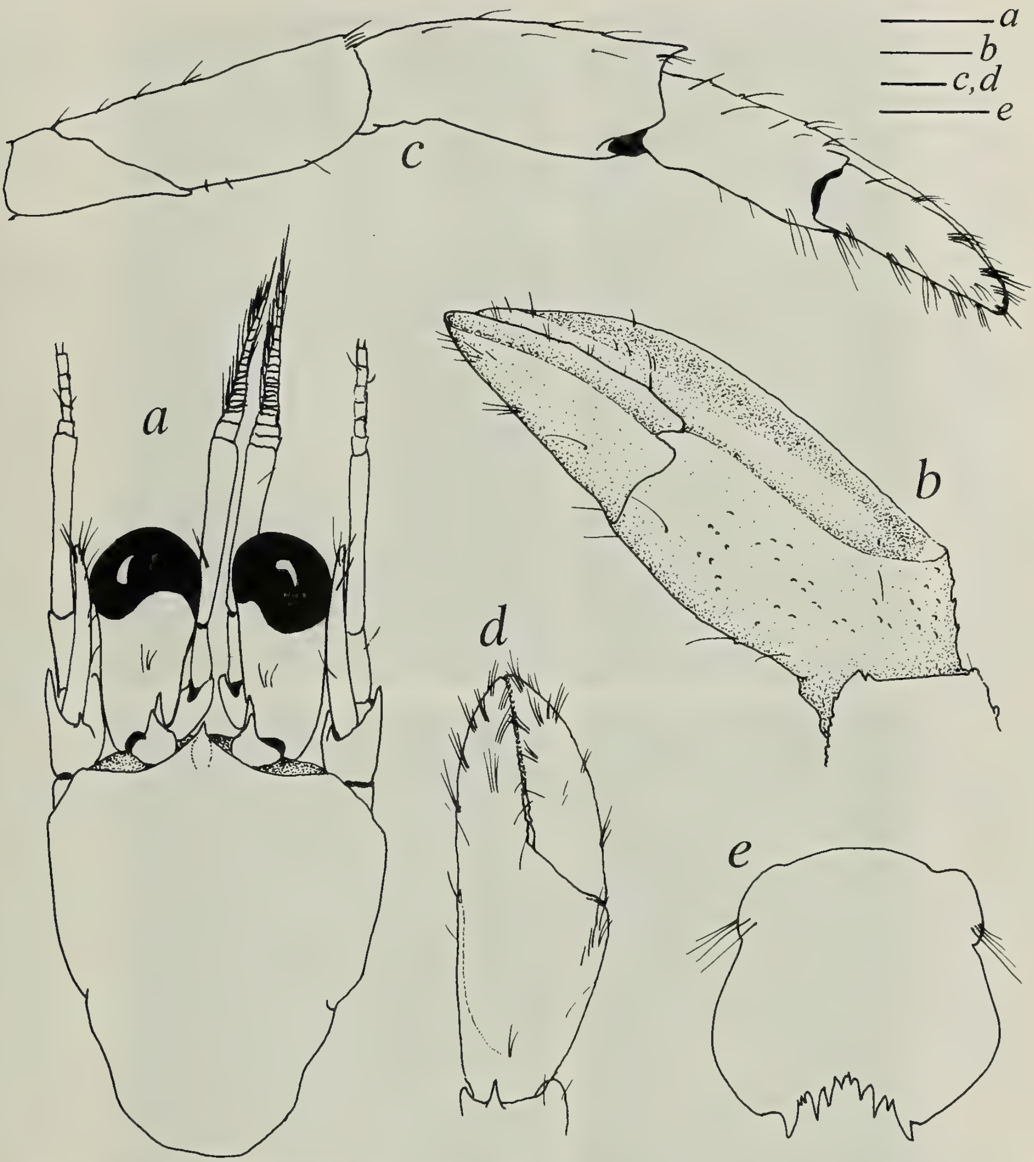

Fig. 10. *Pylopagurus macgeorgei,* new species, holotype ovig ♀ (sl = 3.9 mm), FIU sta B78-8, Cay Sal Banks, USNM 306889. a, shield and cephalic appendages, dorsal; b, right chela, mesiodorsal; c, left cheliped, mesial; d, chela of same, dorsal; e, telson, dorsal. Scales equal 1 mm (a, b), and 0.5 mm (c-e).

margin with 1–4 small spines and several short stiff setae; other margins and surfaces unarmed, but with scattered short setae. Ischium unarmed.

Left cheliped (Figs. 10c, d, 11a) with dactyl slightly longer than palm; surfaces of dactyl, fixed finger and palm all unarmed except for sparse tufts of setae and minute tubercles on dorsoproximal face of palm. Carpus approximately equal to length of merus; dorsodistal margin with small to moderately large spine, dorsal surface with sparse row of tufts of setae; other surfaces unarmed and nearly glabrous. Merus with stiff setae on dorsodistal margin. Ischium unarmed.

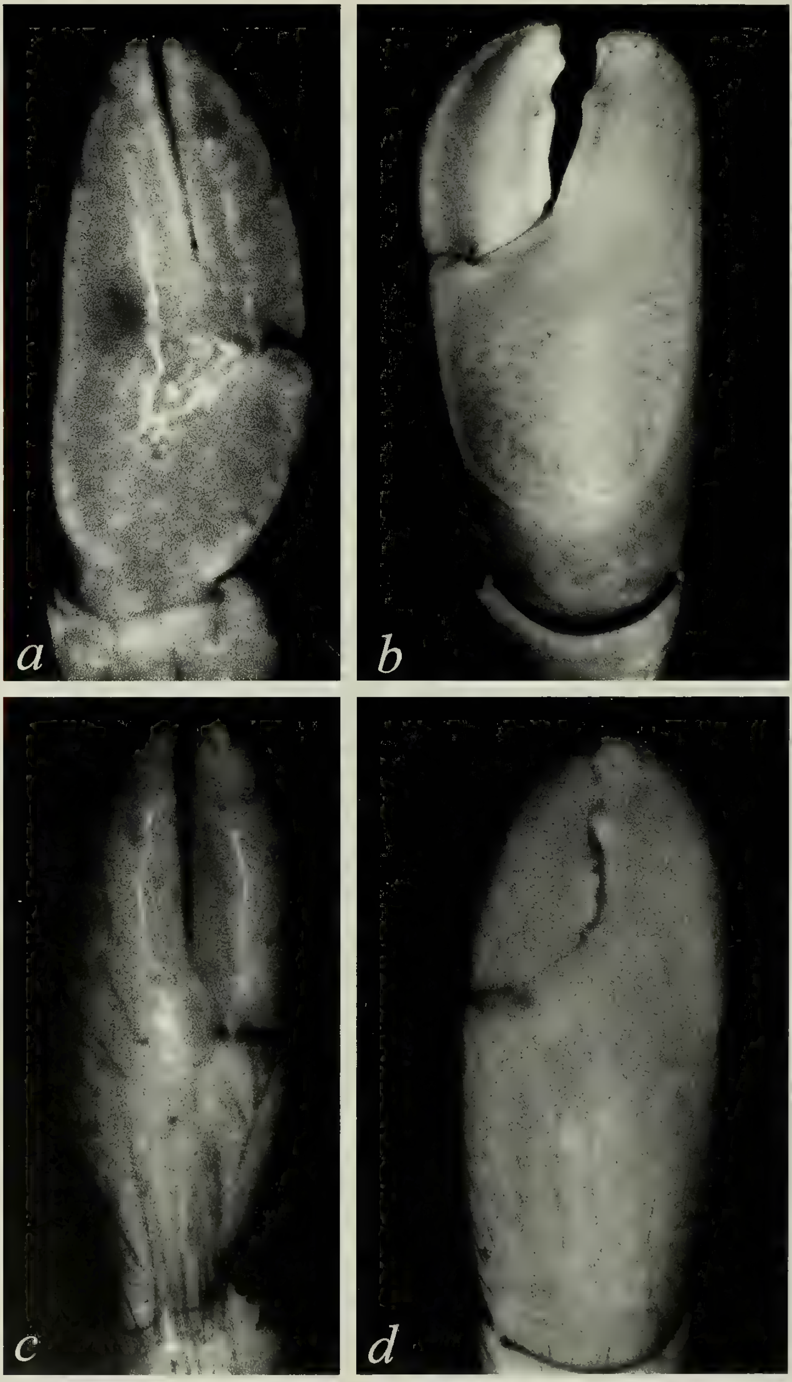

Fig. 11. Chelae of *Pylopagurus macgeorgei,* new species (a, b), and *P. gorei,* new species (c, d), dorsal. a, b, paratype ovig ♀ (sl = 2.6 mm), Straits of Florida, USNM 306890; c, d, paratype ♂ (sl = 3.8 mm), sta O-4572, Gulf of Mexico, USNM 306892. a, left (36.9×); b, right (13.4×); c, left (24.3×); d, right (12.2×).

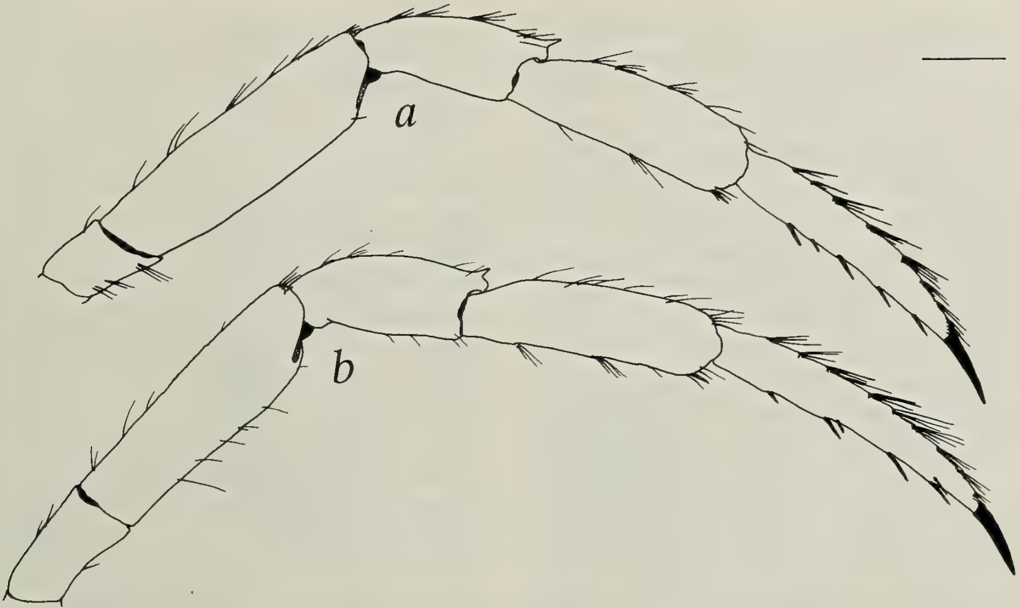

Fig. 12. *Pylopagurus macgeorgei,* new species, holotype ovig ♀ (sl = 3.9 mm), FIU sta B78-8, Cay Sal Banks, USNM 306889. a, right second pereopod, lateral; b, right third pereopod, lateral. Scale equals 1 mm.

Ambulatory legs (Fig. 12) moderately short; similar from left to right. Dactyls about 1.50 times or more as long as propodi; dorsal surfaces each with row of widely-spaced protuberances, each with 1–3 long stiff setae; ventral margins each with row of 5 or 6 corneous spines and few short setae. Propodi 1.25–1.35 times length of carpi; dorsal surfaces each with row of widely-spaced sparse tufts of stiff setae; ventrodistal margins each with 1 or 2 corneous spines, longest on second. Carpi 0.45–0.65 times length of meri, each with prominent dorsodistal spine (smaller on third pereopods), and tufts of setae, at least dorsally. Meri and ischia unarmed, but with dorsal and often also ventral sparse tufts of setae.

Sternite of third pereopods with small, subquadrate or subovate anterior lobe. Sternites of fourth and fifth pereopods in males with capsulate setae. Males often with vas deferens slightly produced on one or both coxae of fifth pereopods to form short, transparent sexual tube(s).

Telson (Fig. 10e) with weak transverse indentation suggesting division into anterior and posterior portions; posterior lobes approximately equal, separated by distinct medial cleft; terminal margins somewhat concave, each with 2 or 3 slender spines interspersed with smaller spines; prominently produced acute or subacute outer angles.

Color.—In life, body and appendages without color.

Habitat.—Scaphopod shells accompanied by anemone.

Distribution.—Western Atlantic and Caribbean Sea, from Bahamas to off Barbados and Colombia; 453–715 m.

Etymology.—This species is dedicated to the late E. J. McGeorge, whose photographs have augmented the descriptions of nearly all of the "*Pylopagurus-Tomopagurus*" group species.

Remarks.—*Pylopagurus macgeorgei,* new species, is superficially quite similar to *P. pattiae,* and because of variation, the only morphological characters truly diagnostic for separating the two taxa are the lengths of the antennal acicles and the armature of the terminal margins of the telson. In *P. pattiae,* the antennal acicles are quite short, rarely reach beyond the bases of the corneas (Fig. 2a); the terminal margins of the telson have one to three short spines (Fig. 2h). In contrast, the antennal acicles of *P. macgeorgei* reach to or beyond the distal corneal margins (Fig. 10a); the terminal margins of the telson each have two or three long, slender spines interspersed with short spines (Fig. 10e). Additionally, the ocular and antennal acicles of *P. macgeorgei* are much narrower than those of *P. pattiae,* and the dactyls of the ambulatory legs are longer (1.50 times or more as long as the propodi). In life, color, or the lack of all color in *P. macgeorgei* will serve to distinguish this taxon.

Equally important is the fact that the two species occupy distinctly different habitats. *Pylopagurus macgeorgei* has only been found in scaphopod shells each with an attached anemone, and at depths in excess of 453 m. In contrast, *P. pattiae* is a relatively shallow-water species (20–82 m) that has been found almost exclusively in corneous, semi-transparent tubes built by polychaetes of the family Onyphidae.

Pylopagurus gorei, new species

Figs. 11c, d, 13

Holotype.—ovig ♀ (sl = 3.0 mm), sta O-4572, 23°23′N, 86°56′W, 549 m, 8 Dec 1953, USNM 306891.

Paratypes.—Eastern coast of United States: 1 ♂ (sl = 1.8 mm), off Florida, 29°38′N, 79°53′W, 520 m, 1 Sep 1977, coll. K. Shaw, USNM 174391.

Gulf of Mexico: 2 ♂ (sl = 3.0–3.8 mm), 1 ♀ (sl = 3.1 mm), sta O-4572, 23°23′N, 86°56′W, 549 m, 8 Dec 1953, USNM 306892.—3 ♂ (sl = 1.5–2.7 mm), sta P-904, 13°45.50′N, 61°05.70′W, 417–589 m, 9 Jul 1969, SMNH 5265, 5266.

Caribbean Sea: 1 ovig ♀ (sl = 2.5 mm), sta SB-3515, Bahamas, 24°03′N, 79°31′W, 576 m, 8 Nov 1961, USNM 306894.—6 ♂, 3 with rhizocephalans (sl = 2.0–2.7 mm), 1 ♀ with rhizocephalan (sl = 2.2 mm), sta P-607, 18°30′N, 87°37′W, 715–787 m, 17–18 Mar 1968, RMNH D48669, USNM 306893.

Description.—Shield (Fig. 13a) longer than broad; anterior margin between rostrum and broadly rounded lateral projections straight or weakly concave; anterolateral margins sloping; posterior margin truncate; dorsal surface glabrous. Rostrum triangular, with acute terminal spine or spinule. Lateral projections unarmed.

Ocular peduncles short, moderately stout, less than 0.50 length of shield, broadening distally. Ocular acicles triangular, terminating acutely, with simple or minutely bifid submarginal spine; separated basally by approximately basal width of 1 acicle.

Antennular peduncles overreaching distal margins of corneas by 0.80–0.95 times length of ultimate segment. Ultimate and penultimate segments with sparse scattered short setae. Basal segment with very tiny spinule on lateral face dorsally.

Antennal peduncles overreaching distal margins of corneas by 0.75–0.90 times length of ultimate segment. Fifth and fourth segments with scattered short setae. Third segment unarmed or with tiny spinule at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in simple or weakly bifid spine; dorsomesial angle with small spine. First segment produced ventrally, unarmed. Antennal acicles reaching beyond distal margins of corneas, but usually not reaching beyond mid-length of fifth peduncular segment. Flagellum with 1 or 2 moderately long and 1 or 2 short setae every 1–3 articles, at least in proximal half. Sternite of third maxillipeds with spine on either side of midline.

Right cheliped (Figs. 11d, 13b) moderately long and slender. Dactyl approximately 0.65–0.75 times length of palm; dorsomesial margin developed as thin slightly elevated, minutely serrate ridge, dorsal surface weakly convex, unarmed; cutting edge with 2 partially coalesced calcareous teeth proximally, 1 more weakly developed tooth

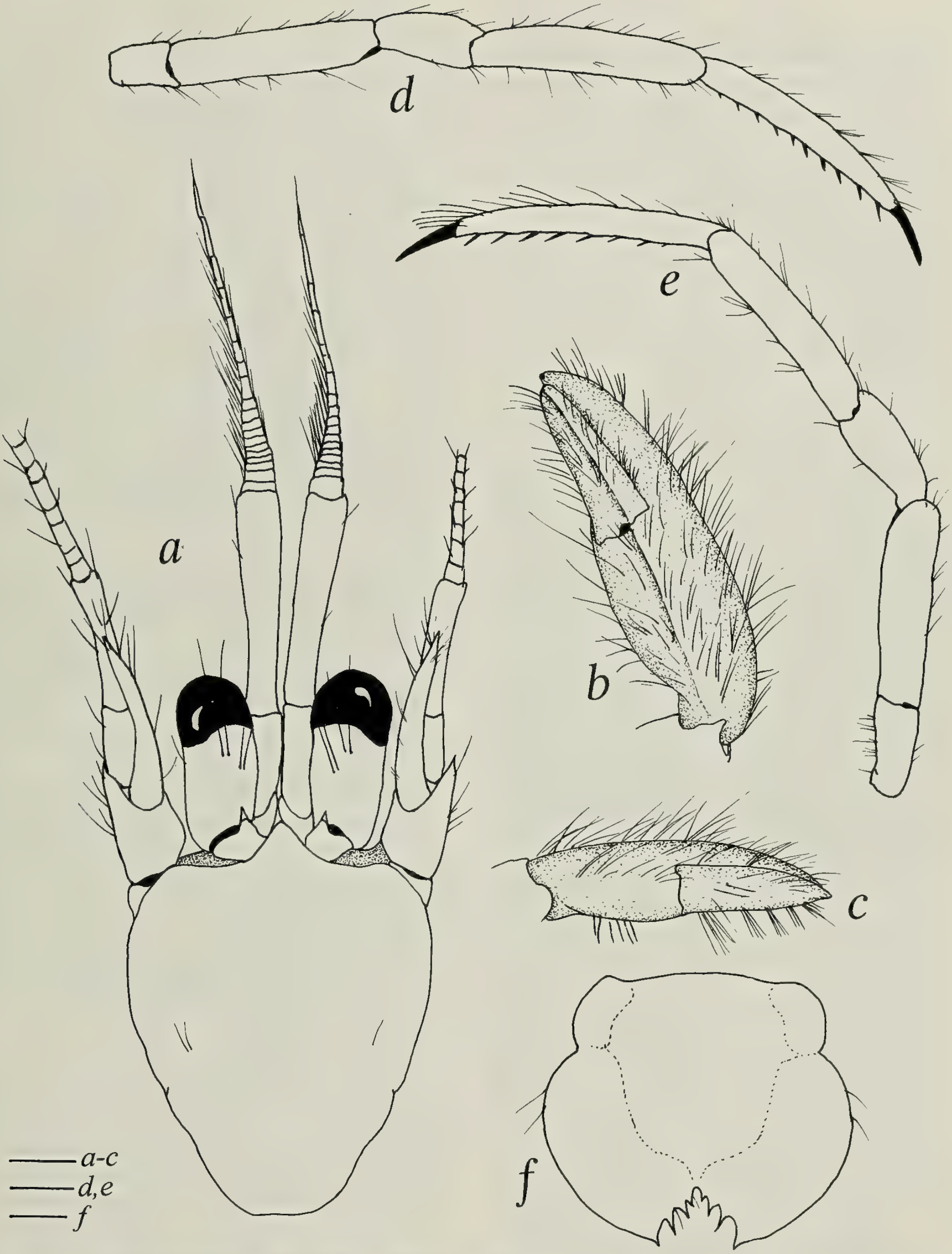

Fig. 13. *Pylopagurus gorei,* new species, paratype ♂ (sl = 3.0 mm), Gulf of Mexico, sta O-4572, USNM 306892. a, shield and cephalic appendages, dorsal; b, right chela, mesial; c, left chela, mesial; d, right second pereopod, lateral; e, right third pereopod, mesial; f, telson, dorsal. Scales equal 0.5 mm (a–c, 1 mm (d, e), and 0.1 mm (f).

distally separated by row of tiny calcareous teeth; terminating in small corneous claw and slightly overlapped by fixed finger; mesial and ventral surfaces with sparse tufts of short setae. Palm (Fig. 13b) approximately 1.25–1.40 times as long as broad; dorsal surface convex, unarmed, but with sparse covering of moderately long setae, dorsal surface of fixed finger weakly concave; dorsomesial and dorsolateral margins elevated to form low, smooth or microscopically serrate ridges; mesial, lateral and ventral surfaces with sparse tufts of short setae; cutting edge of fixed finger marginally calcareous, with 1 broad calcareous tooth approximately at mid-length. Carpus as long as or slightly longer than merus, roundly subtrapezoidal; dorsomesial margin rounded, dorsomesial distal angle with very prominent spine; dorsolateral margin not delimited, convex dorsal surface with numerous moderately long setae; mesial face concave below produced dorsomesial angle, and with numerous very short, very low transverse ridges accompanied by fine setae; lateral and ventral surfaces convex, with scattered setae. Merus triangular; dorsodistal margin with few setae; ventromesial margin with 1 or 2 small blunt tubercles; ventrolateral margin unarmed, surfaces and margins all with scattered setae. Ischium unarmed.

Left cheliped (Figs. 11c, 13c) with dactyl equal to or slightly longer than palm; surfaces of dactyl, fixed finger unarmed but with numerous sparse tufts of long setae; palm with dorsolateral margin delimited by very weak ridge, dorsal surface somewhat elevated in midline, and usually with short row of very tiny blunt or spinulose granules; other surfaces with numerous moderately long to long, fine setae. Carpus approximately equal to length of merus; dorsomesial and dorsolateral distal angles each with prominent spine, dorsal surface with faint row of low protuberances and tufts of setae mesially and laterally, other surfaces unarmed but with sparse tufts of moderate to long setae. Merus unarmed, but with setae dorsally and ventrally. Ischium unarmed.

Ambulatory legs (Fig. 13d, e) moderately long and slender; similar from left to right. Dactyls equal to or longer than propodi; dorsal surfaces with each with row of low protuberances and sparse tufts of long or moderately long setae; ventral margins each with row of 6–8 corneous spines and few short setae. Propodi 1.25 times to nearly twice length of carpi; dorsal surfaces each with row of very low, widely-spaced protuberances and sparse tufts of setae; ventrodistal margins sometimes with 1 stiff bristle. Carpi 0.45–0.65 times length of meri, unarmed but with sparse tufts of setae dorsally and ventrally. Meri and ischia unarmed, but with dorsal and ventral sparse tufts of setae.

Sternite of third pereopods with small, subquadrate or subovate anterior lobe, in males sometimes partially concealed by 1 or 2 capsulate setae. Sternites of fourth and fifth pereopods in males also with capsulate setae. Males without vas deferens produced from gonopores into short tubes.

Telson (Fig. 13f) with weak transverse indentation suggesting division into anterior and posterior portions; posterior lobes approximately equal, separated by distinct median cleft; terminal margins somewhat concave, each with 2–4 usually slender spines sometimes interspersed with smaller spines; prominently produced acute or subacute outer angles.

Color.—Unknown.

Etymology.—This species is named for Dr. Robert H. Gore, esteemed friend and colleague, who, during his tenure in carcinology, contributed substantially to our knowledge of systematics, evolution, and development in decapods, and who is still willing to share from his bountiful reservoir of information on the subjects.

Habitat.—Has only been found inhabiting scaphopod shells, frequently encrusted with bryozoans.

Distribution.—Broadly, but uncommonly distributed in the western Atlantic from the

Gulf of Mexico to the Lesser Antilles; 417–787 m.

Remarks.—*Pylopagurus gorei,* new species, is a member of that group of species in the genus that are characterized by an absence of strong spines on the propodi and carpi of the ambulatory legs. This species is readily distinguished from *P. macgeorgei,* new species, and *P. pattiae* by the absence of an elevated ridge on the posterior dorsal surface of the palm of the right cheliped (Figs. 11d, 13b), and the absence of a dorsodistal carpal spine on the ambulatory legs (Fig. 13d, e).

In contrast to the "feminizing" effect of rhizocephalan infestation seen in some "*Pylopagurus-Tomopagurus*" group species (see Remarks under *P. pattiae*), we found no evidence of morphological alteration in either males or females of *P. gorei,* similarly infected. Nor was any development of short sexual tubes apparent either in infected or uninfected specimens.

Key to species of *Pylopagurus*

1. Antennal acicles short, usually not reaching to bases of corneas, rarely only slightly beyond; dorsal margins of propodus and carpus of right second pereopod unarmed, or rarely microscopically serrate ...... *P. pattiae* (western Atlantic)
– Antennal acicles long or moderately long, reaching at least to mid-length of corneas, often beyond distal margins; dorsal margins of propodus and carpus of right second pereopod variable 2
2. Dorsal surfaces of propodi and carpi of ambulatory legs distinctly denticulate, serrate or spinose 3
– Dorsal surfaces of propodi and carpi of ambulatory legs smooth or with only minute protuberances 4
3. Antennular peduncles overreach distal margins of corneas by nearly entire length of ultimate segment; antennal peduncles overreach distal margins of corneas by more than half length of ultimate segment .. *P. discoidalis* (western Atlantic)
– Antennular peduncles overreach distal margins of corneas by 0.25–0.50 times length of ultimate segment; antennal peduncles reach to distal margins of corneas or beyond by no more than half length of ultimate segment ....*P. holmesi* (eastern Pacific)
4. Chela of right cheliped circumscribed by raised, smooth or crenulated ridge .... *P. macgeorgei,* new species .... (western Atlantic)
– Chela of right cheliped not circumscribed by raised, smooth or crenulated ridge .... *P. gorei,* new species (western Atlantic)

Pylopaguridium, new genus

Type species.—*Pylopaguridium markhami,* new species. Gender: neuter.

Diagnosis.—Eleven pairs of biserial gills. Strongly armed lateral projections widely separated from acute rostrum. Ocular acicles multispinose. Maxillule (Fig. 1g) with external lobe of endopod moderately well developed, not recurved, internal lobe with 1 terminal bristle. Maxilla (Fig. 1h) with proximal lobe of scaphognathite moderately narrow. First maxilliped (Fig. 1i) with slender exopod. Third maxilliped with well developed crista dentata and prominent accessory tooth; merus with prominent spine at dorsodistal margin. Sternite of third maxillipeds unarmed.

Right cheliped markedly larger than left, subrectangular, operculate; angle of articulation of chela and carpus generally perpendicular. Left cheliped with chela small; dactyl and fixed finger dorsoventrally compressed; palm flattened, slightly concave or slightly convex; angle of articulation of chela and carpus perpendicular or only slightly twisted. Ambulatory legs with dorsodistal carpal spine. Fourth pereopods (Fig. 16e) with very small preungual process (not apparent in Fig. 16e, visible under high magnification) on dactyl; propodal rasp consisting of single row of corneous scales.

Sternite of third pereopods with subsemicircular or subovate anterior lobe. Sternites of pereopods 4 and 5 broad. Males with paired gonopores; coxae of fifth pereopods asymmetrical; left produced posteriorly as rounded, gonopore-bearing lobe; gonopore partially masked by tuft of stiff setae on posterior margin, directed anteriorly; 3 unpaired unequally biramous left pleopods (3–5); exopods long, slender, endopods reduced. Females with paired gonopores on coxae of third pereopods; paired first pleopods incompletely 2-segmented and modified as gonopods (Fig. 15g), and 4 unpaired biramous left pleopods, second through fourth with both rami well developed, fifth as in male.

Abdomen flexed. Uropods asymmetrical. Telson with lateral indentations suggesting division into anterior and posterior portions; posterior lobes symmetrical or only slightly asymmetrical, terminal margins armed with 2 to several small spines.

Etymology.—A combination of *Pylo,* indicating the relationship to the "*Pylopagurus-Tomopagurus*" group genera, and *Paguridium,* referring to the genus typified by the enlarged coxa of the male left fifth pereopod.

Distribution.—Western Atlantic from Bahamas to Caribbean Sea off eastern Honduras.

Remarks.—This genus, at present monotypic, while related to other "*Pylopagurus-Tomopagurus*" group genera by the gill number and structure and presence in females of paired first pleopods, is distinguished from all other "*Plyopagurus-Tomopagurus*" group genera, by the asymmetry of the coxae of male fifth pereopods. Additionally, the broad sternal plates of the third through fifth pereopods (thoracic sternites 6–8) are not commonly seen in the majority of "*Pylopagurus-Tomopagurus*" group genera; however, this character may be more strongly influenced by habitat preferences than genetics.

Pylopaguridium markhami, new species
Figs. 14c, d, 15, 16

Holotype.—♂ (sl = 1.8 mm), sta D66, off east side of Fortune Island, Bahamas, 22°11′N, 74°17.40′W, 26 m, 30 Aug 1973, coll. J. C. Markham, USNM 306895.

Paratypes.—Caribbean Sea: 1 ♀ (sl = 2.3 mm), sta D61, off east side of Fortune Island, Bahamas, 22°36.10′N, 74°22.10′W, 17.5 m, 28 Aug 1973, coll. J. C. Markham, SMNH 5264.—1 ♂ (sl = 2.0 mm), 1 ♀ (sl = 1.7 mm), sta D68, off west end, Providence Isles, Turks and Caicos Islands, 21°50.50′N, 72°20.80′W, 23 m, 31 Aug 1973, coll. J. C. Markham, USNM 306896.—1 ♂ (sl = 1.4 mm), sta D71, off west end, Providence Isles, Turks and Caicos Islands, 21°50.50′N, 72°20.80′W, 23 m, 31 Aug 1973, coll. J. C. Markham, RMNH D48668.—1 ♂ (molting, no measurement possible), sta P-630, 15°59.20′N, 86°02′W, 35–37 m, 21 Mar 1968, USNM 306897.

Description.—Shield (Fig. 15a) slightly to considerably longer than broad; anterior margin between rostrum and lateral projections somewhat concave; anterolateral margins sloping; posterior margin rounded; dorsal surface glabrous. Rostrum triangular, drawn out into slender spine. Lateral projections with very prominent marginal or submarginal spine.

Ocular peduncles moderately long and slender, about 0.80 times as long as shield length, somewhat swollen basally and tapering to bases of very slightly dilated corneas. Ocular acicles each with 4 or 5 slender spines; separated basally by approximately basal width of 1 acicle.

Antennular peduncles reaching to distal margins of corneas or beyond by nearly 0.35 times length of ultimate segment. Ultimate segment with 1–3 short seat at dorsolateral distal angle. Penultimate segment glabrous or with 1 or 2 short setae. Basal segment with prominent spine on lateral face dorsally.

Antennal peduncles approximately equal to length of ocular peduncles (including corneas) or somewhat longer. Fifth and fourth segments with few scattered setae. Third segment with prominent spine on ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine. First segment often with minute spinule on laterodistal margin dorsally; ventrodistal margin produced and with small spine laterally. Antennal acicles reaching to bases of corneas or slightly beyond. Antennal flagella with 1 or 2 very short setae on every article proximally, less regular distally.

Right cheliped (Figs. 14d, 15b) longer and appreciably stronger than left. Dactyl approximately 0.85 times length of palm; dorsomesial face proximally and dorsomesial margin depressed ventrally, dorsomesial margin with row of small tubercles or spines; entire dorsal surface covered, but not extremely densely with blunt or spinulose tubercles or small spines; ventral surface with faint transverse rows of very low protuberances; cutting edge with 1 large calcareous tooth in proximal half and row of small calcareous teeth distally; terminating in small corneous claw. Palm approximately as long as carpus; dorsomesial distal angle produced as large tubercle or spine, dorsomesial margin rounded and armed with 2 or 3 longitudinal rows of small spines, tubercles or granules, dorsal surfaces of palm and fixed finger tuberculate or spinulose, 1–3 more prominent and somewhat raised spines or spinulose tubercles on dorsolateral face of palm proximally; dorsolateral margin with row of small tubercles or spines not extending full length of fixed finger; lateral face of fixed finger also tuberculate; lateral face and ventral surface of palm very weakly tuberculate or granular. Carpus approximately equal to length of merus; dorsomesial margin with row of 5 or 6 prominent spines, dorsolateral margin with row of slightly smaller, more closely-spaced spines, dorsal surface with 2–4 additional large to moderately small spines; dorsodistal margin with prominent spine, mesio- and ventrodistal margins minutely spinulose or tuberculate; laterodistal margin with small spine dorsally, ventrolateral margin with spine distally. Merus with prominent spine on dorsodistal margin, dorsal surface with few setae; ventrolateral margin with row of slender acute spines; ventromesial margin with 1 or 2 small spines distally and tiny spinulose protuberances proximally. Ischium unarmed.

Left cheliped (Figs. 14c, 15c, d) with dactyl approximately 1.25 times length of palm; dorsomesial margin not delimited; dorsal, mesial and ventral surfaces with tufts of moderately long, stiff setae, dorsal surface also sometimes with few spinulose protuberances. Palm 0.50–0.75 times length of carpus; dorsal surface elevated in midline, not produced into prominent keel or crest, but armed with double row of small blunt or spinulose tubercles, extending onto fixed finger as single row, not extending to tip; dorsolateral and dorsomesial surfaces each with few small tubercles, dorsolateral margin with row of small spines or spinulose tubercles, dorsomesial margin not delimited; lateral and ventral surfaces varying from tuberculate to only faintly granular. Carpus equal to or slightly shorter than merus; dorsomesial and dorsolateral margins each with row of 4 or 5 spines; ventrolateral margin with 2 or 3 smaller spines distally. Merus subtriangular; dorsal margin unarmed; ventrolateral margin with row of acute spines; ventromesial margin with spine or spinule distally. Ischium unarmed.

Ambulatory legs (Fig. 16a–d) moderately long and stout; similar from left to right. Dactyls slightly longer than propodi; dorsal surfaces with sparse tufts of short setae; ventral margins each with row of 9–15, rather closely-set corneous spines, increasing in size distally. Propodi nearly twice length of carpi; dorsal surface occasionally with few low protuberances and corneous spinules; 1 or 2 corneous spines at ventrodistal angles, and often row of very small corneous spinules on ventral surface. Carpi each with dorsodistal spine and few scattered setae. Meri usually each with spine on ventral margin in distal half (second) or unarmed, but with few sparse setae.

Anterior lobe of sternite of third pereopods (Fig. 15e) with small spines anteriorly.

Telson (Fig. 15h) with very deep, broad median cleft; posterior lobes each with

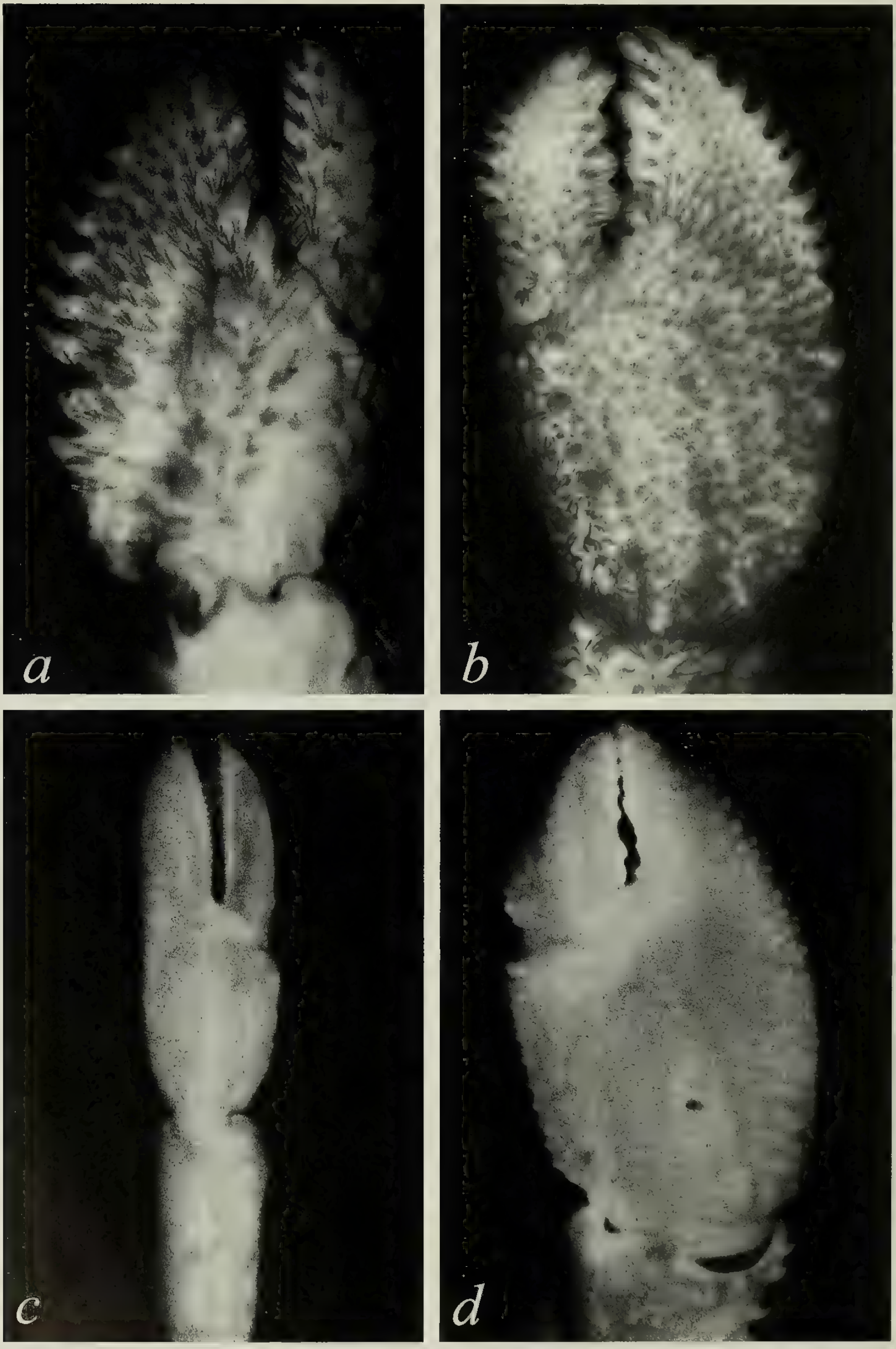

Fig. 14. Chelae of *Haigia diegensis* (Scanland & Hopkins, 1969) (a, b), and *Pylopaguridium markhami*, new species (c, d), dorsal. a, b, ♂ (sl 6.4 mm), Farnsworth Bank, LACM CR19703301; c, d, paratype ♀ (sl = 2.3 mm), sta D61, Bahamas, SNHM 5264. a, left (16.0×); b, right (9.9×); c, left (23.4×); d, right (23.3×).

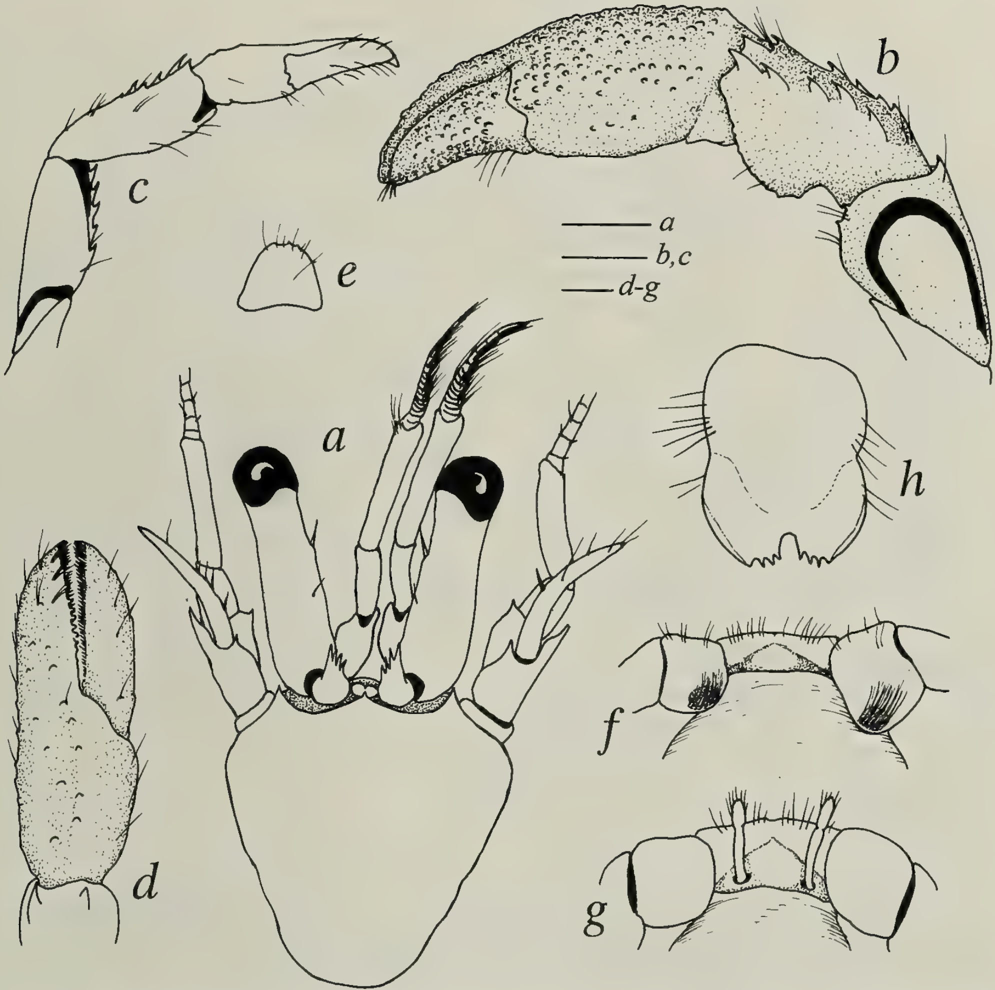

Fig. 15. *Pylopaguridium markhami,* new species. a, b, e, f, holotype ♂ (sl = 1.8 mm), sta D66, Bahamas, USNM 306895; c, d, g, paratypes, sta D68, Turks and Caicos Islands, USNM 306896: c, d, ♂ (sl = 2.0 mm); g, ♀ (sl = 1.7 mm). a, shield and cephalic appendages, dorsal; b, right cheliped, mesial; c, left cheliped, mesial; d, chela of same, dorsal; e, anterior lobe of sternite of third pereopods, ventral; f, coxae and sternite of fifth pereopods, and part of abdomen (lower), ventral; g, coxae and sternite of fifth pereopods, and part of abdomen (lower) showing first pleopods, ventral; telson, dorsal. Scales equal 0.5 mm (a–c), and 0.25 mm (d–g).

nearly straight terminal margins armed with 3 or 4 small spines.

Color.—Shield with faint yellowish tint and blue mottling. Ocular peduncles also with yellow tint and blue mottling. Antennular peduncles with basal segment faint yellow with blue mottling. Antennular peduncles with ultimate segment and flagella purple. Antennal peduncles with faint reddish-brown band on dorsal surface and reddish-brown patch proximally on ultimate segment; antennal acicle with prominent large reddish-brown patch in distal half and lighter, smaller patch proximally. Right cheliped with chela mottled reddish-brown, dactyl and distal part of fixed finger cream with patches of reddish-brown; carpus white distally, mottled reddish-brown and cream on remainder of carpus, merus and ischium. Left cheliped with chela light red-

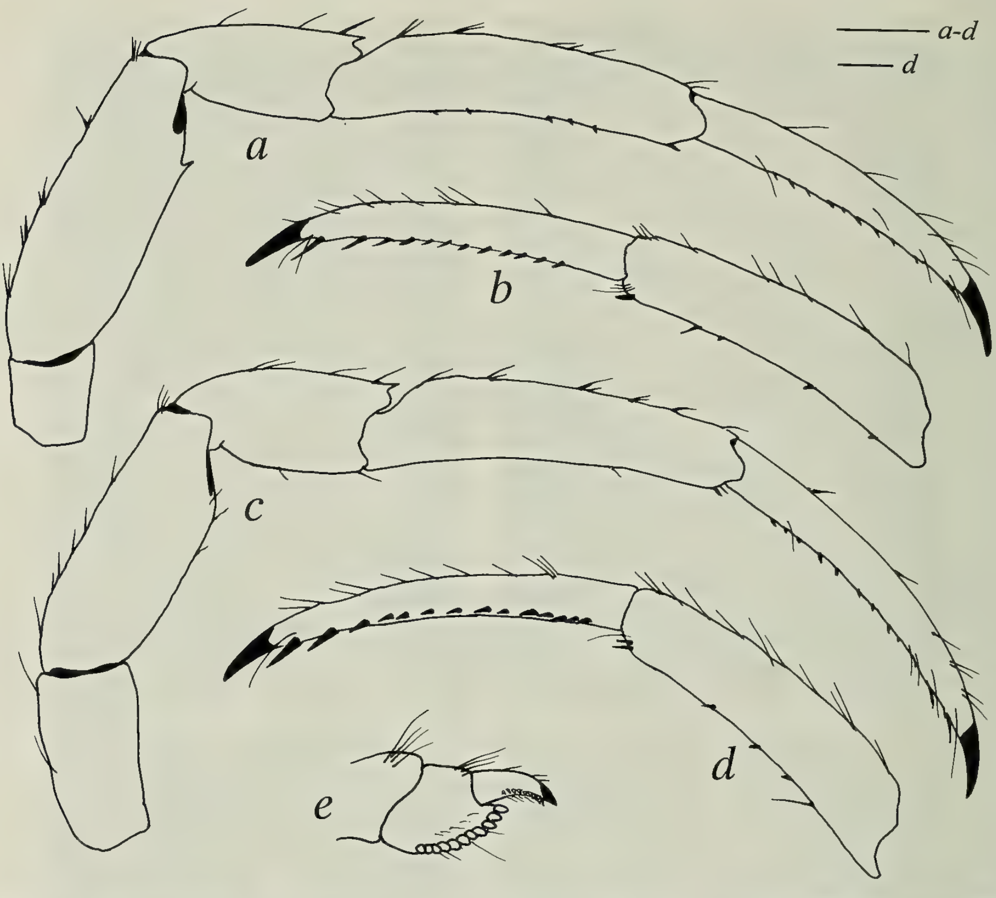

Fig. 16. *Pylopaguridium markhami,* new species. a–d holotype ♂ (sl = 1.8 mm), sta D66, Bahamas, USNM 306895; e, paratype ♂ (sl = 2.0 mm), sta D68, Turks and Caicos Islands, USNM 306896. a, right second pereopod, lateral; b, propodus and dactyl of same, mesial; c, right third pereopod, lateral; d, propodus and dactyl of same, mesial; e, propodus and dactyl of right fourth pereopod, lateral. Scales equal 0.5 m (a–d), and 0.2 mm (e).

dish-brown, spines darker; carpus and merus mottled reddish-brown and cream. Ambulatory legs basically white with reddish-brown short longitudinal patch or stripe on dorsal surface of dactyl proximally; propodi each with similar patch or striped in dorsal midline and similar, but fainter patch on lateral face medially; carpi each with single dorsal patch and 1 or 2 similar but lighter patches on lateral face; meri with small reddish brown patches dorsally and ventrally, median patches tending to form incomplete band on lateral face; ischia each with 1 or 2 dorsal patches or reddish-brown and 1 patch ventrally (color notes from specimen molt).

Etymology.—This species is named for Dr. John C. Markham (Arch Cape Marine Laboratory, Arch Cape, Oregon), its principal collector, as well as our colleague and friend.

Habitat.—Gastropods shells.

Distribution.—Caribbean Sea: Bahamas and Turks and Caicos Islands; off eastern Honduras; 17.5–36 m.

Remarks.—Despite the enlarged left fifth coxa in males of *Pylopaguridium markhami,* new species, it does not appear related to *Paguridium minimum* (Chevreux & Bouvier, 1892) of the monotypic genus *Paguridium* Forest, 1961. In *P. minimum,* the left male gonopore is masked by a tuft of long stiff setae directed from left to right across the gonopore, and reaching beyond the midline of the sternite (Forest 1961:237, fig. 5), whereas in *Pylopaguridium markhami,* the gonopore is only partially concealed by a tuft of setae arising from the posterior margin of the gonopore and directed anteriorly (Fig. 15f). While three unpaired male pleopods are present in *P. markhami,* pleopods are lacking in *Paguridium minimum.* Additionally, females of *Pylopaguridium markhami* have paired first pleopods, whereas females of *Paguridium minimum* lack first pleopods. Among genera of the "*Pylopagurus-Tomopagurus*" group, only in species of the genus *Protoniopagurus* are male pleopods entirely lacking (Lemaitre & McLaughlin 1996).

Haigia McLaughlin, 1981

Haigia McLaughlin, 1981a:5.

Type species.—By monotypy, *Pylopagurus diegensis* Scanland & Hopkins, 1969. Gender: feminine.

Diagnosis.—Eleven pairs of biserial gills. Ocular acicle triangular, with submarginal spine. Maxillule (Fig. 1d) with short internal endopodal lobe with 2 terminal bristles, external lobe elongate, not recurved. Maxilla (Fig. 1e) with proximal lobe of scaphognathite moderately narrow. First maxilliped (Fig. 1f) with slender exopod. Crista dentata of third maxilliped well developed, with 1 accessory tooth. Sternite of third maxillipeds with spine on either side of midline.

Right cheliped with chela subquadrate to subrectangular. Left cheliped with lateral margin of chela somewhat expanded, chela triangular in cross-section but not elevated into prominent keel or crest. Fourth pereopods with propodal rasp consisting of single row of corneous scales.

Sternite of third pereopods with subsemicircular to roundly subrectangular anterior lobe. Sternites 4 and 5 broad, typically without capsulate setae. Coxae of male fifth pereopods symmetrical, gonopores without vas deferens produced to form short sexual tube(s); without paired pleopods, with 3 unpaired unequally biramous left pleopods. Females with paired first pleopods incompletely 2-segmented and modified as gonopods, and with 4 unpaired biramous left pleopods, second through fourth with both rami well developed, fifth with endopod reduced.

Abdomen flexed or straight. Uropods asymmetrical. Telson with lateral indentations suggesting division into anterior and posterior portions; subequal posterior lobes separated by distinct median cleft; terminal margins slightly excavated, straight, with series of small spines.

Distribution.—Apparently restricted to the eastern Pacific from southern California to Baja California and the Gulf of California, Mexico.

Remarks.—Among the "*Pylopagurus-Tomopagurus*" group of genera, *Haigia* appears most similar to *Pylopaguridium,* new genus, in lacking an operculate right chela so common to species of most genera. However, the symmetry of the coxae of the male fifth pereopods immediately separates the species of these two monotypic genera.

Haigia diegensis (Scanland & Hopkins, 1969)

Figs. 14a, b, 17

Pylopagurus diegensis Scanland & Hopkins, 1969:257, fig. 1 (type locality: La Jolla Cove, La Jolla, San Diego County, California).—Haig et al., 1970:21.—Haig, 1977:13.—Wicksten, 1977:24.

Haigia diegensis: McLaughlin, 1981a:5.

Type material.—Holotype: ♂, La Jolla Cove, La Jolla, San Diego County, California, 5 m, 1964, LACM CR19622341 (not seen). Paratypes: 1 ♂ (sl = 3.5 mm), La Jolla Cove, La Jolla, San Diego County, California, 10 m, 1964, USNM 120425; 1

ovig ♀ (sl = 2.2 mm), Los Coronados Island, Baja California, Mexico, 20 m, 1964, USNM 120424.

Material examined.—Eastern Pacific: 1 ♂ (sl = 3.7 mm), off Anacapa Island, 17–18 m, 29 Oct 1962, USNM 111394.—1 ♂ (sl = 5.4 mm), Pelican Cove, Santa Cruz Island, 6–12 m, 12 Aug 1963, colls. Conboy, Scronce, MacGinities, USNM 111391.—6 ovig ♀ (sl = 4.2–5.2 mm), Los Angeles Harbor, 1–2 m, 19 Dec 1990, coll. J. Crain, PMcL.—1 ♂ (sl = 6.4 mm), 1 ♀ (sl = 3.7 mm), Farnsworth Bank, 20–23 m, 12 Dec 1970, LACM CR19703301.

Diagnosis.—Shield (Fig. 17a) longer than broad; rostrum roundly triangular, with terminal spinule; lateral projections broadly triangular, with strong marginal spine. Ocular peduncles slightly more than half shield length, swollen basally and tapering to bases of cornea; ocular acicles roundly triangular, with strong submarginal spine, separated basally by approximately 0.65 times basal width of 1 acicle. Antennular peduncles slightly overreaching distal margins of corneas. Antennal peduncles not quite reaching or slightly overreaching distal margins of corneas.

Right cheliped (Fig. 14b) with tufts of short stiff setae interspersed among marginal spines of subrectangular chela; dactyl moderately broad, dorsal surface with covering of low tubercles, dorsomesial margin with row of strong acute or blunt spines; palm and fixed finger covered with tufts of short setae and scattered tubercles, dorsomesial and dorsolateral margins each with row of strong blunt or subacute spines. Carpus with row of strong acute or subacute spines on dorsomesial margin, dorsal surface with numerous prominent spines, partially concealed by long setae.

Left cheliped (Fig. 14a) with dorsal surfaces of dactyl, fixed finger and palm all with numerous tufts of short, stiff setae; palm with row of strong acute or subacute spines in dorsal midline, extending onto fixed finger mesially, dorsolateral margin with row of strong spines, dorsomesial margin with few low spines or tubercles. Carpus subtriangular, with row of strong spines on dorsal margin, partially obscured by long setae.

Ambulatory legs (Fig. 17b, c) generally similar from left to right. Dactyls usually shorter than propodi, dorsal margins with tufts of moderately long to long setae, ventral margins each with 6 or 7 corneous spines. Propodi with tufts of setae on dorsal, mesial and lateral faces; ventrodistal margins of second each with pair of corneous spines, ventral margins of third each with row of corneous spines. Carpi each with spine at dorsodistal margin. Meri of second each with 1 acute spine near ventrolateral distal angle and 2 or 3 spines on ventrolateral margin distally, meri of third unarmed.

Telson (Fig. 17d) with posterior lobes usually separated by small median cleft, terminal margins with 3 or 4 strong and 2 to several smaller spines; lateral margins angular, with narrow corneous or weakly calcified marginal plate.

Color.—Carapace and ocular peduncles pale pink. Chelipeds and walking legs darker pink. Tubercles on chelae white. Approximate distal half of fingers white on both chelae. Dactyls of walking legs with dark corneous broad tips, and adjacent white ring. Proximal portions of dactyls each circumscribed with broad dark red band (based on Scanland & Hopkins 1969).

Habitat.—A variety of gastropod shells, and occasionally serpulid tubes.

Distribution.—Eastern Pacific, California coast from the Channel Islands to Coronado Islands; Baja, California and Guadeloupe Island, Mexico; 3–23 m.

Remarks.—When originally described in the genus *Pylopagurus* sensu lato, Scanland & Hopkins (1969) related their species to *Rhodochirus hirtimanus* (Faxon, 1893) (as *Pylopagurus*), as the two species were similar in having asymmetrical uropods, a single row of scales in the propodal rasp of the fourth pereopods, and armature of the chelae consisting of large tubercles.

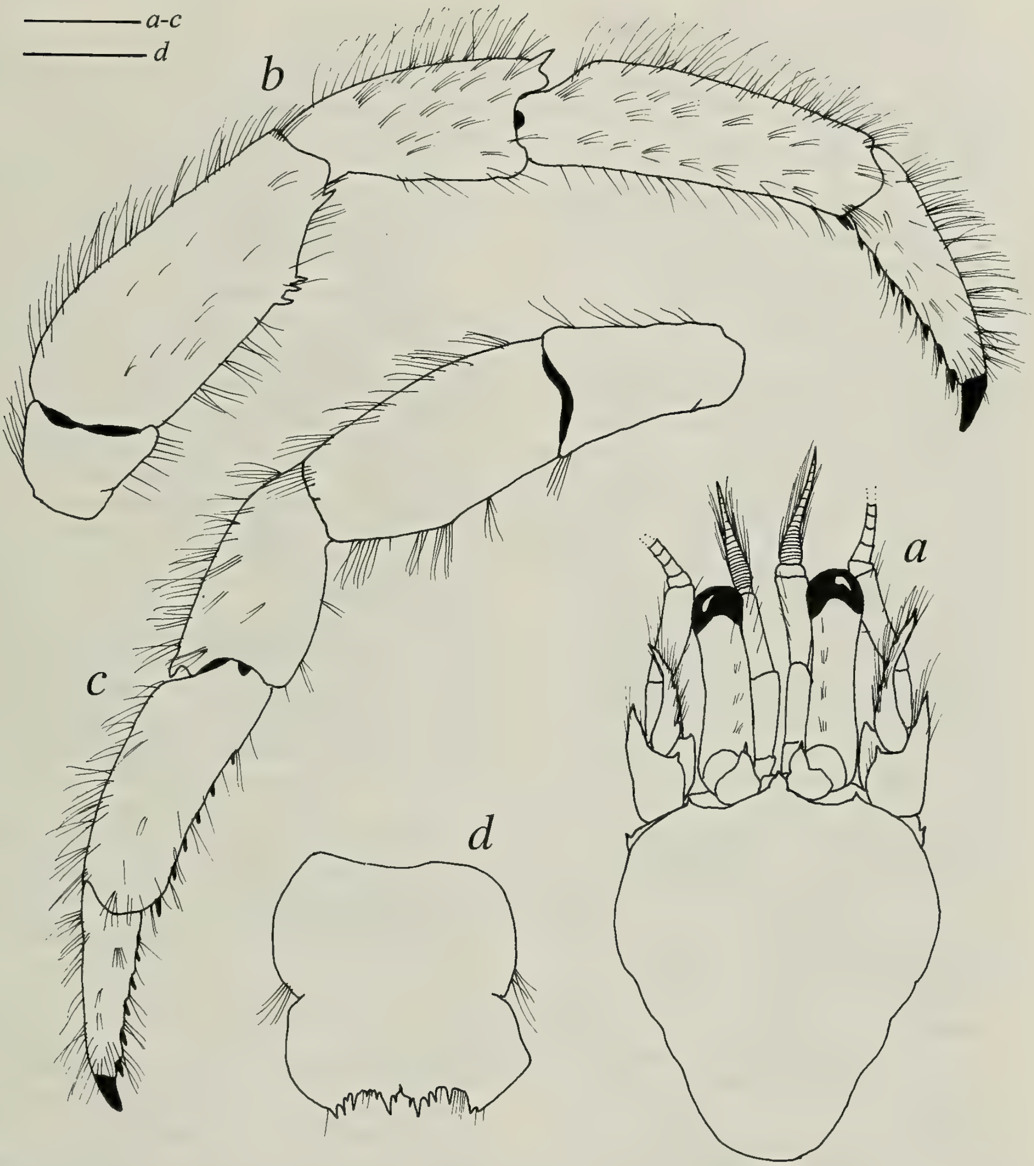

Fig. 17. *Haigia diegensis* (Scanland & Hopkins, 1969). ♂ (sl = 6.4 mm), Farnsworth Bank, LACM CR19703301. a, shield and cephalic appendages, dorsal; b, right second pereopod, lateral; c, right third pereopod, mesial; d, telson, dorsal. Scales equal 2 mm (a–c), and 1 mm (d).

Despite these similarities, McLaughlin (1981a) was of the opinion that the chela armature and telson structure of *P. hirtimanus* suggested a closer relationship to the Atlantic *Pylopagurus rosaceus* A. Milne-Edwards & Bouvier, 1893, and for these two species she proposed the genus *Rhodochirus*. For *Pylopagurus diegensis* she proposed the genus *Haigia*. As is indicated in the generic remarks, as well as in discussion of the genus described below, *Haigia* and *H. diegensis* show more general similarities to *Pylopaguridium,* new genus, and its type species, than either do to most other genera of the "*Pylopagurus-Tomopagurus*" group.

Key to genera of the "*Pylopagurus-Tomopagurus*" group

1. Propodal rasp of fourth pereopod with single row of corneous scales 2
– Propodal rasp of fourth pereopod with multiple rows of corneous scales ... 10
2. Telson with median cleft, terminal margins of posterior lobes each with 1 or more spines 3
– Telson lacking median cleft, terminal margin unarmed .... *Enallopagurus* McLaughlin, 1981a
3. Ocular acicles simple. Coxae of male fifth pereopods symmetrical 4
– Ocular acicles multispinose. Coxae of male fifth pereopods asymmetrical .... *Pylopaguridium*, new genus
4. Chela of right cheliped subovate to subcircular, margins unarmed, weakly tuberculate or minutely crenulate and/or serrate, but never armed with prominent blunt or acute spines or tubercles 5
– Chela of right cheliped variable, margins armed with prominent blunt or acute spines or tubercles 6
5. Fourth pereopods with large, very prominent preungual process at base of claw ... *Phimochirus* McLaughlin, 1981a
– Fourth pereopod without large, very prominent preungual process at base of claw .... *Pylopagurus*
6. Spines of right chela with basal rosettes .... *Rhodochirus* McLaughlin, 1981a
– Spines of right chela without basal rosettes 7
7. Dactyl and fixed finger of left chela excavated ventrally, presenting "spoon-shaped" appearance .... *Tomopagurus*
– Dactyl and fixed finger of left chela not excavated ventrally and not presenting "spoon-shaped" appearance 8
8. Left cheliped with rotation of propodal-carpal articulation 45°–90° from horizontal plane .... *Lophopagurus* (*Australeremus*) .... McLaughlin, 1981a
– Left cheliped with rotation of propodal-carpal articulation much less than 45° from horizontal plane 9
9. Left chela with midline elevated into prominent keel or crest .... *Lophopagurus* (*Lophopagurus*) .... McLaughlin, 1981a
– Left chela with midline sometimes elevated, but not into prominent keel or crest .... *Haigia*
10. Telson with median cleft separating posterior portion into symmetrical or asymmetrical lobes 11
– Telson lacking median cleft, no separation of posterior portion into symmetrical or asymmetrical lobes 13
11. Uropods symmetrical or nearly so, with protopods produced posteriorly .... *Agaricochirus* McLaughlin, 1981a
– Uropods markedly asymmetrical, protopods not produced posteriorly 12
12. Left chela triangular in cross-section, dactyl and fixed finger not dorsoventrally flattened .... *Anisopagurus* McLaughlin, 1981a
– Left chela not triangular in cross-section, dactyl and fixed finger dorsoventrally flattened .... *Manucomplanus* McLaughlin, 1981a
13. Chelae of chelipeds subequal; males without unpaired left pleopods .... *Protoniopagurus*
– Chelae of chelipeds unequal; males with unpaired left pleopods .... *Enallopaguropsis* McLaughlin, 1981a

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A new species of *Calaxius* Sakai & de Saint Laurent, 1989, from the Galapagos Islands (Crustacea: Decapoda: Axiidae)

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Abstract.—*Calaxius galapagensis,* a new species, is described on the basis of two ovigerous females from coral rubble in shallow water at North Plaza off Isla Santa Cruz, Galapagos Islands. The species is compared with the eight previously described species of *Calaxius* Sakai & de Saint Laurent, 1989, and characterized by a strongly tridentate rostral apex, and by rows of corneous spine-like setae on pereopods 3 and 4.

While engaged in an ongoing survey of the crustacean fauna of the Galapagos Islands in August 1997, one of us (CPH) collected two female specimens of a creamy-yellow axiid shrimp bearing robust chelipeds fringed with long setae. The shrimp were at first identified as *Neaxius vivesi* (Bouvier, 1895), which they superficially resemble, but a more careful examination revealed that they were an undescribed species of the axiid genus *Calaxius* Sakai & de Saint Laurent, 1989.

The specimens were collected by hand at a depth of approximately 6 meters along the western end of North Plaza (Plaza Norte), one of a pair of small islets lying off the east side of Isla Santa Cruz. Both specimens were found beneath rocks in coral rubble where they had built burrows. This habitat parallels that of *Axiopsis baronae* Squires, 1977, an axiid shrimp that we have collected throughout the archipelago, (and also known from Pacific Colombia, Peru and Mexico). The specimens were photographed immediately after the dive, then preserved in 70% ethanol. The only other axiids known from the Galapagos are *Eiconaxius cristagalli* (Faxon, 1893), a sponge inquiline known from deep water (717 m) between Isla Santa Cruz and Isla San Cristobal, and *Coralaxius galapagensis* Kensley, 1994, recorded from Sullivan Bay, Isla San Salvador.

USNM - National Museum of Natural History, Smithsonian Institution.

Carapace length is measured from posterior margin of orbit to posterior margin of carapace.

Family Axiidae Huxley, 1879
Calaxius Sakai & de Saint Laurent, 1989
Calaxius galapagensis, new species
Fig. 1

Material examined.—Holotype, USNM 308977, ovigerous female, carapace length 11.9 mm, sta 97-384, west end of North Plaza, 6 m, coll. C. P. Hickman, Jr., 28 Aug 1997. Paratype, Charles Darwin Research Station 97-385, ovigerous female, carapace length 11.0 mm, same data as holotype.

Description of holotype.—Integument hard, brittle, with numerous scattered clumps of setae. Carapace (Fig. 1A) with posterodorsal region faintly rugose/pitted; rostrum (Fig. 1B) twice length of eyes, apically tridentate, with median spine set at lower level than 2 subterminal spines; strong supra-ocular spine; lateral carina extending posteriorly, bearing 2 strong spines posterior to orbit, plus row of 5 spines decreasing in size posteriorly; submedian carina of 5 small spines; median carina having 3 strong spines anterior to tubercle, 5 small spines posterior to tubercle; 3 small spines between anterior median and submedian carinae. Abdominal somite 1 with triangular pleura ventrally subacute; pleura 2–6 (Fig. 1A) ventrally broadly rounded, bearing fringe of setae. Telson (Fig. 1C) as long as basal width, lateral margin with 2 or 3 serrations, posterior margin evenly convex, with 3 articulating spines posterolaterally (spines sometimes lost); dorsal surface bearing 2 pairs of fixed spines.

Rostrum reaching beyond antennular peduncle; flagella subequal in length to carapace. Antennal flagellum missing on both sides; acicle slender, crescent-shaped, reaching about midway along peduncle article 4; peduncle article 3 with strong dorsal and ventral spine. Maxilliped 3 (Fig. 1F), basis with strong posterodistal spine; merus with 2 strong spines in distal half of posterior margin, latter bearing elongate setae; carpus with small posterodistal spine; carpus, propodus and dactylus bearing strong clumps of setae. Pereopod 1, chelipeds (Fig. 1D, E) similar in length and spination, with right slightly more robust than left; ischium having 4 spines on lower margin; merus with row of 7–10 spines on lower margin, 2 distalmost spines strongest, 2 or 3 spines on distal part of upper margin; carpus having single strong spine distally on upper surface, flattened spine on flange of ventrolateral surface; propodus strongly setose, especially dorsally, with row of 5 strong curved spines along upper margin, dorsolateral surface granular, strong spine on lateral surface at base of fixed finger; fixed finger and dactylus with irregular tubercles on cutting edges. Pereopod 2 (Fig. 1G), merus with 3 spines on lower margin; dactylus, propodus and carpus setose along upper and lower margins; cutting edges of chela bearing fine spine-like setae. Pereopod 3 (Fig. 1H), merus with 3 or 4 spines on lower margin; propodus with 5 ventrolateral rows of spine-like setae, 3 rows near upper margin; dactylus with 3 spines on lateral surface. Pereopod 4 (Fig. 1I), merus with 3 spines on lower margin; propodus with 7 rows of spine-like setae along posterior margin, 4 rows near anterior lateral margin; dactylus with double row of fine spine-like setae. Pereopod 5 (Fig. 1J), propodus with 3 spine-like setae on posterodistal margin, row of spine-like setae along distal margin, plus strongly setose patch in distal half; dactylus ventrally hollowed. Pleopod 1 consisting of single slender ramus. Uropodal lateral ramus (Fig. 1C) bearing 6 serrations along lateral margin, 10 spines along transverse suture, 6 spines on dorsal surface; mesial ramus with 4 serrations along lateral margin, row of 5 strong spines on middorsal rounded ridge, distalmost reaching well beyond margin.

Color.—Body overall creamy yellow-orange, with diffuse red patches on dorsal carapace, anterior and posterior margins of pleura, mesial and lateral surface of pereopod 1 propodal palm, especially at base of fingers, margins of pereopodal articles, uropodal and telsonic spines. Tips of pereopod 1 chela fingers white. Strong red patch on epistome. Eggs yellow.

Variation.—Paratype: slight differences in spination from holotype. Rostrum (Fig. 1K) damaged, with apical and left subapical teeth fused. Foraminiferan on dorsal base of rostrum. Four pairs of small spines between median and submedian carinae of carapace (3 in holotype). Eight small spines on dorsal surface of uropodal lateral ramus (6 in holotype) (Fig. 1L); 7 serrations on lateral margin of mesial uropodal ramus (4 in holotype). Telson with 3 articulating spines posterolaterally on each side; tubes of 2 newly settled spirorbid polychaetes present on dorsal surface.

Remarks.—Sakai & de Saint Laurent (1989) included eight species in their new genus *Calaxius,* with *C. acutirostris* Sakai & de Saint Laurent, 1989, designated as the type species. These include three species from the western Atlantic and five from the

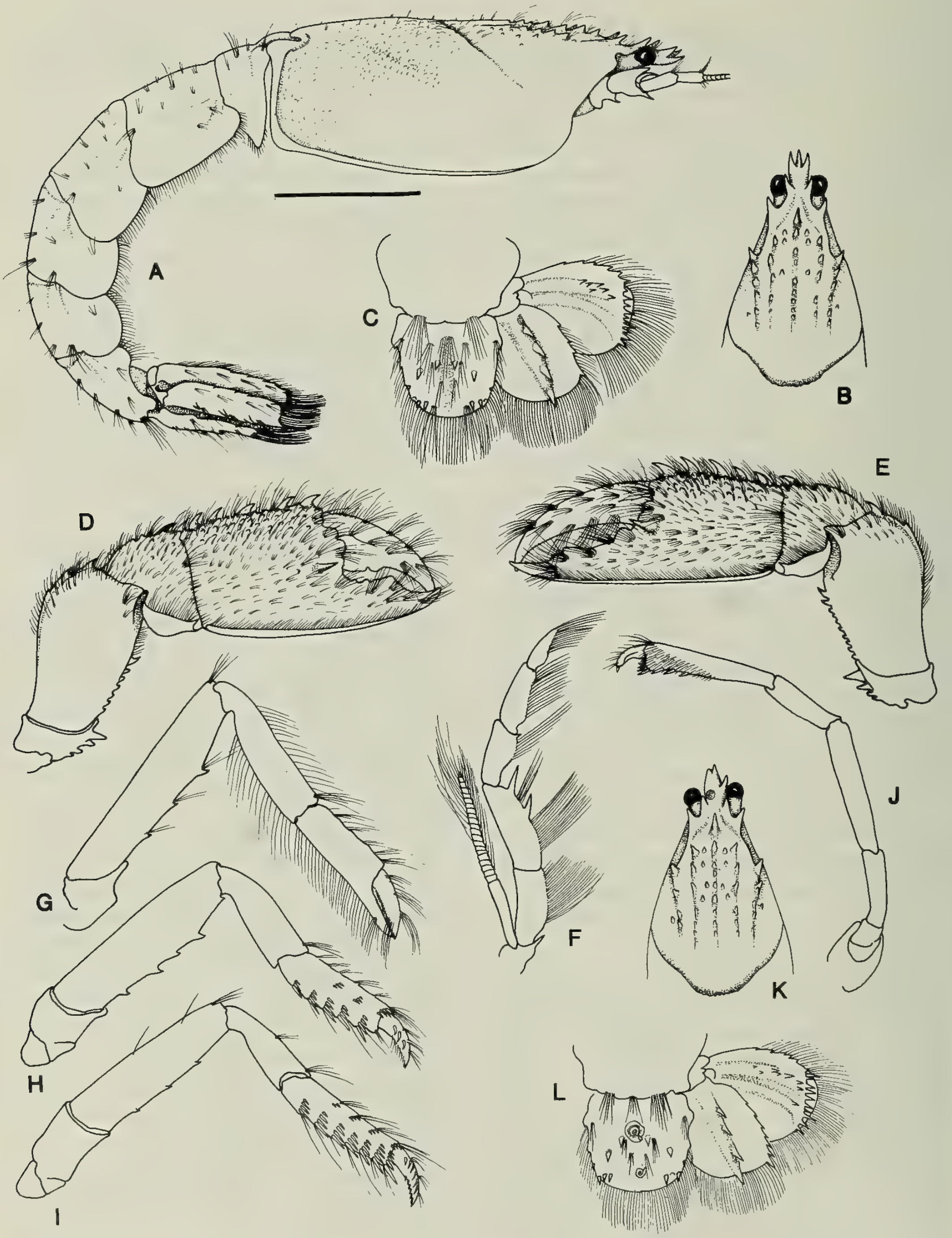

Fig. 1. *Calaxius galapagensis,* new species. A–J, holotype, USNM 308977; K–L, paratype, Charles Darwin Research Station no. 97-384. A, carapace and abdomen in lateral view, scale = 5 mm; B, anterior carapace in dorsal view; C, telson and right uropod; D, right pereopod 1; E, left pereopod 1; F, maxilliped 3; G, pereopod 2; H, pereopod 3; I, pereopod 4; J, pereopod 5; K, anterior carapace in dorsal view (with foraminiferan on rostrum); L, telson (with 2 spirorbid polychaete tubes) and right uropod.

Table 1.—Species of *Calaxius,* with type locality and shape of abdominal pleura.

Species	Type locality	Abdominal pleura
Calaxius acutirostris Sakai & de Saint Laurent, 1989	Madagascar; Philippines, 219–400 m	acute
Calaxius manningi Kensley, Lin & Yu, 2000	Taiwan, 500 m	acute
Calaxius oxypleura (Williams, 1974)	Straits of Florida, 365 m	acute
Calaxius sibogae (De Man, 1925)	Indonesia, 397 m	acute
Calaxius galapagensis, new species	Galapagos, Islands, 6 m	rounded
Calaxius jenneri (Williams, 1974)	North Carolina, 100 m	rounded
Calaxius pailoloensis (Rathbun, 1906)	Hawaii, 250 m	rounded
Calaxius euophthalmus (De Man, 1905)	Indonesia, 397 m	rounded
Calaxius inequalis (Rathbun, 1901)	Puerto Rico, 289–309 m	rounded
Calaxius mimasensis (Sakai, 1967)	Japan, littoral	unknown

Indo-West Pacific and Hawaii. Additionally, *Calaxius manningi* Kensley et al., 2000, was described from Taiwan (Table 1). All of these species agree with the characters given by Poore (1994:97) in his definition of the genus, and are especially characterized by the narrowed and strongly spinose rostrum being about twice the length of the eyes; spinose median, submedian, and lateral carapace carinae; subequal and strongly setose first chelipeds, with the propodal palm dorsally strongly spinose, and a strong spine at the base of the fingers on the lateral surface of the propodus; epipods present on pereopods 1–4; pleurobranchs present above pereopods 2–4; lateral ramus of uropod with transverse suture. The present species agrees on all these features, but differs from all previously described species in the number and distribution of the carapace and pereopod 1 spines, while the strongly tridentate rostral apex seems especially characteristic. None of the previously described species seem to have the strong rows of corneous spine-like setae on the lateral surface of the propodus of pereopods 3 and 4.

The species of *Calaxius* fall into two broad groups, viz. those with strongly triangular and ventrally acute abdominal pleura, and those with ventrally rounded pleura (Table 1). Whether this character is of generic value is uncertain; its distribution does not seem to have any geographical significance.

Etymology.—The specific name is derived from the type locality, the Galapagos Islands.

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A new species of the genus *Anelpistina* (Insecta: Zygentoma: Nicoletiidae) from the Biosphere Reserve Sierra de Huautla

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Abstract.—The Biosphere Reserve Sierra de Huautla was established in 1999 in southern Morelos, Mexico, to protect the tropical dry forest that covers most of the region. From biodiversity studies performed in the reserve, a new species, *Anelpistina doradoi* was found and is described here.

Tropical dry forests (TDF), more than any other ecosystem in Mexico, suffer high rates of deforestation from humans, exceeding even those of the tropical rain forests (TRF). It has been estimated that the extension of land covered by TDF on the Pacific coast of Mesoamerica before the arrival of the Spaniards was approximately 550,000 square km (Janzen 1988). Today, only 2% of that forest remains intact (Janzen 1988), and the estimated current rate of deforestation for Mexico's TDF is around 1.9% annually, which translates to approximately 300,000 hectares per year (Miranda 1996). Within Mexico, the TDF is host to numerous endemic species of plants and animals, and consequently, its loss or misuse could result in a dramatic reduction of the biodiversity of the region. For example, it is estimated that approximately 40% of all plants found in TDF are endemic, whereas only 5% of plants found in Mexico's TRF are endemic (Dorado 2000). By the year 2010, the projected loss in number of species in TDF is between 6.8% and 13.06% (Monroy et al. 2000).

One of the least-studied groups of organisms affected by human activities and deforestation is the Zygentoma (Insecta) or "silverfish," which dwell in the soil and are of substantial ecological importance. In some areas of the Biosphere Reserve Sierra de Huautla, a TDF in southern Morelos, Mexico, silverfish make up to 60% of the macroarthropods found under rocks (pers. obs.). Despite their ubiquity throughout Mexico, however, they are poorly studied (Espinasa 1999a). Although 36 species of silverfish have been described in Mexico, this is but a small fraction of what must exist (Palacios-Vargas 2000), and of the species described, at least 17 (47%) can be found in TDF. Future research should uncover many new species. However, if the present rate of deforestation continues, many of these organisms may disappear and be lost to science forever. This work is a contribution to the knowledge of this fauna.

Materials and Methods

Specimens were collected under rocks and placed in 70% alcohol or taken alive to the laboratory. Dissections were made with aid of a stereo microscope and the different structures of the body were mounted in fixed-preparations with Hoyer's solution. All illustrations were made with a camera lucida attached to a compound microscope.

Types were deposited in the following collections: ♂ Holotype, 5 ♂ paratypes and 7 ♀ paratypes in LESM-DB-MEX (Laboratory of Ecology and Systematic of Microarthropods. Department of Biology, Faculty of Sciences, UNAM. Mexico D.F.).

Catalog numbers: ZYG-7. 11 ♂ paratypes and 3 ♀ paratypes are in author's collection at CEAMISH, UAEM.

Anelpistina doradoi, new species
Figs. 1–4

Type material.—México, Morelos, Tlaquiltenango municipality, Huautla ejido, tens of meters behind the Biological Station Sierra de Huautla at Cruz Pintada and the dam of Lorenzo Vásquez, 18°27′43.4″N, 99°02′07.6″W, Under rocks, 8 Jun 2000 and 22 Jul 2000, C. E. Granados-García and L. Espinasa cols. Male holotype, 16 ♂ paratypes, 10 ♀ paratypes.

Description.—Maximum body length 7.5 mm. Maximum conserved length of antennae 5.0 mm and of caudal appendages 3.5 mm. When complete, the antennae measure slightly more than half the length of body, and caudal appendages measure approximately half the length of body. Body proportions as in Fig. 1A. General color light yellow to white.

Basal article of antennae in males without projections. Pedicellus of antennae in adult male as in Fig. 1B, almost as long as 1st article and with unicellular glands clustered approximately in 3 groups, one of them very long. Pedicellus in juvenile male half as long as 1st article and with almost no unicellular glands (Fig. 1C). Female basal articles of antennae simple. Head with macrochaeta and microchaeta as in Fig. 1D, with approximately 8 + 8 macrochaetae on border of insertion of antennae.

Mouthparts relatively long, maxilla as in Fig. 1E. Last article of maxillary palp approximately ⅓ longer than penultimate. Apex of maxillary palp with 2 conules, one longer than wide and the other wider than long. Labial palp as in Fig. 1F, apical article barely longer than wide and only slightly longer than next to last article. Penultimate article with bulge containing 2 macrochaetae. Labium and 1st article of labial palp with macrochaetae. Mandibles without very small pegs on bigger tooth and chaetotaxy as in Fig. 1G.

Pro-, meso- and metanotum with approximately 5 macrochaetae on lateral borders apart from several setae of varied sizes, in (Fig. 2A). Legs as in Fig. 2B. Hind tibia approximately 5× longer than wide, slightly shorter than tarsus. Claws of normal size.

Abdominal terga and sterna as in other members of genus. Abdominal sterna II-VII subdivided into coxites and sternite. Sterna VIII and IX of male entire. Appendages of urosternum IV of adult male extremely long, similar to *A. carrizalensis* (Wygodzinsky, 1946) and *A. ruckeri* (Silvestri, 1905), but curved inward (Fig. 2E). Urosternum VIII of male long and shallowly emarginate on posterior margin (Fig. 3A–B). Urosternum IX of male as in Fig. 3A–B without a row of sensory cones or highly sclerotized submedian longitudinal macrochaetae. Behind insertion of parameres, in center, with a small group of short distinct setae. Point of insertion of parameres in urostermum IX is deep, and in adult, internal face of coxal processes with spiniform macrochaetae highly sclerotized. Stylets II–VIII as usual for subfamily. Stylets IX larger than others, with 2 macrochaetae and an extra subapical pair. Terminal spine with small teeth. In males and females styles without modifications. Urotergite X shallowly emarginated in both sexes, posterior angles with 2 + 2 macrochaetae and a few relatively strong setae, length of inner macrochaetae almost equal to distance between them (Fig. 3C).

Penis and parameres as in Fig. 3A–B. Parameres attaining slightly above ½ the length of stylets IX in adults. Surface of parameres with short setae. Subgenital plate of female rounded (Fig. 4A–C). Ovipositor in female adults surpassing apex of stylets IX by slightly less than 3× length of stylets (Fig. 4C). Gonapophyses with approximately 21 articles.

Cerci of adult male with a longer than wide basal article, sometimes followed by a wider than long, then a very long article bearing numerous spines, followed by nu-

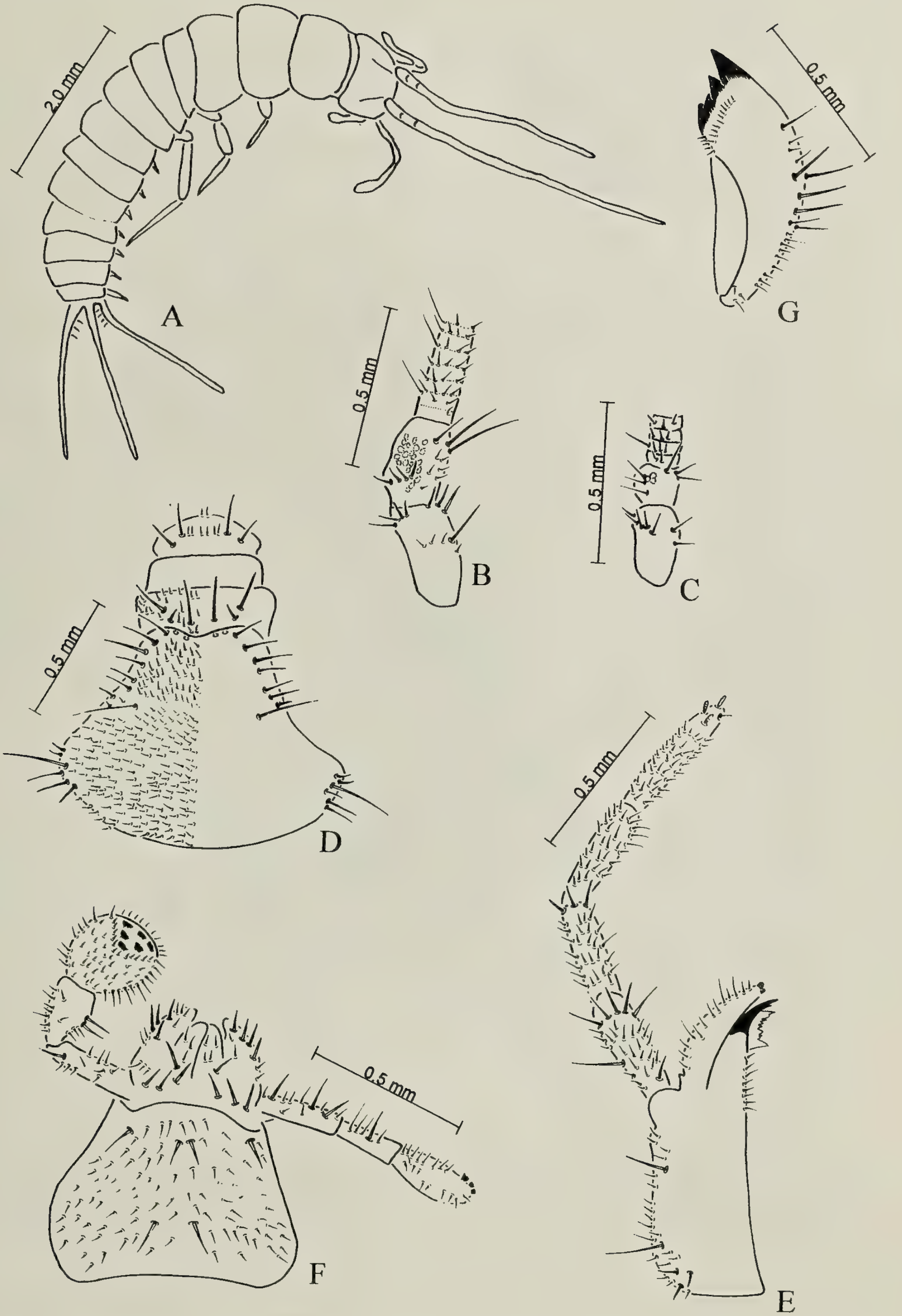

Fig. 1. *Anelpistina doradoi,* new species. A, Adult male paratype; B, D–G, Adult male holotype; C, juvenile male paratype; A, Dorsal view; B–C, Postembryonic development in male basal portion of antenna; D, Head; E, Maxilla; F, Labial palp and labium; G, Mandible.

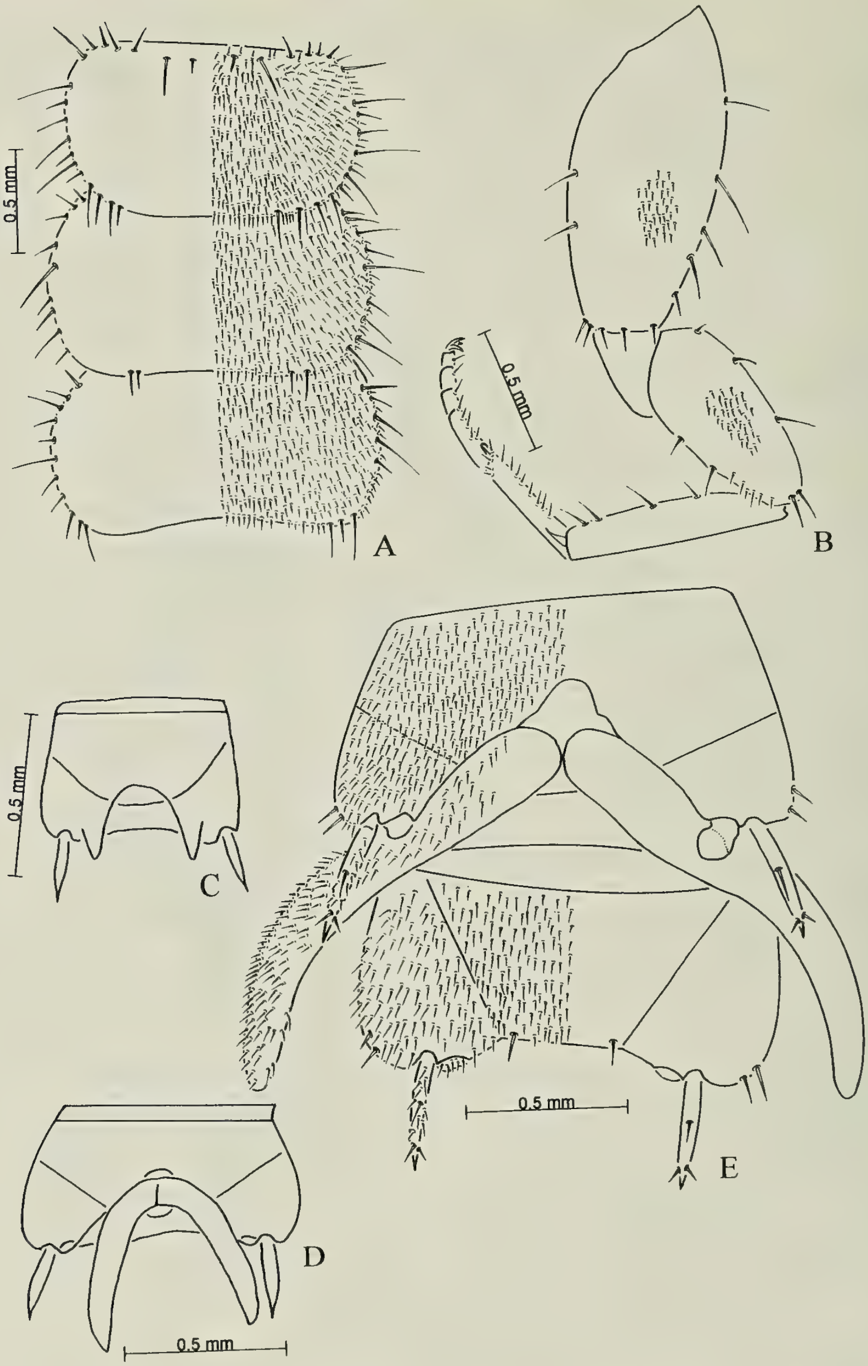

Fig. 2. *Anelpistina doradoi,* new species. A–B, E, Adult male holotype; C–D, Juvenile male paratypes; A, Thoracic nota; B, Hind leg; C–E, Postembryonic development in male appendages of urosternum IV.

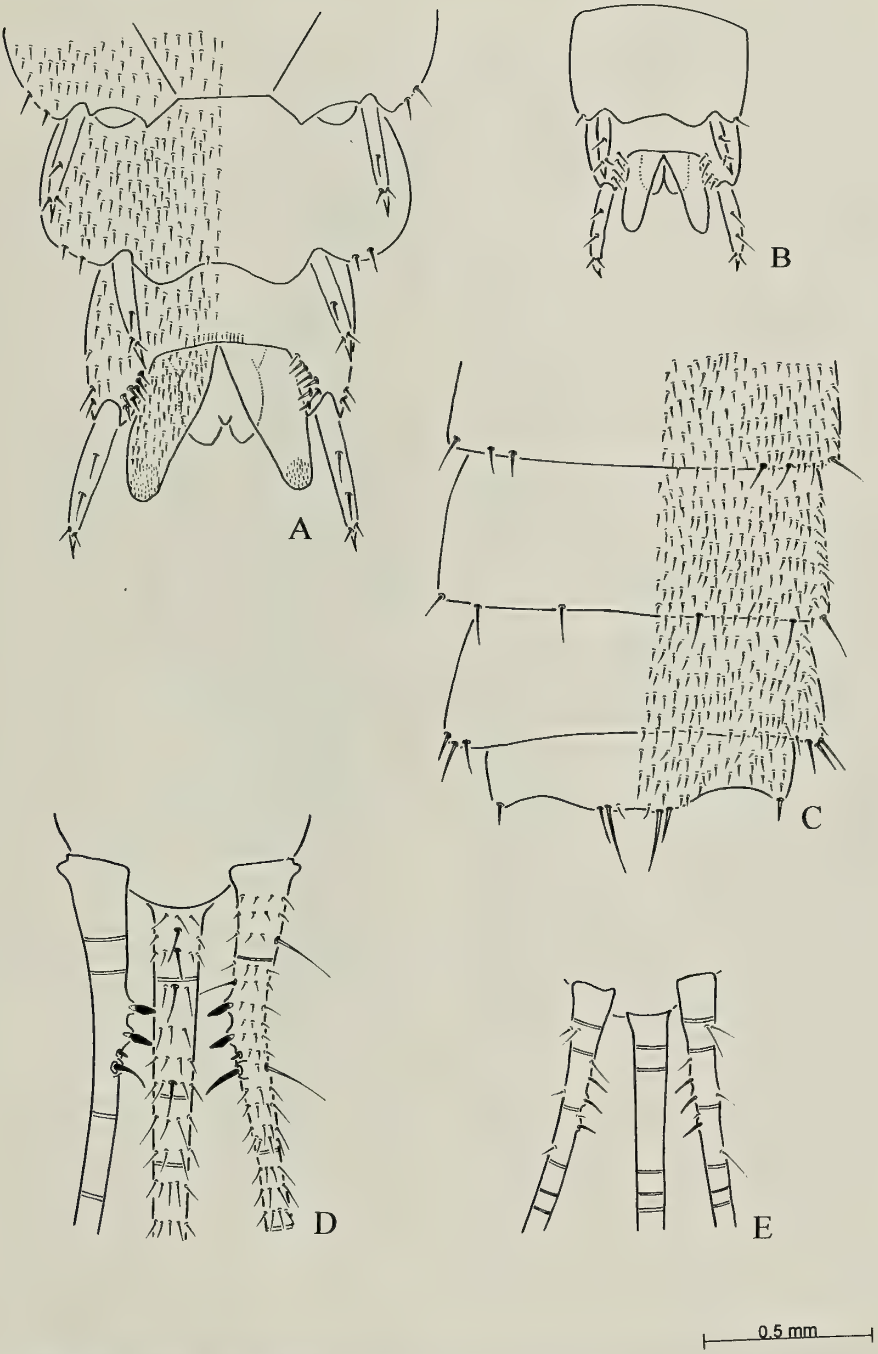

Fig. 3. *Anelpistina doradoi,* new species. A, C–D, dult male holotype; B, E, juvenile male paratype; A–B, Postembryonic development in male genital area; C, Apex of abdomen, dorsal view; D–E, Postembryonic development in male cerci.

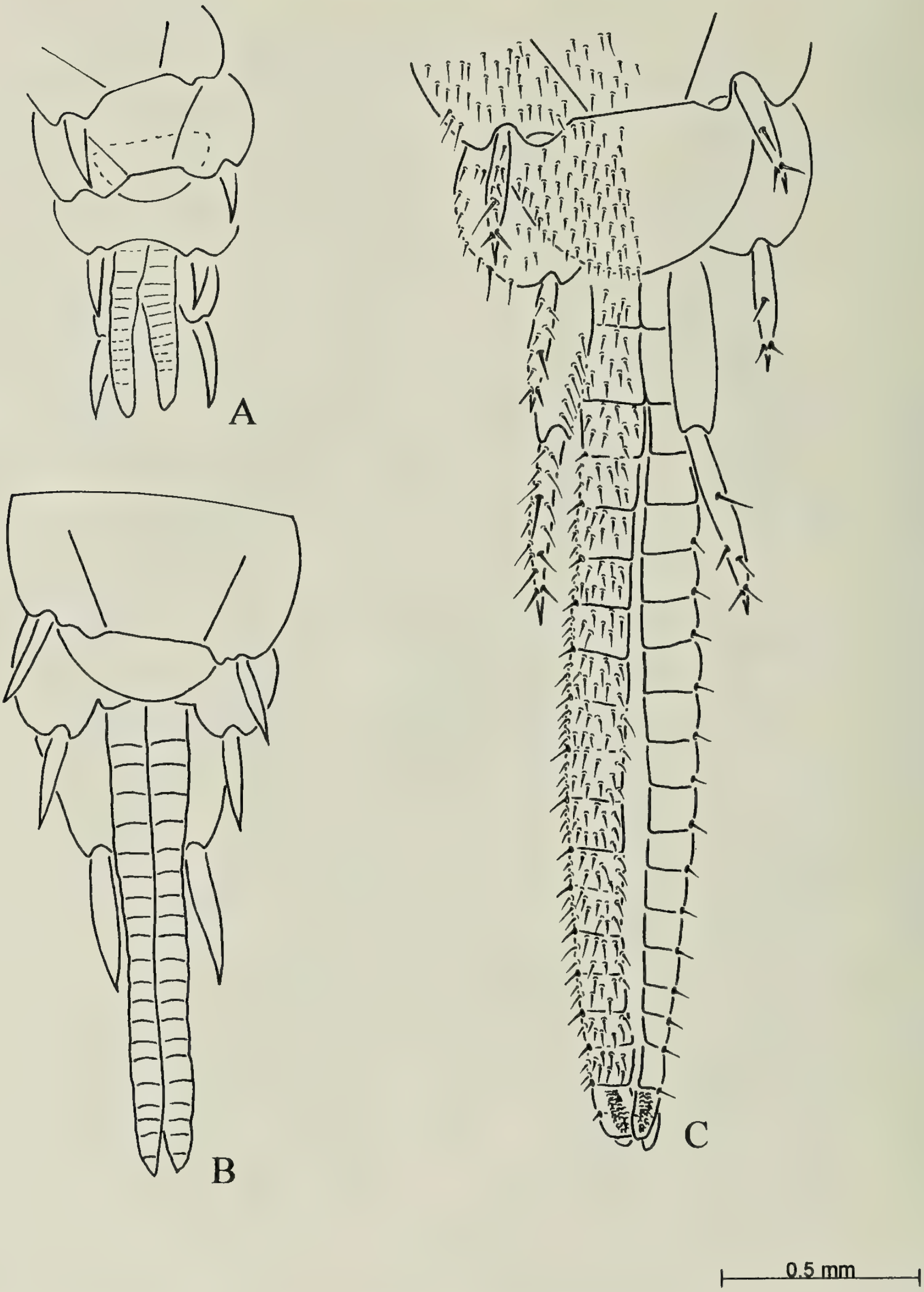

Fig. 4. *Anelpistina doradoi,* new species. A–C, Postembryonic development in female ovipositor and subgenital plate.

merous short articles of simple chaetotaxy. Spines consist of two strong, subacute ones inserted in tubercles, a very small one and a long, acute and slightly curved one (Fig. 3D). In some individuals, spines in cerci are asymmetrical; one of the cercus spines is as stated above and the other has 3 strong, subacute spines inserted in tubercles and then the other two small and long ones. Female cerci simple.

Postembryonic development in male complex. In younger instars of less than 4.5 mm, the pedicellus of antennae half as long as 1st article and without unicellular glands (Fig. 1C), appendages of urosternum IV either absent or small (Fig. 2C), parameres attaining slightly below ½ of stylets IX (Fig. 3B), urosternum IX coxal processes without spiniform macrochaetae, and cerci without spines or spines slender and not highly sclerotized (Fig. 3E). Individuals of 4.5 mm to less than 5 mm acquire 4 spiniform macrochaetae highly sclerotized on the coxal processes of urosternum IX (Fig. 3B). Individuals of more than 5 mm progressively acquire the adult length of pedicellus and their unicellular glands (Fig. 1B), appendages of urosternum IV become of medium size (Fig. 2D) and then adult size (Fig. 2E), parameres attain slightly above 1/2 of stylets IX (Fig. 3A), urosternum IX coxal processes acquire 6 and then 8 spiniform macrochaeta (Fig. 3A), and the cerci attain the robust spines (Fig. 3D). The shortest male collected is 4.0 mm and the longest 7.5 mm.

In females, the length of ovipositor increases proportionally with body size. At a length of 3 mm, ovipositor barely surpasses base of stylets IX. At 4 mm, it reaches apex of stylets IX (Fig. 4A). Longer body sizes of up to 7 mm bring an increase of size (Fig. 3B) until ovipositor surpasses apex of stylets IX by slightly less than 3× length of stylets (Fig. 3C). The shortest female collected is 3.0 mm and the longest 7.0 mm.

Range.—Known only from the type locality.

Etymology.—The species is named for Dr. Oscar Dorado, Director of the Centro de Educación Ambiental e Investigación Sierra de Huautla (CEAMISH) at the Autonamous University of the State of Morelos (UAEM), to recognize his efforts in establishing Sierra de Huautla, the type locality of this new species, as a biosphere reserve.

Remarks.—Adult males of Anelpistina can be easily subdivided by the morphology of the appendages of urosternum IV (Fig. 2C–E). *Anelpistina decui* (Wygodzinsky & Holinger 1977) and *A. inappendicata* (Espinasa 1999b) lack them. In *A. weyrauchi* (Wygodzinsky 1959), the medium-sized appendages have a small subapical projection on outer margin, and two projections at both sides of insertion of stylets. Adults of *A. anophtalma* (Bilimek 1867), *A. wheeleri* (Silvestri 1905), *A. miranda* (Silvestri 1912), *A. boneti* (Wygodzinsky 1946), *A. bolivari* (Wygodzinsky 1946), and *A. cuaxilotla* (Espinasa 1999b) have simple appendages of medium size, their length being slightly longer than the length of urosternum IV and less than 5× longer than wide. *Anelpistina ruckeri* and *A. carrizalensis* have simple appendages of very long size, their length being approximately equal to twice the length of urosternum IV and more than 6× longer than wide. To this last group belongs the new species, but it can be differentiated from *A. ruckeri* and *A. carrizalensis* because in both species appendages of urosternum IV are curved outward and urotergite X is deeply emarginated on the posterior border, while only in the new species appendages are curved inward (Fig. 2E) and urotergite X is only shallowly emarginated (Fig. 3C).

Furthermore, the new species can be differentiated from other congeners by its particular set of spines on cerci. While *A. wheeler, A. ruckeri* (although not shown in Silvestri's 1905 drawings), *A. carrizalensis* and *A. inappendicata* have nine or more spines of subequal size, and *A. decui, A. weyrauchi, A. anophtalma, A. miranda, A. boneti, A. bolivari,* and *A. cuaxilotla* spines consist basically of a long, acute and slightly curved one inserted in a tubercle, a very small one, a strong, subacute one inserted in tubercle, and sometimes a fourth very small one, the new species has the same three distal spines, but then instead of no spine or a very small one, it has another one or two strong, subacute ones inserted in tubercles (Fig. 3D).

Females are more difficult to differentiate within the genus, and the change in length of the ovipositor on the postembryonic development might cause confusion. For the new species, ovipositor in female adults surpasses apex of stylets IX by slightly less than thrice the length of stylets (average of 2.72 times in females measuring 7 mm, range from 2.6–2.8, $n = 3$) and gonapophyses with approximately 21 articles. *A. weyrauchi* has a much longer ovipositor (surpasses 5×) with 30 articles. Every other species with the exception of *A. wheeleri* and *A. miranda* have in different degrees, smaller ovipositors with fewer articles. Females of *A. ruckeri* have not been described.

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Parmops echinatus, a new species of flashlight fish (Beryciformes: Anomalopidae) from Fiji

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Abstract.—A second species of the genus *Parmops* is described from two specimens collected in 440m and 550m respectively in Fiji. *Parmops echinatus* n.sp. is distinguished most prominently from *P. coruscans* in lacking midventral scutes and an external tooth patch on the lateral face of the dentary, and in having papillose ridges on the gular isthmus, 15 dorsal-fin soft rays, 12 anal-fin soft rays, 15 or 16 pectoral-fins rays, 34 pored lateral-line scales and 14 + 17 vertebrae.

The species of the family Anomalopidae were reviewed most recently by McCosker & Rosenblatt (1987). Shortly thereafter, Johnson & Rosenblatt (1988) described the anatomy of the mechanisms of light-organ occlusion in the family, introduced a new genus, and proposed a phylogeny of the family. Since that time two additional genera and species have been described (Rosenblatt & Johnson 1991, Baldwin et al. 1997) bringing the total to six genera and seven species. Except for the two monotypic New World genera, one each in the western Atlantic and eastern Pacific, all known anomalopids have Indo-West-Pacific distributions. Material from Fiji that has become available recently contains a second and larger specimen of *Parmops coruscans* and two specimens of an undescribed species that we refer to *Parmops.* The purposes of this paper are to describe the new species, compare it with and amplify the description of *P. coruscans,* and to modify the generic diagnosis of the genus *Parmops.*

Parmops echinatus, new species
Fig. 1

Holotype.—USNM 361379, 46.0 mm SL, sex unknown, off Viti Levu, Fiji, west of Beqa Island and north of Yanuca Island, from a prawn trap in 250 fathoms (440 m) 20 Sept 1983, University of the South Pacific (USP) R/V *Aphareus.*

Paratype.—UNSM 361380, 88.5 mm SL, sex unknown, off the Suva Barrier Reef, from a prawn trap in 300 fathoms (550m), 9 Jul 1981, USP R/V *Nautilus.* Both specimens now faded and in poor condition.

Diagnosis.—A *Parmops* without midventral scutes or an external tooth patch on anterolateral face of dentary near tip, gular isthmus with papillose ridges, posterior supramaxilla comprising one or two autogenous pieces posteriorly, and 5 dorsal-fin spines, 15 dorsal-fin soft rays, 12 anal-fin soft rays, 15 or 16 pectoral-fin rays, 14+17 vertebrae, and 34 pored lateral-line scales.

Description.—Counts and measurements, in mm, of the holotype and (paratype): dorsal-fin rays V-I,15 (VI,15); anal-fin rays II,11(II,11); pectoral-fin rays ii12ii (ii11ii); pelvic-fin rays I,5 (I,5); caudal-fin rays 8,10+9,8 (8,10+9,8); branchiostegals 8 (8); gill rakers 8+22 (8+21); pored lateral-line scales 34 (34); scales above lateral line 8 (8); scales between pelvic girdle and anus 12 (12); vertebrae 14+17. Head length

Fig. 1. Holotype of *Parmops coruscans,* USNM 361379, 46 mm SL, right side reversed.

18.8 (28.6); head depth 17.4 (29.4); head width 10.0 (19.9); interorbit width 5.0 (8.8); predorsal length 20.8 (36.5); prepelvic length 18.1 (33.5); body depth 18.3 (38.5); caudal-peduncle depth 4.9 (10.0); caudal-peduncle length 11.8 (28.6); snout length 4.6 (7.0); orbit diameter 8.2 (13.7); light-organ length 8.6 (11.7); light-organ depth 2.7 (5.4); pectoral-fin length 9.5 (23.4); pelvic-fin length 7.9 (15.3).

Body compressed, width of head 1.8 in depth, body depth 1.7 in post-head length. Snout blunt, profile sloping forward with little curvature from occiput. Nostrils above anterodorsal margin of eye, the posterior approximately twice as large as anterior. Mouth strongly oblique, tip of lower jaw at level of mid orbit, upper jaw slightly included. Maxilla extending posteriorly to vertical through anterior ⅓ of eye; posteroventral corner not dentigerous, but lightly papillose. Posterior supramaxilla ovoid, with an anterior process; posterior end of supramaxilla comprising one autogenous plate in the holotype, two in the paratype. Anterior supramaxilla much smaller, comprising one piece in the holotype, two in the paratype. No enlarged external teeth on dentaries. Vomer toothless, palatines with bands of teeth. Posterior margin of supracleithrum smooth. Infraorbitals 1–4 enlarged and laterally flared to form ventromedially sloping shelf effectively widening and deepening subocular pocket that accommodates light organ. Lacrimal with two pores and three larger cavities. Postorbital with two skin-covered openings at corner, followed by three openings, the central the largest. Preopercular canal without bony bridges, except at corner. Mandibular canal with two pores anteriorly followed by trough roofed by bone only at junction with preopercular canal. Canals of cranium apparently entire but not in good condition. A single fleshy papilla on rear margin of orbit. Subocular light organ and shutter as in *P. coruscans* (Jonhson & Rosenblatt 1991, fig. 2). Ovoid organ free except at anterior end, rotatable so that luminous face can be rotated dowward into pocket formed by flared infraorbitals. Outer margin of adpressed organ well below infraorbital rim. Black elastic shutter membrane attached along lateral margin of suborbital pocket, lying flat on floor of pocket when relaxed, with free margin medially. Scales strongly spinoid, with rows of almost erect spines on exposed portion. Scales on ventral midline not enlarged or scute-like. Head scales is in *P. coruscans.* Gular isthmus with well-developed papillae on transverse ridges. Basal scale sheaths on dorsal- and anal-fin soft rays strongly developed, with a distal enlarged row, covering about 40% of fin. Pseudobranch with about 23 filaments. Spinous dorsal fin low, most spines and soft rays damaged, as are the anal-fin rays. Pectoral fin angulate, its ventral margin sloping anteriorly. Pelvic fins extending to within about 40% of eye diameter of anus. Color now faded to brown, but undoubtedly black in life.

Etymology.—From the Latin, *echinatus,* spiny, with reference to the strongly ctenoid scales and well-developed spination on head and fin rays.

Occlusion mechanism.—The light organ and associated structures are as in *P. coruscans.* (See Rosenblatt and Johnson, 1991, pp. 331-332, fig. 2).

Generic placement.—Parmops echinatus agrees with the character states defining *P. coruscans* given in tables 1 and 2 of Rosenblatt & Johnson (1991), except that there are more epineural bones (see Remarks below), 14+17 vertebrae (vs. 14+16), no external patch of enlarged teeth on dentary, and no midventral scutes. The latter feature requires modification of the diagnosis of the genus provided by Rosenblatt & Johnson (1991), which included "a row of enlarged scutes on the belly." *P. echinatus* is the only member of the family (indeed, for that matter, of the Trachichthyoidei) without midventral scutes or external teeth on the dentary. The latter can be interpreted as a matter of degree, as there are teeth on the dorsal surface of the dentary that are visible anteriorly with the mouth closed, but they do not extend around the anterolateral tip to contact the serrate ridges along the ventral surface of the dentary as in *P. coruscans.* The midventral scales are neither ridged nor enlarged. Considering the ubiquity of scutes and external dentary teeth in trachichthyoids, their absence in *P. echinatus* is most parsimoniously interpreted as the result of independent reversals. With reference to the most recent cladogram of anomalopid genera (Baldwin et al. 1997, fig. 4), *P. echinatus* exhibits four of the five synapomorphies uniting the *Protoblepharon - Photoblepharon* clade (the exception being the external dentary tooth patch), the four uniting the *Parmops - Photoblepharon* clade, and lacks the two uniting *Phthanophaneron* with *Kryptophanaron* and the one uniting the latter two genera. Its placement as the sister taxon of *P. coruscans* (and thus within the genus *Parmops*) is supported by the apomorphic expanded infraorbitals and the resultant subocular pocket configuration it shares with that species.

Remarks.—The Fiji material includes the second known specimen of *P. coruscans* (USNM 361381), which is considerably larger than the holotype. It was caught off Suva Barrier Reef in 240 fathoms (440 m) in August 1983 in a prawn/Nautilus trap from the USP R/V *Nautilus.* Its counts and measurements in mm are:

Dorsal-fin rays V-I,16; anal-fin rays II, 12; pectoral-fin rays ii13ii; pelvic-fin rays I, 5; caudal-fin rays 10,10+9,10; branchiostegal rays 8; gill rakers 11+23; lateral-line scales 31; scale rows above lateral line 8; vertebrae 14+16. Standard length 66.5; head length 25.2; predorsal length 30.5; prepelvic length 34.5; body depth 34.0; caudal-peduncle length 21.9; caudal-peduncle depth 8.4; head length 25.2; snout length 6.4; eye diameter 11.4; orbit diameter 13.1; light-organ length 8.3; light-organ depth 3.1; pectoral-fin length 17.0; pelvic-fin length 15.2; first dorsal spine length 4.5; fifth dorsal spine length 6.4; upper caudal-lobe length 17.6; middle caudal-fin ray length 8.3.

The larger specimen agrees well with the description of the much smaller holotype, except that the pectoral fin is proportionately longer, (about 1.2, rather than 1.5, in the head), the second anal-fin spine is fully transformed and unsegmented, the posteroventral corner of the maxilla is strongly dentigerous, and the anterior supramaxilla is fused to the maxilla. The median fins of the holotype are damaged. In the present specimen the borders of the soft dorsal and anal fins slope evenly backward and the caudal fin is forked, as is typical for the family.

Johnson & Rosenblatt (1988, table 1) reported incorrectly that *Phthanophaneron,* *Kryptophanaron,* and *Photoblepharon* have epineural bones (their "epipleural ribs") on only the first two vertebrae. There is considerably more variability. Patterson & Johnson 1995 (table 7) recorded additional ossified epineurals on V8–12 in *Photoblepharon* and Baldwin et al. (1997) reported them on V9–14 in *Protoblepharon. Kryptophanaron* may have either no ossified epineural ligaments or partial ossification of those on V12 or V12–13. Both species of *Parmops* have ossified epineurals extending to V13–14; in both specimens of *P. echinatus* and the holotype of *P. coruscans,* they begin on V8 whereas in the larger specimen of *P. coruscans* they appear to form a continuous series from V1 to V14.

Acknowledgments

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Further characterization of *Caracara creightoni* Brodkorb based on fossils from the Quaternary of Cuba (Aves: Falconidae)

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Abstract.—*Caracara creightoni,* previously known from three fragmentary fossils from New Providence Island, Bahamas, is here documented from two Quaternary sites in Cuba. It appears to have been a smaller species than *C. cheriway,* but with a more robust bill and quadrate and other cranial differences, relatively shorter wings, and more robust hindlimb elements. The living species *C. cheriway* appears to be a relatively recent arrival in Cuba so that it is likely that fossils of *Caracara* from the West Indies may all belong to extinct endemic species.

In his report on Quaternary birds from a sinkhole on New Providence Island, Bahamas, Brodkorb (1959) erected a new species, *Caracara creightoni,* based only on a single fragment of carpometacarpus consisting mainly of the major metacarpal. Although Olson (1976) regarded this with skepticism, he was forced to concede that it came from a caracara and that it had a few apparently distinctive features. Nevertheless, he adopted a very conservative approach and considered all of the then-named fossil forms of *Polyborus* (now *Caracara* again—see Banks & Dove 1992) to be referable to *Caracara plancus* sensu lato. This conclusion was reversed following the discovery at the type locality of an incomplete quadrate and the distal end of a tibiotarsus that were distinct from *C. plancus,* so that *C. creightoni* was reinstated as a good species despite the paucity of material (Olson & Hilgartner 1982).

An incomplete skull and two portions of femora from Quaternary sites in Cuba were referred to *Caracara creightoni* by Suárez & Arredondo (1997), although these were not described or illustrated. The identification of the femoral portions we now regard as uncertain because of the difficulty of identifying incomplete specimens, but we here describe the skull along with additional more recently collected postcranial material from Cuba in an attempt to further characterize the species *C. creightoni.* Unfortunately, although vertebrate fossils have been found in many localities in Cuba, very few have been accurately dated and all of those discussed herein can only be assumed to be Quaternary in age (Suárez 2000).

Comparative material examined.—Complete skeletons unless otherwise noted: *Caracara cheriway* USNM 11679 (partial postcranial), 19664 (skull), 19670-71, 19682 (skull), 321805, 322338, 343845-46, 346402, 428041, 431612, 553229-30. *Caracara plancus* 18478, 227375 (skull), 345779-80, 488293 (skull), 490931, 614583-84. *Caracara lutosus* 19916.

Systematics

Class Aves
Family Falconidae
Genus *Caracara* Merrem, 1826
Caracara creightoni Brodkorb, 1959
Figs. 1–3

Referred material.—Skull consisting of most of the rostrum, the interorbital bridge,

Table 1.—Skull measurements (mm) of species of *Caracara*. Sequence in modern taxa is: range (mean) n.

Measurement	*C. creightoni*	*C. cheriway*	*C. plancus*
Length of premaxilla from anterior margin of naris to tip	22.6+	18.7–20.2 (19.9) 9	18.8–20.8 (19.9) 7
Depth of premaxilla from ventral margin of nostril to tomium	14.0	10.4–11.4 (11.0) 10	9.7–12.1 (10.8) 7
Width of premaxilla at midpoint through tomia	9.6	8.4–9.6 (9.3) 9	8.6–11.6 (10.0) 7
Width of bridge between nostrils	7.6	5.1–6.2 (5.7) 10	5.2–7.1 (6.1) 7
Width of frontals (interorbital bridge) at posterior margins of lacrimal scars	19.2	18.5–21.0 (19.7) 10	17.0–23.2 (21.9) 7
Dorsal width of cranium posterior to postorbital processes	41.0	29.1–41.2 (40.0) 9	36.9–43.0 (40.5) 7
Posterior width of cranium through temporal fossae	33.2	32.2–34.9 (32.9) 10	31.8–36.4 (34.5) 7
Distance from dorsal margin of foramen magnum to nuchal crest	13.5	11.0–11.9 (11.4) 9	10.3–12.7 (11.3) 7
Depth of foramen magnum (to dorsal surface of occipital condyle)	6.3	6.8–7.5 (7.1) 9	6.7–7.8 (7.2) 7

and the braincase lacking some of the antero-ventral portions, OA 3928; Cuba, Matanzas Province, Municipality of Cárdenas, 1.5 km SE of the town of Cantel, Cueva Calero. This site also contained numerous human skeletons and bones of extinct reptiles, birds, and mammals (Martínez & Rives 1990), but it is not known whether the excavation was sufficiently controlled to exclude the possibility that the caracara skull did not come from lower strata and may not have been directly associated with archaeological material.

Complete left ulna, MPSG 75; right carpometacarpus lacking minor metacarpal, MPSG 77 and the proximal half of a left carpometacarpus MPSG 110; left tibiotarsus lacking internal condyle, MPSG 79; distal end of right tibiotarsus lacking posterior rim of internal condyle, MPSG 83; complete left tarsometatarsus MPSG 103; distal half of left tarsometatarsus, MPSG 106; Cuba, Provincia de Villa Clara, Munícípio de Coralillo, El Charcón, "Solapa del Megalocnus." This site is a small pit (*casimba*) less than 2 m in diameter that is filled with water in most years. In 1997, a year of drought, discovery of bones of the ground sloth *Megalocnus* in the exposed mud led to the excavation of the site and the collection of remains of other mammals, reptiles, and birds, including a condor (*Gymnogyps*—see Suárez 2000), as well as *Caracara creightoni.* At least two, and probably three, individuals of *Caracara* are represented because the distal portion of one tibiotarsus is considerably larger than the other, yet the two left tarsometatarsi are about equal in size.

Descriptions and comparisons.—Compared with *Caracara cheriway, C. plancus,* or *C. lutosus, C. creightoni* has the premaxilla large and high, and more laterally compressed in ventral view; dorsal arc more rounded (less tapered) in lateral view; culmen broader with bridge between nostrils greater; distance between nostril and tomium deeper (Table 1); nostrils smaller and more ovoid, not distinctly reniform. Interorbital bridge relatively narrow compared with overall size of skull (Table 1). Nuchal crest higher (more dorsal and anterior) on skull, with distance to foramen magnum greater (Table 1); dorsal margin of foramen magnum straighter, not curved; foramen magnum oval rather than rounded, wider but dorso-ventral dimension less.

All of the complete postcranial bones are shorter than in any modern individuals of *Caracara* (Tables 2, 3). All but two of the

Table 2.—Measurements (mm) of wing elements of species of *Carcara*. Sequence in modern taxa is: range (mean) n.

Measurement	*C. creightoni*	*C. cheriway*	*C. plancus*
Ulna			
Length	101.2	106.5–121.0 (114.1) 11	114.5–142.3 (138.8) 6
Proximal width	8.5	8.8–10.2 (9.5) 11	9.5–12.0 (10.8) 6
Shaft width at midpoint	5.0	4.9–5.5 (5.2) 11	5.2–6.9 (6.2) 6
Distal width	9.1	9.5–10.6 (10.2) 11	9.8–13.1 (11.5) 6
Caprometacarpus			
Length	50.7	55.6–63.8 (61.9) 11	59.9–75.5 (66.5) 6
Length of major metacarpal from distal margin of alular metacarpal to distal condyle	40.3, 44.9*	43.9–50.8 (48.2) 11	47.3–60.8 (53.6) 6
Proximal width through trochlea	5.8	6.1–7.0 (6.6) 11	6.3–8.3 (7.3) 6
Proximal depth	13.4	12.6–16.2 (15.0) 11	14.2–19.9 (16.9) 6

* = holotype, from Brodkorb (1959: 353).

other measurements of wing elements are smaller than in *C. cheriway,* whereas most of the other measurements of hindlimb elements fall within those of *C. cheriway.* Ulna with scar for anterior articular ligament larger. Tibiotarsus with fibular crest longer relative to total length of bone; intercondylar sulcus wider.

Remarks.—The new Cuban material referred here to *Caracara creightoni* reaffirms the differences from *C. cheriway* and *C. plancus* that were tentatively inferred from the very fragmentary remains previously known from the Bahamas (Olson & Hilgartner 1982). The skull, although not larger overall, has a more massive and differently shaped bill, nostril, and foramen magnum, among other differences. Presumably these are associated with some difference in feeding habits. The large size of the quadrate from the Bahamas is assumed to be correlated with the cranial differences observed in the Cuban fossil.

Likewise, the small size of the wing elements from Cuba are in accordance with the small size of the holotypical carpometacarpus of *Caracara creightoni* from the Bahamas. The leg elements identified here from Cuba are shorter than in *C. cheriway* yet most of the other measurements fall within the range of that species, indicating a more robust hindlimb. Again, the Cuban

Table 3.—Measurements (mm) of leg elements of species of *Caracara*. Sequence in modern taxa is: range (mean) n.

Measurement	*C. creightoni*	*C. cheriway*	*C. plancus*
Tibiotarsus			
Length	101.6	105.7–116.8 (111.7) 11	105.6–129.6 (117.7) 6
Length of fibular crest	18.4	12.6–19.9 (16.3) 10	14.5–20.5 (17.3) 6
Proximal width	14.2	13.7–15.3 (14.7) 11	13.8–18.7 (16.6) 6
Shaft width at midpoint	6.2	6.0–6.6 (6.3) 11	5.7–7.9 (7.1) 6
Distal width	13.3, 14.2*	13.7–15.3 (14.7) 11	11.6–15.8 (14.3) 6
Tarsometatarsus			
Length	82.1	85.8–97.3 (91.6) 11	87.5–108.0 (98.0) 6
Proximal width	12.4	12.3–13.6 (13.0) 11	12.4–16.0 (15.6) 6
Shaft width at midpoint	5.4	5.1–5.7 (5.4) 11	4.8–6.7 (5.9) 6
Distal width	13.8	12.6–16.2 (15.0) 11	14.2–19.9 (16.9) 6

* = topotype, from Olson and Hilgartner (1982: 30).

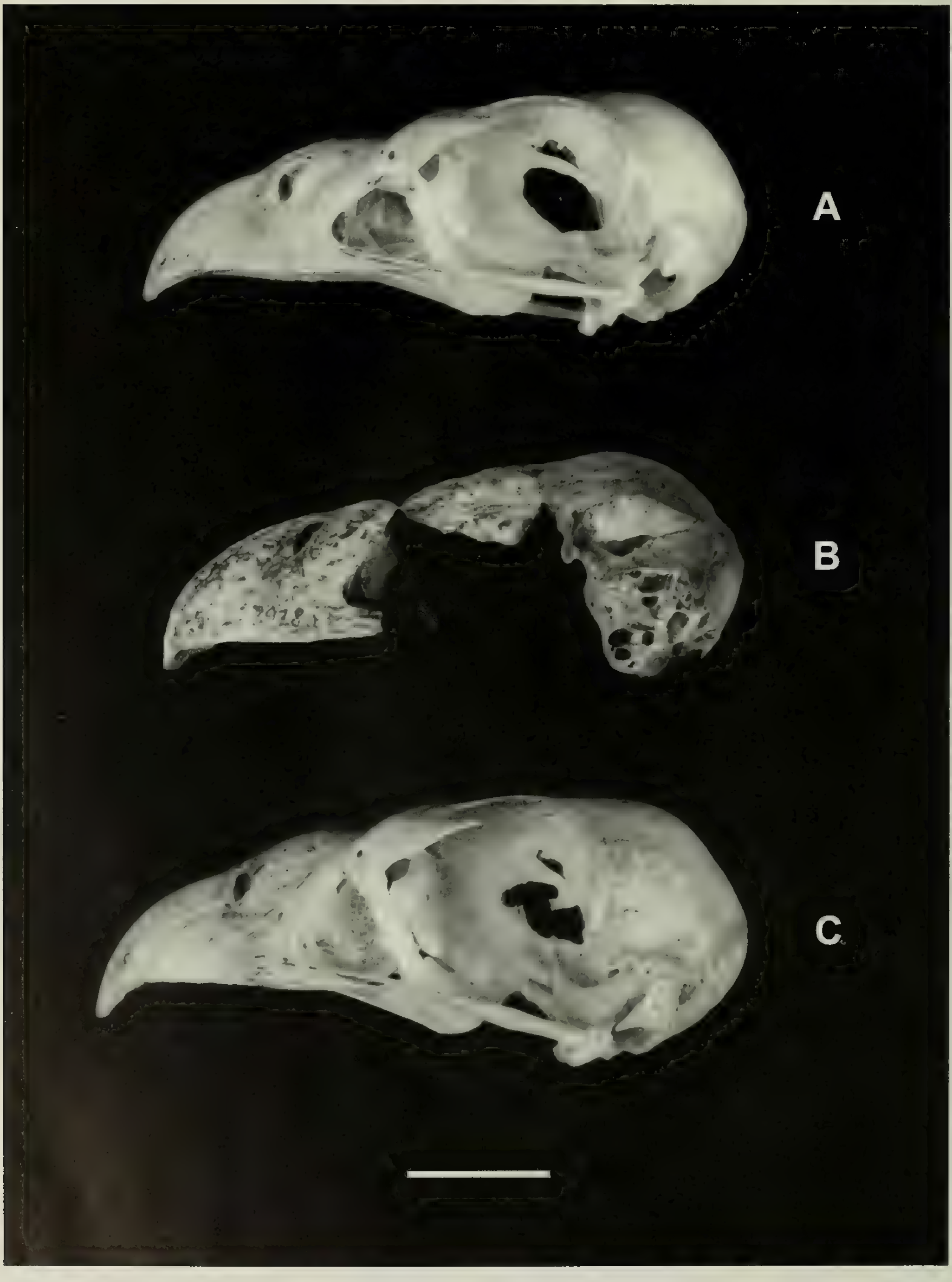

Fig. 1. Lateral view of skulls of *Caracara*. A, *C. cheriway* USNM 322338; B, *C. creightoni* OA 3928; C, *C. plancus* USNM 614584. Scale = 2 cm.

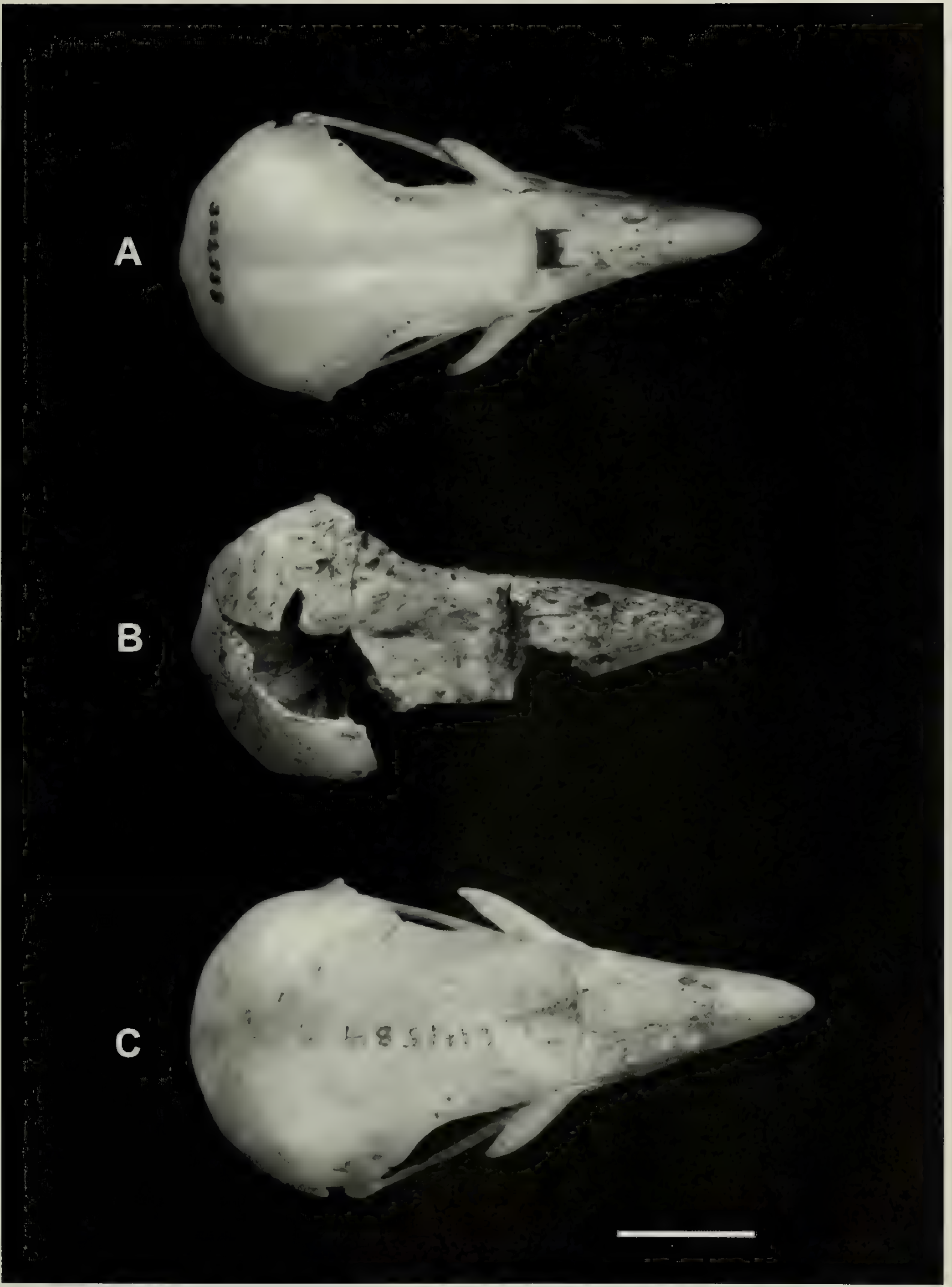

Fig. 2. Dorsal view of skulls of *Caracara*. A, *C. cheriway* USNM 322338; B, *C. creightoni* OA 3928; C, *C. plancus* USNM 614584. Scale = 2 cm.

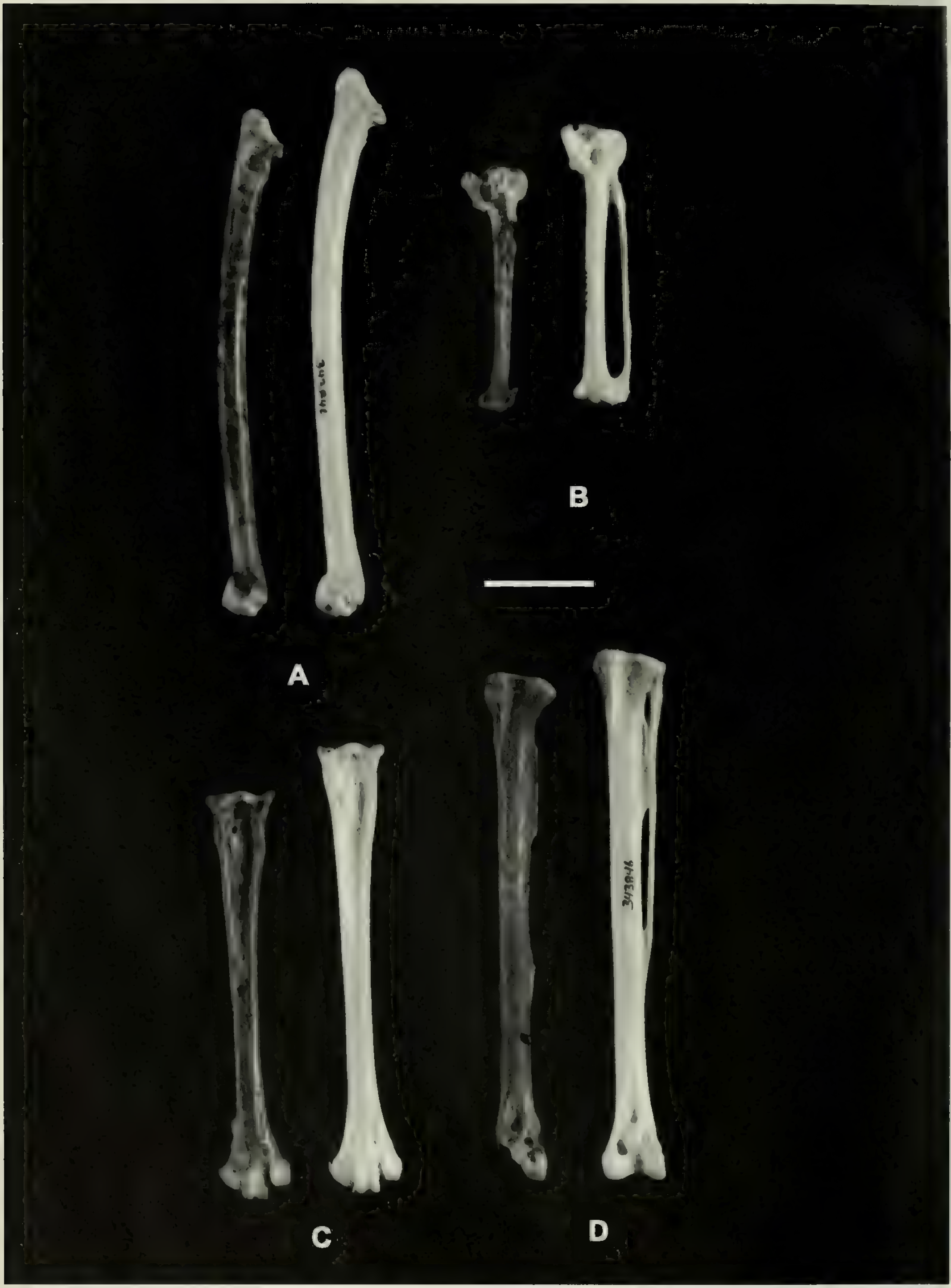

Fig. 3. Limb elements of *Caracara creightoni* (on the left in each pair) compared with *C. cheriway* (on the right in each pair). A, left ulnae in internal view (MPSG 75, USNM 343846); B, right carpometacarpi in internal view (MPSG 77, USNM 343846); C, left tarsometatarsi in anterior view (MPSG 103, USNM 343846); D, left tibiotarsi in anterior view (MPSG 103, USNM 343846). Scale = 2 cm.

material agrees with that from the Bahamas in the noticeably wide intercondylar sulcus of the tibiotarsus.

The historically known taxa of crested caracaras (*Caracara*) were revised by Dove & Banks (1999) who recognized three species: *C. lutosus* Ridgway endemic to Guadeloupe Island, Mexico, and now extinct; a southern species, *C. plancus,* Miller found in South America south of the Amazon; and a northern species, *C. cheriway* Jacquin, in Middle America and northern South America, with outlying populations in southern Florida and Cuba. Each of these three species was regarded as monotypic, with none of the previously named geographic variants being considered valid. Thus, the only resident crested caracaras in the West Indies today are the populations of *C. cheriway* in Cuba and the Isle of Pines.

Emslie (1998) reported that fossils of *Caracara plancus* (=*C. cheriway*) are absent in older deposits in Florida and occur only in the late Pleistocene. The same is probably true of Cuba, where *C. cheriway* may be a relatively recent arrival, as it shows no differences from mainland populations. Fossils thought to be referable to *C. cheriway* have been found in Cuba, but none have been well documented or dated. Furthermore, most fossils of caracaras would be difficult to determine to species when fragmentary, so exceptional conditions of preservation, stratigraphy, or dating may be needed to show whether *C. cheriway* and *C. creightoni* were ever contemporaneous.

Morgan (1994) referred the distal end of a tarsometatarsus from a cave on Grand Cayman to *Polyborus* (=*Caracara*) *creightoni,* with the observation that it was larger than in any of 10 specimens of *C. plancus* (sensu lato) from "throughout its range," and had the inner and outer trochleae more widely separated from the middle trochlea than in *C. plancus.* This does not agree with the tarsometatarsi of *C. creightoni* from Cuba, however, which are not of large size. On the other hand, a species of *Caracara* with a very large tarsometatarsus has been found in fossil deposits in Jamaica (S. L. Olson, unpubl.) and it seems likely that the specimen from Grand Cayman will prove to be referable to that species rather than *C. creightoni.* The relationship that this may bear to the species *Polyborus latebrosus* that Wetmore (1920) named from the Quaternary of Puerto Rico will be explored in a later paper. In light of the probable recentness of colonization of the West Indies by *Caracara cheriway,* it seems more likely now that fossils of *Caracara* from the West Indies be referable to endemic taxa that have all become extinct.

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A new species of large flightless rail of the *Rallus longirostris/elegans* complex (Aves: Rallidae) from the late Pleistocene of Bermuda

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Abstract.—*Rallus recessus,* new species, probably derived from the King Rail *R. elegans,* is described from a cave deposit exposed in quarrying operations on the island of Bermuda. This species had the reduced elements of the wing and pectoral girdle and more robust hindlimbs typical of flightless rails. It is the only member of the largest size-class of the genus *Rallus* known to have colonized an oceanic island and become flightless. It was present on Bermuda during the last (Wisconsinan) glacial period and appears to have become extinct naturally due to changing environmental conditions associated with changes in sea level.

Fluctuating sea-levels dramatically altered the land area of the North Atlantic island of Bermuda during the Pleistocene, causing natural turnover in major elements of the island's biota, particularly birds. At least two different avifaunas have been recognized from undated caves and fissures exposed in limestone quarrying operations. One of these is characterized by the presence of a crane, a duck, and two medium to small flightless rails—*Grus latipes, Anas pachysceles, Rallus ibycus,* and *Porzana piercei* (Wetmore 1960, Olson & Wingate 2000). These species are absent in the other fauna, which is dominated by a large, flightless derivative of the *Rallus longirostris/elegans* complex that has been alluded to previously as an unnamed species (Olson 1977, 1997; Olson & Wingate 2000).

These distinct avifaunas are thought to have existed during two different glacial periods of the Pleistocene when sea-levels were lower and the land area of Bermuda was greater than at present. Olson & Wingate (2000) made an assumption that the crane fauna was older than the fauna with the large rail. Although this assumption is now known to be correct, the crane fauna is probably not as old as they hypothesized.

The following description of the large rail is based entirely on the specimens collected in 1960 from "Rail Cave" in Government Quarry. Additional material of the species has since been found in two other deposits that are under investigation by P. J. Hearty (James Cook University, Queensland, Australia) and Olson. One of these promises to allow a very precise chronological reconstruction of the geology and paleontology of Bermuda in the late Quaternary, which will be presented elsewhere. For the present, we have been able to determine that the undescribed large rail existed during the last (Wisconsinan) glacial period. Therefore, we here proceed with naming it in order to be able to refer to it unambiguously in future publications.

Materials and Methods

Disassociated fossil elements are cataloged in the collections of the Florida Museum of Natural History and all specimens take the prefix UF PB, which we have omitted except in the citations of the holotype

Table 1.—Measurements (mm) of selected skeletal elements of *Rallus recessus,* new species.

	n	Range	Mean	S.D.
Cranium				
Length from naso-frontal hinge	14	29.2–33.3	32.2	1.21
Width at postorbital processes	15	15.9–17.1	16.6	0.31
Width interorbital bridge	19	3.9–5.2	4.6	0.39
Sternum				
Length along midline (from notch)	16	30.4–36.7	33.0	1.70
Width across coracoidal sulci	17	12.0–14.6	13.1	0.71
Depth of carina	24	6.0–9.2	7.5	0.75
Coracoid				
Length	38	20.5–25.1	23.3	1.30
Humerus				
Length	60	39.7–47.4	43.7	1.91
Proximal width	59	8.4–10.5	9.4	0.45
Shaft width	60	2.2–2.9	2.6	0.15
Distal width	60	5.6–6.7	6.1	0.31
Ulna				
Length	45	29.3–37.3	34.1	1.84
Radius				
Length	18	28.1–34.3	31.4	1.81
Carpometacarpus				
Length	27	20.5–24.5	22.9	1.18
Proximal depth	27	5.0–5.9	5.5	0.29
Pelvis				
Sacrum length	27	32.8–42.9	38.2	2.45
Width across antitrochanters	10	17.5–21.2	20.1	1.25
Femur				
Length	26	44.3–52.4	49.1	2.12
Proximal width	26	7.9–9.5	8.8	0.45
Distal width	26	7.5–8.8	8.3	0.37
Tibiotarsus				
Length from proximal articular surface	30	58.0–71.9	66.3	3.61
Distal width	30	6.0–7.2	6.6	0.31
Tarsometatarsus				
Length	29	36.6–44.6	40.9	2.21
Proximal width	29	6.3–7.6	7.0	0.36
Distal width	29	6.7–8.1	7.4	0.40

and the figure legends. There is a great deal more material available than is listed among the type material. As paratypes we have listed those specimens that either were used in the descriptions, are illustrated, or were used for any of the cited measurements. Measurements of long bones of the limbs usually do not include broken or juvenile specimens, which accordingly are not among the listed paratypes. Measurements were taken with digital calipers to 0.01 mm and rounded to the nearest 0.1 mm.

Comparative material examined.—Skeletons (complete unless otherwise indicated) of the following species in the collections of the National Museum of Natural History, Smithsonian Institution (USNM). *Rallus aquaticus* 431545, 553039, 553041; *R. lim-*

Fig. 1. Comparison of skulls (*a, d*) and sterna (*b–c, e*) of *Rallus* in lateral view. *a, R. recessus,* new species, holotype UF PB5108; *d, e, R. elegans* female USNM 499437; *b, c, R. recessus,* new species, UF PB5124, UF PB5126. Scale bar = 2 cm.

icola 489973, 525915, 525917; *R. elegans* 499437, 525886, 610780, UF 22870, UF 24314, UF 24318; *R. longirostris* 525876, 525873, 525879; *R. longirostris* × *R. elegans* 525887.

Systematics

Family Rallidae
Genus *Rallus* Linnaeus

Referable to *Rallus,* sensu stricto, by the very long, slender bill and by the lack of characters suggesting relationship to the long-billed rails of the genus *Pardirallus* (including *Ortygonax*), which are not closely related to *Rallus* (Olson 1973).

Rallus recessus, new species
Figs. 1–5

Holotype.—Cranium and rostrum consisting of the pila supranasalis and premaxillary symphysis but lacking the lateral nasal bar and ventral portions UF PB5108. Collected in February/March 1960 by Pierce Brodkorb and David B. Wingate.

Type locality.—Bermuda, Hamilton Parish, Government Quarry, from a fissure called "Rail Cave" that was exposed in quarrying operations and that has since been quarried away.

Chronology.—Late Pleistocene, last (Wisconsinan) glacial period.

Measurements (mm) of holotype.—Total

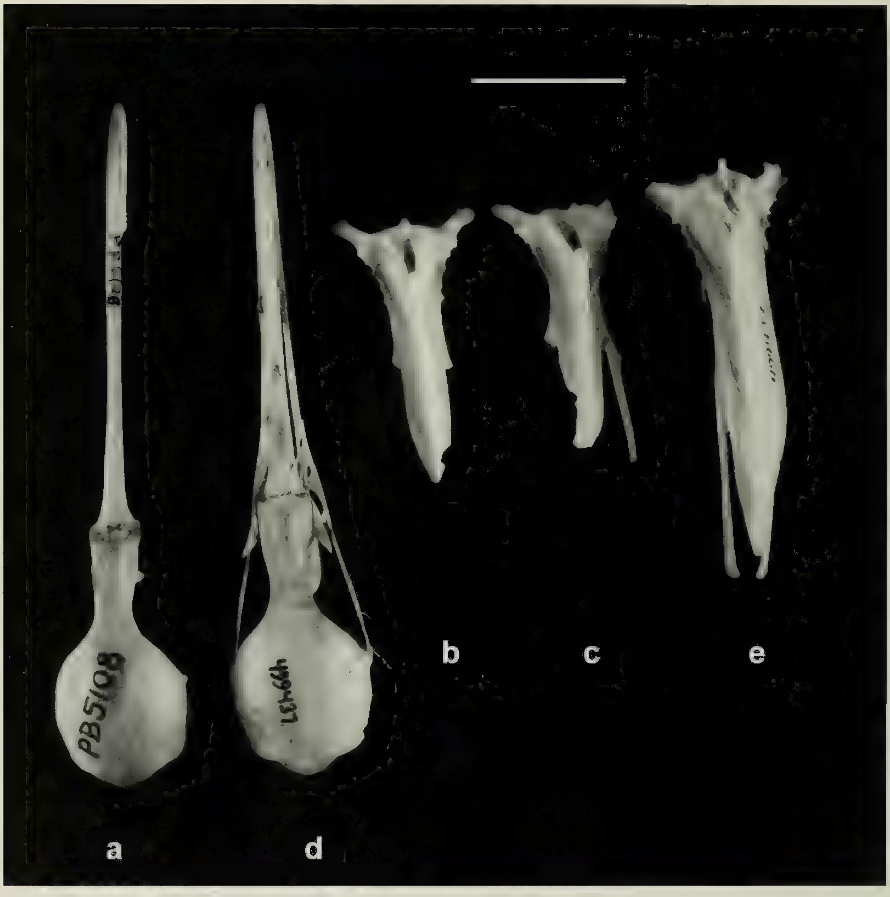

Fig. 2. Comparison of skulls in dorsal view (*a, d*) and sterna in ventral view (*b–c, e*) of *Rallus. a, R. recessus,* new species, holotype UF PB5108; *d, e, R. elegans* female USNM 499437; *b, c, R. recessus,* new species, UF PB5124, UFPB 5126. Scale bar = 2 cm.

length, 93.6; rostrum from nasofrontal hinge to tip, 62.7; length of premaxillary symphysis, 21.1; length of cranium from naso-frontal hinge, 33.1; width of cranium at postorbital processes, 17.0; width of interorbital bridge 4.8.

Paratypes.—Crania with rostra 5104, 5115. Rostrum 5103. Crania (a few consisting of only the interorbital bridge) 5101–5103, 5105–5107, 5109–5114, 5116–5117, 5295–5298. Sterna 5119–5129, 5131–5135, 5137–5138, 5140–5141, 5143, 5145, 5294, 5894. Coracoids 5284, 5395–5400, 5856, 5858–5865, 5867, 5869–5875, 5878–5887, 5890–5893. Scapula 5285. Humeri 5146–5158, 5160–5174, 5180–5196, 5198–5203, 5205–5208, 5822–5826. Radii 5836–5843, 5848–5857. Ulnae 5213–5219, 5221–5226, 5228–5236, 5242, 5243, 5244, 5245, 5246, 5247, 5248–5264. Carpometacarpi 5269–5278, 5280–5283, 5340–5342, 5344–5353. Pelves 5287, 5408, 5896–5902, 5904, 5906–5915, 5917–5919, 5922–5924, 5926. Femora (right) 5288, 5302, 5304–5307, 5309–5310, 5312–5314, 5316–5322, 5327, 5328, 5332–5936. Tibiotarsi (right) 5289, 5332, 5368, 5385–5386, 5388–5394, 5717–5726, 5833–5834, 5937–5941, 5948. Tarsometatarsi (right) 5290, 5746–5760, 5791–5795, 5797–5798–5798bis? = 5799?, 5800–5803, 5813.

Measurements (mm) of paratypes.—Rostrum: length from naso-frontal hinge, 61.5, 62.5, 62.7, 63.8; length of premaxillary

Fig. 3. Comparison of pectoral and wing elements of *Rallus recessus,* new species (*a–e*) with *R. elegans* (*f, i, j,* USNM 499437 female; *g, h,* USNM 610781 female). *a, f,* left coracoids in ventral view (*a,* UF PB 5860); *b, g,* left scapulae in dorsal view (*b,* UF PB5385); *c, h,* left humeri in anconal view (*c,* UF PB5160); *d,* left ulna and radius in internal view (ulna UF PB 5214; radius UF PB 5856); *i,* right ulna and radius in internal view; *e, j,* left carpometacarpi in internal view (*e,* UF PB5340). Scale bar = 2 cm.

symphysis, 21.1, 21.1, 21.6, 22.0. Scapula: length 42.4. For other measurements see Table 1.

Associated paratype.—An articulated incomplete skeleton covered with flowstone was collected on a block of limestone from Rail Cave and is now on exhibit in the Bermuda Aquarium, Museum and Zoo (BAMZ 2000 190 001). Not all of the skeleton is present and the measurements of the remaining elements will in most cases probably be slightly too large because of their casing of flowstone. In size, the specimen would be at the small end of size variation in the species, presumably a female. The following length measurements (mm) were obtained. Total length of skull and bill 77.7; rostrum from nasofrontal hinge 49.6; cranium from nasofrontal hinge 19.6; mandible 66.2; coracoid 20.5; humerus 39.9; femur 44; tibiotarsus 60; tarsometatarsus 37.5.

Etymology.—Latin, *recessus,* used here with a double meaning; first, to refer to recession of the sea during the glacial period that this species occupied Bermuda (*recessus marini aestus* being low tide in Latin), and also to the second meaning of the word, a nook, corner, or secret spot, in reference to the hidden chamber in which the type material was secreted.

Diagnosis.—Larger than any of the species of *Rallus* (sensu stricto, Olson 1973) except those of the *R. longirostris/elegans*

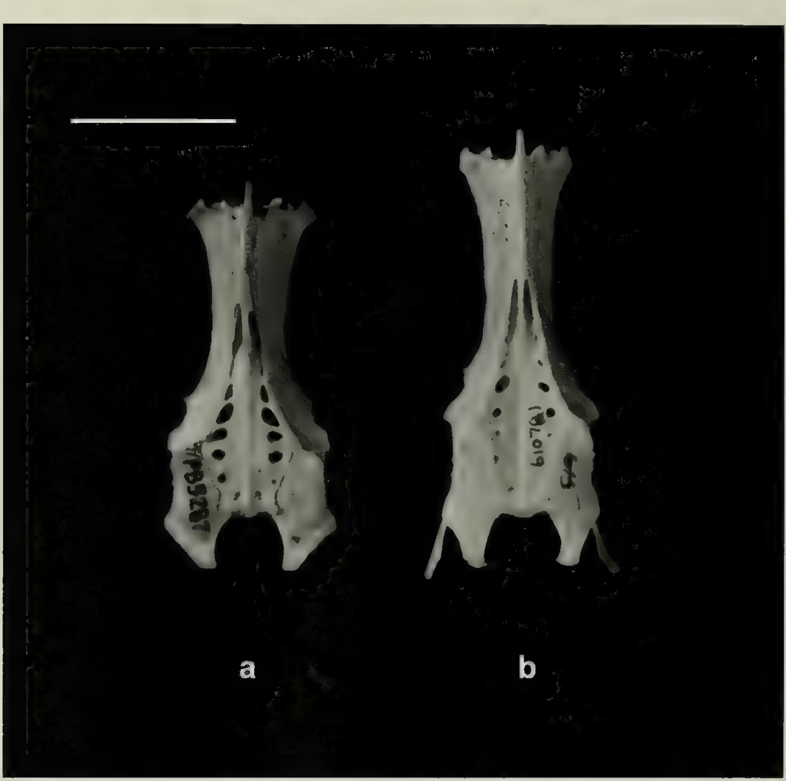

Fig. 4. Comparison of pelves of *Rallus* in dorsal view. *a, R. recessus,* new species, UF PB5287; *b, R. elegans* (USNM 610781 female). Scale bar = 2 cm.

complex. Differs from related species in characters associated with flightlessness and in having a proportionately longer and more slender bill, with a longer and more decurved premaxillary symphysis. The width of the interorbital bridge is intermediate between that of *R. longirostris* and *R. elegans.* Flight apparatus greatly reduced in development. Hindlimb elements shorter and much more robust.

Description.—In addition to the longer, more decurved bill, this species has the orbits reduced so the frontal area in lateral view slopes more steeply. There are no impressions for salt glands on the interorbital bridge, unlike *R. longirostris.* The cranium is narrow, which is less like *R. elegans.*

Compared with *Rallus longirostris/elegans,* the sternum is shorter and wider with the carina greatly reduced, although a small manubrial spine is present and there is no deep notch between the coracoidal sulci as in many flightless rails. The sternocoracoidal process of the coracoid is more pointed and projecting. The humerus has the head smaller, the capital groove wider, the shaft more curved and the brachial depression deeper. The ulna is very short and more curved and the carpometacarpus small.

The pelvis is wider with the postacetabular portion proportionately shorter, the ischial area in lateral view is much less deep, the ilia do not extend as far posteriorly beyond the sacrum, and the ilioischiadic fenestra is smaller. The hindlimb elements are shorter, both absolutely and relatively, and more robust, particularly the shafts.

Remarks.—The large species of *Rallus* included in the *R. longirostris/elegans* complex are confined to the New World. Their interelationships, biogeography, and hypothetical history have been discussed by Olson (1997), who argued on the basis of the interorbital bridge that the Bermuda bird

Fig. 5. Comparison of hindlimb elements in anterior view of *Rallus recessus,* new species (*a–f*) with *R. elegans* (*g–i*—USNM 499437 female). *a, b,* right femora UF PB5036, UF PB5309; *c, d,* right tibiotarsi UF PB5941, UF PB5722; *e, f,* right tarsometatarsi UF PB5796, UF PB5800. Scale bar = 2 cm.

was a derivative of *Rallus elegans* that had become adapted to somewhat higher salt stress, rather than a derivative of *R. longirostris.* According to Olson's hypothesis, *R. elegans* was the original North America stock of large *Rallus* that was later displaced from Gulf and Atlantic salt marsh habitats by an invasion of *R. longirostris.* Although the salt-marsh Clapper Rail, *R. longirostris,* has been found as a very rare vagrant to Bermuda, the King Rail, *R. elegans,* has not yet been recorded there (Amos 1991).

Acknowledgments

As in our previous paper (Olson & Wingate 2000) we are indebted to officials at the Bermuda Government Quarry, the late Pierce Brodkorb, Marc Frank, and David W. Steadman for assistance in obtaining and studying the specimens, Paul J. Hearty for geological insights, Helen James for statistics, and John Steiner, Victor E. Krantz, and Brian Schmidt for photography and arrangement of figures. We thank Lisa Green and Wolfgang Sterrer of the Bermuda Aquarium, Natural History Museum and Zoo (BAMZ) for access to the associated paratype and many other considerations. This is contribution #37, Bermuda Biodiversity Project (BBP), of the BAMZ.

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Sharamynodon (Mammalia: Perissodactyla) from the Eocene of the Ily basin, Kazakstan and the antiquity of Asian amynodonts

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Abstract.—The brontothere bone bed at Kyzyl Murun near Aktau Mountain in the Ily basin of eastern Kazakstan is a 0.5-m-thick layer of green bentonitic mudstone in the Kyzylbulak Formation that yields numerous skeletons of the middle Eocene (Irdinmanhan) brontothere *Protitan.* An incomplete skull, lower jaw and some fragmentary postcrania from this bed belong to an amynodontid rhinoceros. This specimen can be assigned to *Sharamynodon mongoliensis* (Osborn) because it displays numerous diagnostic features of that taxon, including three closely spaced incisors, a short nasal incision that extends back to the postcanine diastema, a deep and tall preorbital fossa, and a relatively short preorbital portion of the skull. This is the first record of *Sharamynodon* from Kazakstan and the oldest Kazak amynodontid. Previous reports of this taxon indicate it had a broad geographic (China, Mongolia, Japan) and temporal (Irdinmanhan-Ergilian, i.e., middle-latest Eocene) distribution in Asia. There is no evidence that any Asian amynodont record is older than Irdinmanhan. Thus, we consider the record of "*Andarakodon*" from Andarak, Kyrgyzstan to be Irdinmanhan, not older. Indeed, "*Andarakodon*" is a junior subjective synonym of *Sharamynodon.*

Amynodontids were middle Eocene-early Miocene rhinocerotoids known from Asia, North America and Europe. Typically considered to have been amphibious, they actually represent a range of body plans from subcursorial and terrestrial to graviportal and amphibious (Wall 1982, 1989). In eastern Asia (Japan, Korea, China and Mongolia), amynodontids first appeared during the middle Eocene (Irdinmanhan land-mammal "age" [lma] of Russell & Zhai 1987) and persisted until the end of the Oligocene (Tabenbulukian lma). The latest known Asian amynodontids are two specimens of the derived, hypsodont genus *Cadurcotherium* from the lower Miocene Bugti Formation of Pakistan (Pilgrim 1912, Raza & Meyer 1984). The westernmost Asian occurrences of amynodontids are in Kazakstan (Fig. 1), where five amynodontid taxa have been named (Lucas & Emry 1996, Lucas et al. 1996). Here, we add to this record the occurrence of *Sharamynodon mongoliensis* in Irdinmanhan-age strata of the Ily basin (Fig. 1). We also re-evaluate the taxonomy and age of the supposedly oldest Asian amnyodont records from Kyrgyzstan to reaffirm that Amynodontidae first appear in Asia during the Irdinmanhan.

Abbreviations used.—When used in dental notations, upper case letters denote upper (skull) teeth and lower case letters denote lower (dentary) teeth. Institutional abbreviations are: AMNH – Department of Vertebrate Paleontology, American Museum of Natural History, New York; KAN – Institute of Zoology, Academy of Sciences of the Republic of Kazakstan, Almaty.

Fig. 1. Map of Kazakstan showing location of the *Sharamynodon* locality at Aktau Mountain.

Systematic Paleontology

Family Amynodontidae Scott & Osborn, 1883

Genus *Sharamynodon* Kretzoi, 1942

Sharamynodon mongoliensis (Osborn, 1936)

Figs. 2–3

Referred specimen.—KAN-N2/872, incomplete skull, lower jaw frargments and teeth isolated from these elements. Most of the right side of the skull is preserved, but the specimen is laterally crushed. The right P2-M3 are present, and M3 is not fully erupted. The left P3 is present, as are the right upper canine and right I1. The lower right canine, right i1-2, right p2-3 and symphysis are preserved, as are fragments of the postcrania, most notably the scapular glenoid.

Locality and horizon.—Brontothere bonebed at Kyzyl Murun, near Aktau Mountain, Ily basin, eastern Kazakstan (Fig. 1). The bonebed, at UTM 44361142E, 4872826N, is a 0.5-m-thick green bentonitic mudstone of the Kyzulbulak Formation (= unit 26 of Lucas et al. 1997, fig. 3).

Description.—The skull (Fig. 2) has an approximate maximum length of 430 mm and is very similar to AMNH 20278, the holotype skull of *Sharamynodon mongoliensis* (Osborn, 1936, fig. 3). Among its diagnostic characteristics are a relatively short preorbital region of the skull, a short nasal incision that extends to above the postcanine diastema, a weak ascending process of the premaxilla, a deep and tall preorbital fossa, a small postorbital process, presence of three closely spaced incisors, relatively small canines and a long postcanine diastemata.

The upper canine (Fig. 3A) is characteristically amynodontid in being laterally compressed and having a triangular crown in lateral view because of the prominent wear facet on its anterior face for the corresponding lower canine. Crown length = 18.4 mm.

The I1 (Fig. 3B–C) has a tall, blade-like crown with a pointed tip. The crown is convex anterior, less convex posterior and has a low, lingual cingulum that extends up the crown surface. Crown width = 12.8 mm.

The P2 (Fig. 3L) has a triangular crown dominated by a tall, thick ectoloph that peaks at the paracone. Lingually, a ridge begins at the protocone and extends anterolabially. Lingual to this ridge is a low cingulum that connects to the anterior and posterior edges of the ectoloph, thus enclosing the trigon basin. A small loph projects lingually from the ectoloph posterior to the paracone. P2 length = 19.1 mm, w = 19.8 mm.

The P3 (Fig. 3K) is much more molariform than the P2. It has a nearly square occlusal outline. A tall ectoloph dominates the crown, and it has four distinct ribs that project labially—a small parastyle anteriorly, a very large paracone, a smaller metacone and a very small metastyle posteriorly. The protoloph is a thick crest confluent with the ectoloph. A low cingulum extends from the parastyle lingually then posteriorly and labially to close the trigon basin. It is broken by two cristae—one on the anterior edge of the protoloph near the parastyle, the other directly lingual to the protoloph. As on the P2, a small cristid projects lingually into the trigon basin from the ectoloph at the metacone. P3 length = 23.1 mm, width = 27.3 mm. The P4 (Fig. 3J) is very similar to but larger and relatively wider (more transverse) than the P3. P4 length = 26.5 mm, width = 36.4 mm.

The M1 (Fig. 3M) is incomplete—much of its anterior half is missing. It is a square tooth with a large ectoloph and two prominent lophs (protoloph and metaloph) essentially perpendicular to the ectoloph. A cingulum circles the anterior, lingual and posterior edges of the crown but is discontinuous just lingual to the metaloph and paraloph. M1 width is about 43.6 mm.

The M2-3 have been plastically deformed, mostly in the labial-lingual direction. Distortion of the M2 (Fig. 3P–Q) has pushed the two lophs together antero-posteriorly. The ectoloph is very large, long and slightly concave labially. Anteriorly, there is a prominent parastyle followed immediately by an equal-sized paracone rib. There is no trace of a metacone, and there is a nearly complete lingual cingulum. M2 length = 56.2 mm, width = 49.4 mm (but note that distortion has altered the tooth shape significantly).

The M3 (Fig. 3N–O) is extremely deformed so that the ectoloph has been "squeezed" over the protoloph and metaloph. This tooth has a long, concave-labial ectoloph with a large paracone closely appressed to a slightly smaller parastyle. A prominent metacone terminates the ectoloph posteriorly. Like M2, the M3 has tall, transverse metaloph and protoloph and a nearly complete lingual cingulum. M3 length = 60.5 mm, width = 43.1 mm (but note that distortion has altered the tooth shape significantly).

The i1 (Fig. 3D–E) has a nearly round crown that peaks at a central cuspid. A ridge divides the lingual face of the crown

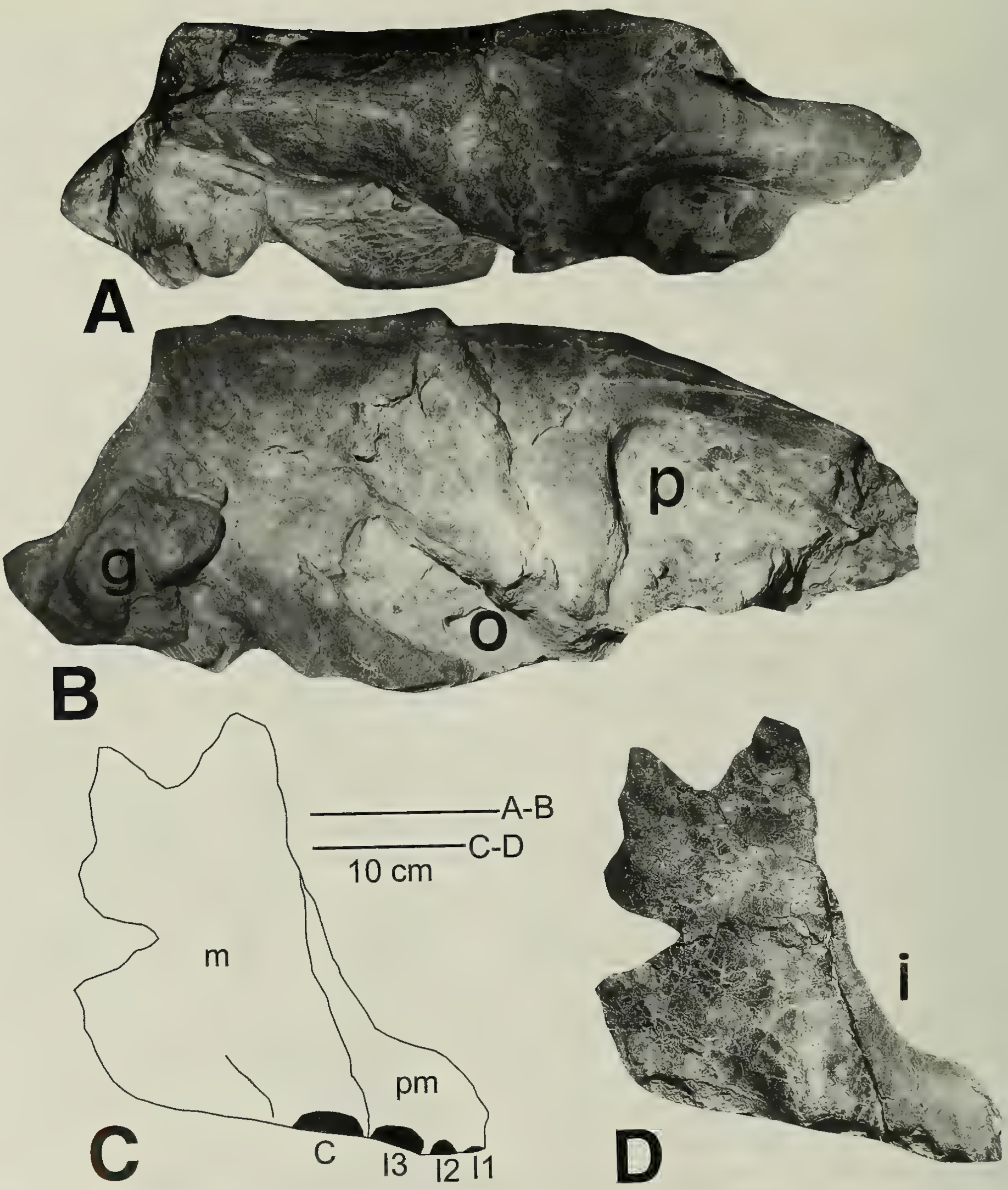

Fig. 2. KAN-N2/872, incomplete skull of *Sharamynodon mongoliensis* from the Ily basin, Kazakstan. A–B, Incomplete skull, dorsal (A) and right lateral (B) views. C–D, lateral views of premaxilla-maxilla. Abbreviations are: g - glenoid process, i - nasal incision, m - maxilla, o - orbit, p - preorbital fossa, pm - premaxilla.

into two "pockets," and the labial face is convex with a basal cingulid. Width of i1 = 12.8 mm.

The i2 (Fig. 3F–G) is similar to the i1 but larger. It also differs from i1 in not having such a distinct ridge on the lingual face of the crown. Width of i2 = 14.7 mm.

The p2 is a nearly rectangular tooth with a tall protoconid and prominent lingual cingulid. A cristid oblique connects the protoconid to the posterior end of the tooth. The p2 length = 14.7 mm, width = 10.2 mm.

The p3 (Fig. 3H–I) is very similar to the

Fig. 3. KAN-N2/872, teeth of *Sharamynodon mongoliensis* from the Ily basin, Kazakstan. A, upper right canine, medial view. B–C, right I1, in medial (B) and lateral (C) views. D–E, right i1, in medial (D) and lateral (E) views. F–G, right i2, in lingual (F) and labial (G) views. H–I right p3, in occlusal (H) and lingual (I) views. J, right P4, occlusal view. K, right P3, occlusal view. L, right P2, occlusal view. M, right M1, occlusal view. N–O, right M3, in buccal (N) and occlusal (O) views. P–Q, right M2, in boccal (P) and occlusal (Q) views.

p2 but larger and more molariform. This rectangular tooth also differs from p2 in having a distinct paracristid and hypolophid. The p3 length = 20.6 mm, width = 13.7 mm.

Discussion.—KAN-N2/872 displays all the diagnostic features of *Sharamynodon* listed by Wall (1989, p. 346) as distinctive of that taxon. It is very similar in morphology and size to AMNH 20278, the holotype of *Sharamynodon mongoliensis* (Osborn, 1936). Therefore, assignment of KAN-N2/872 to *S. mongoliensis* is certain.

Antiquity of Asian Amynodontidae

Lucas & Emry (1996) reviewed records of amynodont rhinoceroses from Kazakstan (also see Lucas et al. 1996). Prior to the record of *Sharamynodon* documented here, these were records in Ergilian-Shandgolian (late Eocene-early Oligocene) strata. The brontothere bonebed at Kyzyl-Murun in the Ily basin yields numerous skeletons of the characteristically Irdinmanhan brontothere *Protitan* (Emry et al. 1997). Therefore, the *Sharamynodon mongoliensis* record from Kyzyl Murun is the oldest Kazak amynodontid. Other *Sharamynodon* records—in China, Mongolia and Japan—range in age from Irdinmanhan to Ergilian (Russell & Zhai 1987).

In China and Mongolia, the oldest records of amynodontids are in strata of Irdinmanhan age; indeed, the FAD (first appearance datum) of Amynodontidae has been used as one of the criteria to define the beginning of Irdinmanhan time (Tong et al. 1995; Lucas 2000). Irdinmanhan is generally considered to be middle Eocene in age, a correlative of the North American Bridgerian LMA and the later part of the European Rhenanian LMA (Fig. 4) (Holroyd & Ciochon 1994, Ting 1998, Lucas 1998, 2000). Localities in China, Mongolia and Kazakstan of the immediately older time interval, the Arshantan LMA, conspicuously lack amynodontids (Tong et al. 1995; Lucas 2000).

In Kyrgyzstan, there are two mammal localities of Eocene age. The Toruaygyr locality lacks amynodontids and yields the Arshantan index fossil *Gobiatherium* (Agadjanian & Kondrashov 1999, Erfurt et al. 1999, Lucas 2000). Supposed records from Toruaygyr of *Teleolophus* (Reshetov 1979, Erfurt et al. 1999), which has its FAD at the beginning of the Irdinmanhan, are unsubstantiated, so assigning an Irdinmanhan age to Toruaygyr, as done by Erfurt et al. (1999), is difficult to accept. Toruaygyr is older, of Arshantan age, and notably lacks amynodontids.

The other Kyrgyz Eocene mammal locality is Andarak, which is actually two geographically close sites at approximately the same stratigraphic level (Averianov & Godinot 1998 provide the most recent review). This site yields several taxa whose FAD's are during Irdinmanhan time, including Amynodontidae, Eomoropidae and Anthracotheriidae. Therefore, the Irdinmanhan age of Andarak is certain (Lucas 2000).

Nevertheless, Averianov & Potapova (1996) concluded that the Andarak amynodontid is the oldest Asian amynodontid, assigning it an early Eocene age. Beliayeva (1971) originally described amynodontid specimens from Andarak as *Lushiamynodon* (?) *kirghisensis*. Averianov & Potapova (1996) redescribed this material, and additional specimens, assigning them to a new genus, *Andarakodon,* type species *A. kirghisensis* (Beliayeva). (Note that the species name "*kirghisiensis*" used by Averianov & Potapova (1996) is a lapsus calami for the original "*kirghisensis*" of Beliayeva.)

However, we conclude that *Andarakodon* is not a valid genus, nor is it the oldest amynodontid. Beliayeva's original tentative assignment of the Andarak amynodontid to *Lushiamynodon* was correct, but note that we agree with Wall (1989) that *Lushiamynodon* Chow & Xu, 1965 is a junior subjective synonym of *Sharamynodon* Kretzoi, 1942. Therefore, we identify the Andarak amynodontid as *Sharamynodon kirghisensis* (Beliayeva, 1971).

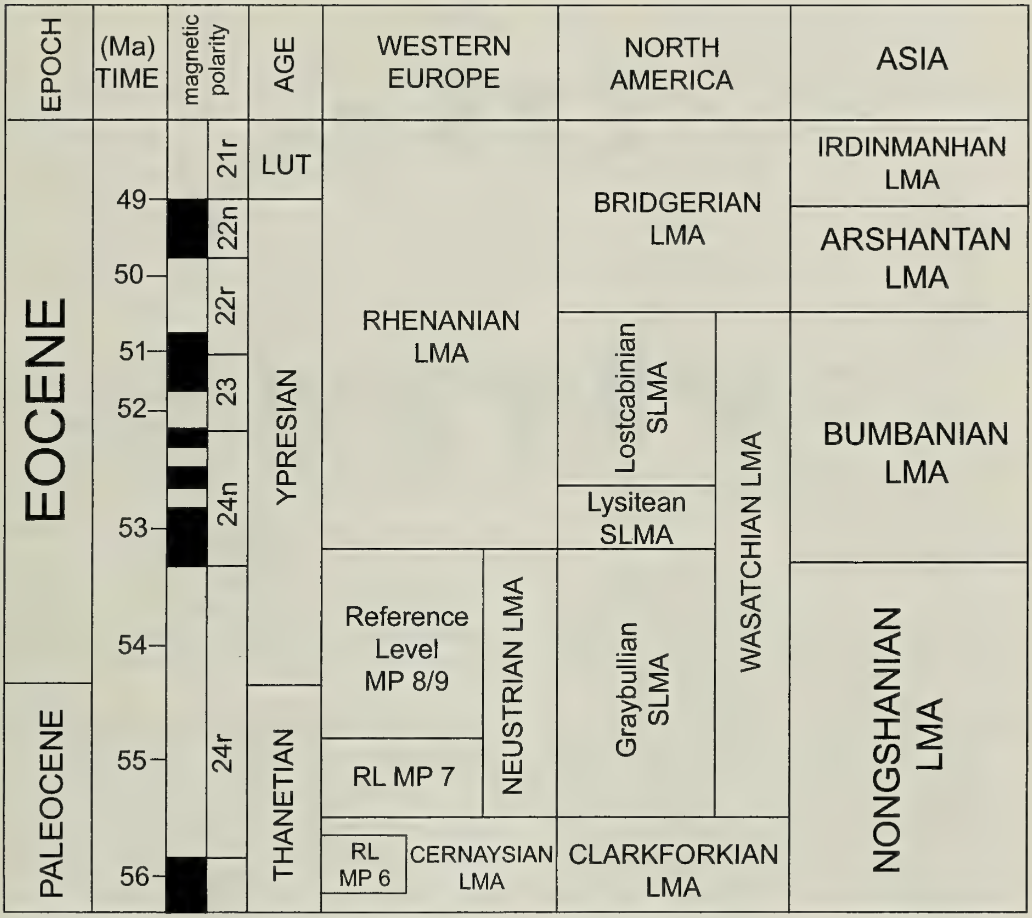

Fig. 4. Correlation of European, North American and Asian lmas across the Paleocene/Eocene boundary (modified from Lucas 1998).

Averianov & Potapova (1996, p. 1062) listed three supposedly distinctive features of *Andarakodon* in their generic diagnosis:

> Small amynodontid with relatively low-crowned cheek teeth; upper molar with nearly complete and well marked lingual cingulum.
> Infraorbital foramen placed over P4.

However, small size and relatively low-crowned cheek teeth are characteristic of several Eocene amynodontid genera, including *Sharamynodon* (Wall 1989). The upper molars of *Sharamynodon* have well developed, nearly complete lingual cingula (Fig. 3; Osborn 1936, fig. 4; Chow & Xu 1965, pl. 1, fig. 1; Xu 1966, pl. 4, fig. 1). And, the claim that *Andarakodon* has an infraorbital foramen above the P4 and also that the anterior root of the zygomatic arch is above M1 (for these reasons Averianov & Potapova 1996 assigned the genus to the metamynodontini sensu Wall 1989) is not supported by the photographs of the Kyrgyz fossils. These illustrations (Averianov & Potapova 1996, fig. 1) indicate that the preorbital fossa extends back to over M1 and that the anterior root of the zygomatic arch is over the anterior edge of M2, exactly as in *Sharamynodon* (Osborn 1936, fig. 3). The upper premolar and molar morphology of "*Andarakodon*" (Beliayeva 1971, fig. 1; Averianov & Potapova 1996, fig. 1) also is identical to that of *Sharamynodon* (Fig. 5).

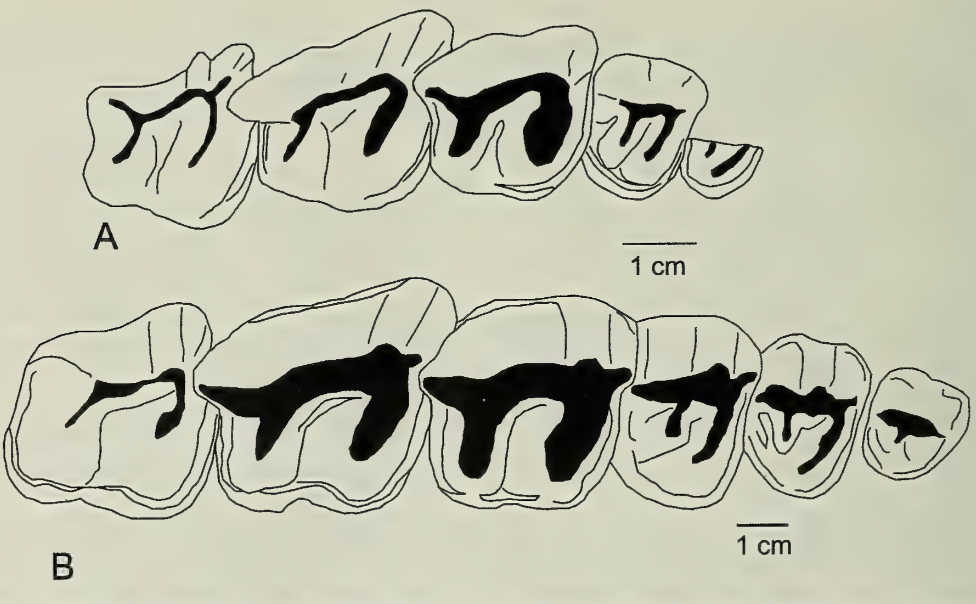

Fig. 5. Occlusal views of upper cheek teeth of "*Andarakodon*" *kirghisensis* (above, after Averianov & Potapova 1996) compared to those of *Sharamynodon mongoliensis* (below, after Osborn 1936).

Therefore, we regard *Andarakodon* as a junior subjective synonym of *Sharamynodon.* The Kyrgyz material of *Sharamynodon* is smaller than *S. mongoliensis,* but about the same size as Chinese *S. meichiapuensis.* However, pending further study, we regard the Kyrgyz species *S. kirghisensis* as valid.

Averianov & Udovichenko (1993) argued that the Andarak localities are of early Eocene (late Ypresian) age. They based this on selachian taxa from the marginal marine Andarak localities that have an upper Ypresian (nannoplankton zone NP 12) stratigraphic range in Western Europe. However, whether or not these stratigraphic ranges can be directly applied to correlation in Middle Asia is open to question.

If an Ypresian age is accepted for Andarak this suggests that at least part of Irdinmanhan time is Ypresian. This is possible, but unlikely given mammal-based correlation of the Irdinmanhan to the North American Bridgerian (Fig. 4). Nevertheless, despite any uncertainty about the marine cross-correlation of the Irdinmanhan lma, there is no evidence that Andarak is older than any other Irdinmanhan locality. This means that the Andarak amynodontid is not the oldest amynodontid. It is, within resolution, no older than any other Asian records, which indicate an Asian FAD of amynodontids at the beginning of the Irdinmanahan lma.

Acknowledgments

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
114(2):526–528. 2001.

A new species of *Ageratina* from Chiapas, Mexico (Eupatorieae: Asteraceae)

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Abstract.—Ageratina (Neogreenella) *resinifera* is described as new based on a Breedlove collection from Chiapas, Mexico, having glabrous leaves with internal resiniferous lenses.

A review of the backlog of unidentified specimens has led to the discovery of an additional species of *Ageratina* Spach from Mexico. The new species is compared with other species by reference to the Robinson key to Mesoamerican *Ageratina* (1990). It should be noted that the 1990 key has a misplaced part, the second half of couplet 7 was erroneously placed after couplet 10 instead of after couplet 16. This correction is taken into account in the following mention of the key placement of the new species. Placement in the Turner (1997) key is also stated.

Ageratina (Neogreenella) *resinifera* H. Rob., sp. nov.
Fig. 1

Type: Mexico: Chiapas: Munic. Motozintla de Mendoza: high ridge with evergreen cloud forest near Niquivil at the junction with a small side ridge to Cerro Boqueron, 2600 m, 16 Dec 1976, Breedlove 42812 (holotype CAS-DS).

Plantae fruticosae ca. 0.6 m altae; caules subglabrae. Folia glabra in areolis resinosilenticularia. Corollae albae 4.5 mm longae in nervis fauciorum lineate resiniferae.

Erect shrubs to 0.6 m tall, vegetative branching not seen; stems pale brownish, sparsely minutely puberulous, glabrescent. Leaves opposite; petioles 0.5–1.2 cm long; blades ovate, mostly 3.5–6.0 cm long, 1.8–3.5 cm wide, base rounded to obtuse, margins subentire to remotely subserrulate, apex slightly short-acuminate, surfaces glabrous, darker green adaxially, pale abaxially, veinlets and resiniferous internal vesicles or lenses prominulous; strongly triplinervate, spreading at a 25–30°-angle, from 2–4 mm above base of blade. Inflorescences terminal on leafy branches, rounded-corymbiform, with branches at a ca. 45°-angle; peduncles 6–10 mm long, densely appressed-puberulous. Heads 7–8 mm long; involucre ca. 3 mm long and wide; bracts 13–15, slightly subimbricate, oblong, 1.3–3.0 mm long, 0.9-1.3 mm wide, tips erect, short-acute to rounded, tinged with red, outer surface minutely puberulous. Florets 7–9 in head; corollas white with pink tips, ca. 4.5 mm long, glabrous, basal tube 1 mm long, throat ca. 2.5 mm long, with yellow resin in ducts along veins, lobes ca. 0.7 mm long. Achenes ca. 2.5 mm long, setulose on ribs and upper sides with small binary hairs, glabrous in middle and below; pappus without evident outer series of shorter bristles, moderately deciduous, ca. 4 mm long, at maturity totally exceeding involucre, bristles pink at base, slightly broadened at tips.

Ageratina resinifera is known only from the type. The prominent, resiniferous lenses in the areoles of the leaves are distinctive. The species would key out best in the Robinson (1990) key before couplet 17, on the basis of the resiniferous lenses in the leaf aeroles. This placement avoids the need to

Figure 1. *Ageratina resinifera* H.Rob., holotype, *Breedlove 42812* (CAS-DS).

alter couplet 17 to accomodate a supposedly non-scrambling erect shrub with 7–9 florets in the heads. The single specimen of the new species consists of separated branches without branching nodes. Thus, the angle of branching is not known. In the key to subg. *Neogreenella* by Turner (1997), the species keys to couplet 27, best fitting *A. ligustrina* (DC.) R.M.King & H.Rob., but having resinous lenses in the leaves rather than glandular dots. If the species is keyed as having a dimorphic pappus, it would end at couplet 81, with *A. saltillensis* (B.L.Rob.) R.M.King & H.Rob., a species of more xeric northern Mexico that also has glandular dots on the abaxial leaf surfaces rather than resiniferous lenses in the areoles.

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New species of *Fleischmannia* from Panama and Andean South America (Asteraceae: Eupatorieae)

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Abstract.—Fifteen species of *Fleischmannia* are named as new, *F. hammelii* from Panama, *F. killipii* and *F. narinoensis* from Colombia, *F. ceronii, F. dodsonii, F. kingii, F. microstemoides,* and *F. zakii* from Ecuador, and *F. altihuanucana, F. cajamarcensis, F. davidsmithii, F. petiolata, F. quirozii, F. sagasteguii,* and *F. vargasii* from Peru. Distinctions of other Colombian, Ecuadorian and Peruvian species are discussed.

During the course of previous identification and floristic studies, many specimens of *Fleischmannia* were put aside for later study. One part of this backlog was studied for the Flora Mesoamericana, and two new species were described (Robinson 1991). Preparation of a treatment for the Flora of Ecuador has been the occasion for a more complete review of the remaining backlog of material. The result is the presentation of the following 15 new species of the genus. This includes one species from Panama that is in the Flora Mesoamericana range, two species from Colombia, five species from Ecuador, and seven from Peru.

Fleischmannia was first described to accomodate a single Mesoamerican species that had a pappus of five well spaced, slender bristles and a well developed anther appendage (Schultz-Bip. 1850). It was named by Schultz-Bipontinus in honor of his teacher at Erlangen, Hon. Prof. Dr. Gottfried Fleischmann. The concept was expanded over the next 100 years to include a number of additional species, some with reduced anther appendages. The value of the generic separation from *Eupatorium* by the five pappus bristles was questioned at least twice, at least indirectly by Schultz-Bipontinus himself (Seemann 1852–1857) and more directly by B. L. Robinson (1926). It remained for R. M. King & H. Robinson (1966, 1970a, 1970b) to remove all previously added species of the genus except the type. Two species were transferred to *Hofmeisteria* (King & Robinson 1966) and one to *Ageratina* (King & Robinson 1970b). About the same time, 52 species from *Eupatorium* were transferred to *Fleischmannia* on the basis of newly discovered characteristics by which the genus could be very naturally defined (King & Robinson 1970a).

The characteristics of *Fleischmannia* as defined by King & Robinson (1970a) indicated a very distinct genus that lacked striking macroscopic distinctions but was sharply differentiated by a combination of microscopic features. The base of the corolla tube is ribbed when dry because of the five thickened veins; the lobes of the corolla have a prorate papillosity, where only the upper ends of the elongate cells project as papillae; and the anther collars are slender with dense transverse annulate thickenings that totally obscure the cellular structure. Geographically and in general habit, *Fleischmannia* species are often confused with members of *Ageratina* Spach, even though the two genera are not closely related. *Fleischmannia* species usually differ by the additional characteristics of subimbricate (distinctly shingled) versus eximbricate (scarcely overlapping) involucral bracts, the lack versus the presence of an enlarged basal stylar node, and the prorosity versus the non-prorate papillosity of the corolla lobes that is not restricted to the inside surface. The corollas of *Ageratina* are white or reddish whereas those of *Fleischmannia* are often lavender to purplish or bluish. The involucral bracts are more subimbricate in some species of *Ageratina* and nearly eximbricate in a few *Fleischmannia,* and the style is without a basal node in a few central Andean *Ageratina,* but the chromosome numbers of *Fleischmannia* are always based on $n = 10$ or, rarely, $n = 4$, whereas those of *Ageratina* are based on $n = 17$ or 40–42 or are apomicts.

In the present concerted study of *Fleischmannia,* many variations have been noted in the specimens, and it has sometimes been difficult to determine which features were of taxonomic value. The new Panamanian species has a reduced number of pappus bristles, a characteristic of some other Mesoamerican species, but not of those from South America. Some Mesoamerican species have peripheral achenes totally lacking a pappus, but all achenes have a pappus with many bristles in South American species. The persistence of yellow in the achene ribs does not seem so constant in the Andean species as it does in the Mesoamerican ones, but it has been used to some extent in the following species concepts. Glandular dots on the leaves seem to be present in most Andean species, but they are sometimes difficult to see; their absence in some Ecuadorian species such as *F. lloensis* (Hieron.) R. M. King & H. Rob. and *F. pastazae* (B. L. Rob.) R. M. King & H. Rob. is not totally proven. Minute, stipitate glands on stems, leaves, peduncles, or involucral bracts seem useful in four of the new species, although some stipitate glands sometimes occur on the abaxial leaf surfaces in the common *F. pratensis* (Klatt) R. M. King & H. Rob. Heads sizes and floret number in the heads seem to distinguish some species adequately in spite of some observed variability. Inflorescence density alone depends partly on peduncle length and partly on head size, but dense versus lax head disposition seems to be a useful character.

Corolla color seems to distinguish some species in spite of some cited variation. The color might prove more valuable if collectors could be relied upon to check carefully, distinguish corolla color from bract color, and be careful with immature specimens.

The widespread *Fleischmannia microstemon* (Cass.) R. M. King & H. Rob. and *F. pratensis* usually occur in the Andean areas from which the new species are described, and these widespread species maintain the characteristics as cited in the Flora of Panama (King & Robinson 1975).

Panama

Fleischmannia hammellii H. Rob., sp. nov.

Fig. 1

Type.—Panama: Pcia. Chiriquí: N of Tolé, herb on rocks along Río Curibora, flowers lavender, 17 Feb 1979, *Hammel 6263* (holotype US; isotype MO).

A *Fleischmannia capillari* in setae pappi ca. 10 similis sed in foliis anguste ellipticis et ramis inflorescentiae minute stipitato-glanduliferis differt.

Herbs with clustered stems to 4 dm tall, with few slender mostly short and ascending branches; stems brownish, densely short-hirtellous. Leaves opposite; petioles 2–3 mm long; blades membraneous, narrowly elliptical, mostly 10–20 mm long, 3–5 mm wide, base cuneate, distal margins bluntly 2–4 serrulate, apex bluntly acute, adaxial surface green, pilosulous, abaxially paler, densely pilosulous to hirtellous on main veins, with glandular dots; triplinervation from base of blade. Inflorescences diffuse, branches opposite proximally, alternate distally, ascending, with foliose bracts smaller distally; branches and peduncles densely covered with minute stipitate glands; peduncles slender, 5–12 mm long. Heads 3.5 mm high and wide; involucral bracts ca. 23, lanceolate, inner more oblong, weakly subimbricate in ca. 3 series, 1.5–3.0 mm long, 0.3–0.4 mm wide, apices narrowly acuminate, abaxially mostly glabrous, outer bracts minutely pilosulous. Florets ca. 35; corollas lavender, ca. 2 mm long, basal tube ca. 0.3 mm long, throat ca. 1.4 mm long, sometimes with colored resin in ducts, lobes ca. 0.3 mm long, with only few minute short hairs outside; styles narrowly linear. Achenes ca. 1.5 mm long, with persistently pale ribs, sides and ribs setulose with scattered short binary hairs; pappus of 10–12 non-contiguous, slender bristles ca. 1.8 mm long.

Fleischmannia hammelii is known only from the type. The species is like *F. capillipes* (Benth. ex Örsted) R. M. King & H. Rob. on the basis of the weakly subimbricate involucre and the 10-12 widely spaced setae of the pappus. The new species differs by the small, narrow leaves and the numerous, minute, stipitate glands in the inflorescence. The species is named for the collector, Barry Hammel.

Colombia

Of the Colombian species, *Fleischmannia granatensis* R. M. King & H. Rob. with lavender florets, has now been found in the north and northwest at lower elevations and at higher elevations in Cundinamarca. The species seems close to the widespread *F. pratensis,* but it has more pointed leaves and involucral bracts and has denser stem pubescence. The heads seem particularly densely clustered in glomerules. Other species in Colombia with black achenes include the more robust *F. mayorii* (B. L. Rob.) R. M. King & H. Rob. with the triplinervation usually above the base of the leaf blade and florets lavender, and *F. pennellii* (B. L. Rob.) R. M. King & H. Rob., with broadly rounded, non-scarious apices on the involucral bracts and florets that are white. Other Colombian species with dense inflorescences and pale-ribbed achenes and white florets include *F. klattiana* and *F. magdalenensis,* the latter nearly glabrous with rather succulent leaves. More diminutive species of western Colombia include *F. misera* (B. L. Rob.) R. M. King & H. Rob., *F. cuatrecasasii* R. M. King & H. Rob., *F. sideritides* (Benth. in Örsted) R. M. King & H. Rob. and *F. lellingeri* R. M. King & H. Rob., the first three with laxly deposed heads and the last with small clusters of heads terminal on elongate branches.

The following two species are described as new from Colombia.

Fleischmannia killipii H. Rob., sp. nov.
Fig. 2

Type.—Colombia: Depto. Santander: between El Roble and Tona, 1500-1900 m, 17 Feb 1927, *Killip & A. C. Smith 19414* (holotype US, isotypes GH, NY).

A *F. steyermarkii* in foliis celtidiformis simila sed in caulibus puberulis et laminis foliorum herbaceis et capitulis remotioribus et bracteis involucri basilaribus brevioribus differt.

Scrambling subshrubs to 1.3 m tall, with branches spreading at an 80–90° angle; stems greenish brown, minutely puberulous to glabrescent; internodes often 9–13 cm long. Leaves opposite; petioles 1.2–2.7 cm long, broadened and fleshy at base; blades herbaceous, narrowly ovate, mostly 4–8 cm long, 1.0–2.8 cm wide, base rounded, with small acumination at petiole, margins crenulate to crenate-serrate, with 9–12 teeth on each side, apex narrowly acuminate, adaxial surface shortly pilose, abaxial surface pilosulous on veins, with glandular dots; triplinervation from basal acumination of blade, secondary and largest tertiary veins pale, strongly ascending. Inflorescences thyrsoid with laxly corymbiform branches; peduncles 3–15 mm long, minutely puberulous. Heads ca. 7 mm long, 3 mm wide when closed; involucral bracts ca. 20 in ca. 4 series, 0.8–5.0 mm long, outermost minutely ovate, puberulous outside, inner bracts oblong to narrowly oblong, apices rounded, sides scarious to a third of width,

Fleischmannia hammelii H Rob
Holotipe.
det. H Robinson 2000

PANAMA
Province of Chiriquí
Family: COMPOSITAE
Fleischmannia capillipes (Benth. in Örsted) K. & R.
N of Tolé.
Herb on rocks along Rio Cuvibora.
Flowers lavender.
Barry Hammel 6263 17 Feb. 1979

Fig. 1. *Fleischmannia hammelii* H. Rob., holotype, *Hammel 6263* (US).

glabrous abaxially. Florets ca. 20; corollas white, ca. 2.5 mm long, basal tube ca. 0.5 mm long, throat ca. 1.5 mm long, without colored resin in ducts, lobes ca. 0.4 mm long, with few or no hairs outside; styles linear. Achenes ca. 1.8 mm long, black with, rarely, somewhat pale ribs, setulose with minute binary hairs on ribs and distally on sides; pappus ca. 2.5 mm long, bristles scarcely broadened and almost contiguous at base.

Fleischmannia killipii is known only from the type from a wooded area at 1500–1900 m in Santander. The narrow, acuminate leaves with strongly ascending secondary and tertiary veins are reminiscent of *F. steyermarkii* R. M. King & H. Rob. of the Cordillera del Avila of Venezuela. The Venezuelan species differs most obviously by its glabrous stems, the membranaceous leaf blades with glabrous adaxial surfaces, and more isolated rather dense clusters of few heads.

Fleischmannia narinoensis H. Rob., sp. nov.

Fig. 3

Type.—Colombia: Depto. Nariño: Reserva Natural La Planada, 7 km above Chucunés (on road between Tuquerres and Ricaurte); along trail to Pialapí, past entrance to La Planada Field Station, 1°06′N, 77°53′W, 150–200 m, 10 Mar 1990, *Croat 71273* (holotype PSO; isotypes MO, US).

E speciebus majoribus plantis in sicco atro-brunnescentes in bracteis involucri obtusis et in corollis albis distincta.

Herbs or vines, becoming dark brownish when dry, to 2.5 m high, with branching often at a 90° angle; stems pilose to sparsely hirsutulous; internodes of primary stems to 13 cm long. Leaves opposite; petioles slender, 0.7–2.5 cm long; blades membranaceous, ovate, mostly 2.5–6.5 cm long, 0.9–4.0 cm wide, base obtuse to truncate, margins serrate with up to 13 teeth on each side, apex sharply acute to scarcely acuminate, adaxial surface pilose, abaxial surface pilose on veins, darkly minutely gland-dotted; triplinervation ascending from base of blade. Inflorescences of lax, widely spreading cymes, divaricately branching; peduncles 2–8 mm long, densely puberulous to hirtellous. Heads mostly 5–7 mm long, 4–5 mm wide; involucral bracts ca. 25, in ca. 4 series, outer lanceolate, 1.5–2.5 mm long, pilosulous abaxially, inner oblong, to 5.5 mm long, rounded to mucronate at tip, margins usually broadly lustrous, mostly glabrous outside. Florets ca. 25; corollas white, ca. 3.4 mm long, basal tube ca. 0.8 mm long, throat ca. 1.8 mm long, with dark resin in ducts, lobes ca. 0.8 mm long, with few, short, scarcely noticeable hairs; style branches linear. Achenes ca. 1.6 mm long, with few binary hairs on the often somewhat persistently pale angles; pappus of many bristles, to 3 mm long, white or sordid.

Paratypes.—Colombia: Nariño: Reserva Natural La Planada, a 7 km de Chucunés, 1°10′N, 77°58′W, 1800 m, 2 Nov 1987, *Benavides 8818* (MO, PSO, US). Trayecto San Isidro–La Planada, 1°10′N, 77°58′W, 1500-1800 m, 13 Feb 1988. *Benavides 9219* (MO, PSO, US). Quebrada: El Mar - La Calladita, 1°10′, 77°58′W, 1500-1800 m, 29 Apr 1988, *Benavides 9553* (MO). Trail from La Planada to Pielapi, wet lower montane cloud forest, 1°04′N, 78°02′W, 1600–1800 m, 22 Jul 1988, *Gentry, Benavides et al. 63587* (MO, PSO, US). La Planada, 7 km above Chucunés on road between Tuquerres and Ricaurate, along trail to summit of hill behind Centro de Científicos, 1°01′N, 78°01′W, 1780 m, 28 Jul 1988, *Croat 69659* (MO, PSO, US). Reserva Natural La Planada, 7 km above Chucunés on road between Tuquerres and Ricaurte, primary forest and margins of old pasture along Sendero La Vieja, 1°06′N, 77°54′W, 1780-1850 m, vine, to 2.5 m in tree, 7 Mar 1990, *Croat 71140* (MO, PSO, US). 7 km above Chucunés (on road between Tuguerres and Ricaurte); along trail above La Posada to El Mojenes, disturbed virgin forest and pasture margin along forest, 1°06′N, 77°53′W, 1800-1900,

Fig. 2. *Fleischmannia killipii* H. Rob., isotype, *Killip & Smith 19414* (US).

12 Mar 1990, *Croat 71336* (MO, PSO, US). La Planada Biological Reserve, ca. 7 km S of Chucunez, along trail to Pialapi, 1°10′N, 77°53′W, 1800-1900 m, disturbed premontane forest and open potreros, along road edge, scandent herb, phyllaries green, florets white, 6 Aug 1990, *Luteyn & Steela Sylvia S. 13899* (NY, US).

Fleischmannia narinoensis is rather distinctive in the laxly divaricate branching of the inflorescence with mostly non-contiguous heads and the blunt involucral bracts with often broad and lustrous margins. While it may not be absolutely characteristic, all the specimens examined are dark brown when dry, differing from the usually greenish color of dried material of other species.

Ecuador

Preparation for the Flora of Ecuador treatment has led to discovery of the following five previously undescribed species. The total number of species presently recognized in the country is 13. This takes into account the reduction of *Fleischmannia aequinoctalis* (B. L. Rob.) R. M. King & H. Rob. to synonymy under *F. obscurifolia* (Hieron.) R. M. King & H. Rob. and the resurrection of *F. huigrensis* (B. L. Rob.) R. M. King & H. Rob. from the synonymy of the *F. obscurifolia.*

Fleischmannia ceronii H. Rob., sp. nov.

Fig. 4

Type.—Ecuador: Pcia. Pichincha: Reserva Geobotánica del Pululahua, Sector Moras Pungo - Papa Tena, Segundo Chipantasi y Franisco Santillán, 00°05′N, 78°30′W, 2900-3100 m, 17 Aug 1988, *Cerón & Cerón 4484* (holotype US, isotype MO).

Ad *F. granatensem* et *F. pratensem* in habitus similis sed in foliis supra velutinis et subtus non vel obscure glandulo-punctatis differt.

Erect to procumbent subshrubs or shrubs to 1 m high; branching mostly at a 35-50° angle; stems brown, hirsute to hirsutulous with reddish or brownish hairs; internodes mostly 2-12 cm long. Leaves opposite; petioles 0.5–2.0 cm long; blades herbaceous, broadly ovate, mostly 1.5–5.0 cm long, 1.2–2.8 cm wide, base rounded to subtruncate, slightly acuminate at petiole, margins crenulate to crenate-serrate, with 9–13 teeth on each side, apex acute to scarcely acuminate, adaxial surface velutinous with whitish to reddish hairs, abaxial surface densely pale pilose to subtomentose on and between veins, without evident glandular dots; triplinervation from basal acumination of blade. Inflorescences terminal on primary stems and long lateral branches, forming isolated small dense corymbiform clusters; peduncles 2–4 mm long, densely puberulous to tomentellous. Heads 5–6 mm long; involucral bracts ca. 20 in ca. 4 series, 1–4 mm long, outer bracts puberulous abaxially, ovate, acute, inner bracts sparsely puberulous, narrowly oblong to linear, short-acute. Florets ca. 19; corollas greenish-white, 2.5–4.0 mm long, basal tube ca. 0.5 mm long, throat 1.5–1.8 mm long, with reddish ducts, lobes 0.4–0.5 mm long, with many short hairs abaxially; style branches linear. Achenes 1.5–1.8 mm long, black with ribs rarely persistently yellow, glabrous to sparsely scabrid with spiculiform binary hairs; pappus 2.3–2.5 mm long, bristles slightly broader and contiguous at base.

Paratype.—Ecuador: Pcia. Pichincha: Cantón Quito: Parroquia Calacalí, Reserva Geobotánica Pululahua, Línea de cumbre La Ventanilla - Sincholagua, 00°05′N, 78°30′W, 3100 m, 12 Nov 1989, *Cerón & Montesdeoca 7687* (MO, US).

Fleischmannia ceronii is known only from two collections, both from the Reserva Geobotánica del Pululahua in Pichincha, in humid premontane forest at 2900–3100 m elevation. The species seems close to the widely distributed *F. pratensis,* but differs by the densely pubescent leaves and the whitish corollas.

Fleischmannia dodsonii H. Rob., sp. nov.

Fig. 5

Type.—Ecuador: Pcia. Los Rios: Cantón Vinces: Between Mocacho and Palenque on

COLOMBIA

ASTERACEAE

[illegible]

Isotype

NARINO
Reserva Natural La Planada: 7 km above Chucunés (on road between Tuquerres and Ricaurte); along trail to Pialapí, past entrance to La Planada Field Station.
1°06'N 77°53'W 150-200 m

Vine to 2 m long; flowers white.

10 March 1990

Thomas B. Croat 71273
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 3. *Fleischmannia narinoensis* H. Rob., holotype, *Croat 71272* (US).

Fig. 4. *Fleischmannia ceronii* H. Rob., holotype, *Cerón & Cerón 4484* (US).

Estero Peñafiel, 70 m, 15 Aug 1978, *Dodson, Dodson, Embree & Perry 7058* (holotype US, isotype SEL).

A speciebus pluribus in caulibus et foliis et pedunculis et bracteis involucri minute stipitate glanduliferis distincta.

Scandent herbs ca. 0.5 m tall, branches at a ca. 80° angle; stems brownish, hirtellous and with minute stipitate glands. Leaves opposite proximally, subopposite or alternate distally; petioles 0.4–1.1 cm long; blades ovate, at least 1.2–1.5 cm long, 1.0 cm wide, base obtuse, margins crenate-serrate, 2–4 teeth on each side, apex acute to scarcely acuminate, surfaces hirtellous with minute, stipitate glands, abaxially with brownish glandular dots; triplinervation from base of blade. Inflorescences laxly corymbiform with numerous small clusters of few heads; peduncles mostly 4–6 mm long, densely covered with minute, stipitate glands. Heads 5–6 mm long; involucral bracts ca. 18 in ca. 3 series, 1–4 mm long, mostly densely covered with minute, stipitate glands abaxially, the outer bracts ovate-lanceolate to subulate, the inner ones narrowly oblong, obtuse and apiculate, narrowly scarious. Florets ca. 30; corollas pink, ca. 2.5 mm long, basal tube ca. 0.5 mm long, throat ca. 1.8 mm long, with dark resin in ducts, lobes ca. 0.4 mm long, with short hairs outside; style branches linear. Achenes ca. 1.2 mm long, mostly black, ribs sometimes somewhat persistently yellowish, ribs and upper sides minutely scabrid with spiculiform binary hairs; pappus ca. 2.2 mm long, bristles not broader and not or scarcely contiguous at base.

Fleischmannia dodsonii is known only from the type, which was collected in lowland western Ecuador at 70 m in a cut-over area along a path to a forest. The many, minute, stipitate glands are particularly distinctive. The specimen is in poor condition, and the rather few, small leaves may be somewhat unrepresentative. The Peruvian species named below, *F. quirozii,* also has many, minute, stipitate glands, but it differs in the usually alternate branching, the larger heads with 50 or more florets, and the persistently yellow ribs on the achenes. The species is named for the collector, Calaway H. Dodson, founder of the Río Palenque Science Center, Los Rios, Ecuador, and formerly head of the Selby Botanical Garden.

Fleischmannia kingii H. Rob., sp. nov.

Fig. 6

Type.—Ecuador: Pcia. Loja: 12–20 km S of San Lucas on road to Loja, 6200 ft., 27 Jan 1979, *King & Almeda 7846* (holotype US, isotypes CAS, MO).

A *F. ferreyrii* in ramis ascendentibus et attenuatis similis sed in inflorescentiis corymbiformibus densioribus et in costis acheniarum persistentiter flavis et in setis pappi base angustioribus et non contiguis distincta.

Scrambling subshrub to ca. 1 m high, with long, spreading branches at a 45–60° angle; stems brownish, puberulous to pilosulous; internodes often 6–9 cm long. Leaves mostly opposite, alternate and smaller distally; petioles mostly 0.3–1.0 cm long; blades herbaceous, ovate, mostly 1.5–2.5 cm long, 0.7–1.5 cm wide, base obtuse, margins crenate, 4–8 teeth on each side, apex acute, adaxial surface pilose, abaxially pilose or puberulous on veins, glandular dots obscure; triplinervation from base of blade. Inflorescences terminal on elongate branches, ending in rather densely corymbiform cymes; peduncles 2.5–7.0 mm long, densely puberulous. Heads 5.0–5.5 mm long; involucral bracts 18–20 in 3–4 series, 1–4 mm long, outermost bracts subulate, puberulous abaxially, inner bracts oblong to oblong-linear, obtuse and apiculate, glabrous abaxially. Florets 19–24; corollas white, 2.5–2.8 mm long, basal tube ca. 0.4 mm long, throat 1.8–2.9 mm long, ducts sometimes reddish, lobes ca. 0.4 mm long, with few or no hairs; style branches broadened distally. Achenes 1.8 mm long, ribs persistently yellow, ribs and some upper sides setulose with short binary hairs; pappus ca. 2.5 mm long, bristles not narrowed distally, narrow and not or scarcely contiguous at base.

Fleischmannia kingii is known only from the type, collected on a roadside at 6200 ft. in southern Ecuador. Its closest relationship

Fig. 5. *Fleischmannia dodsonii* H. Rob., holotype, *Dodson, Dodson, Embree & Perry 7058* (US).

is probably to Peruvian species such as *F. ferreyrii* R. M. King & H. Rob.; but the latter has distinctly cymiform inflorescences, black achenes, and broadened contiguous bases of the pappus bristles. The species is named for the first collector and noted student of the Eupatorieae, Robert Merrill King.

Fig. 6. *Fleischmannia kingii* H. Rob., holotype, *King & Ameda 7846* (US).

Fleischmannia microstemoides H. Rob., sp. nov.

Fig. 7

Type.—Ecuador: Pcia. Pastaza: Road Puyo - Macas, ca. 15 km southeast of Puyo, 28 Nov. 1974, *Lugo S. 4688* (holotype US, isotype GB).

A *F. microstemon* simila sed in laminis foliorum herbaceis acutis vel obtusis non acuminatis in inflorescentiis cymosis robustioribus in ramis lateralibus brevioribus paucioribus vel nullis in bracteis involucri acutioribus et in corollis 2.5–3.0 mm longis distincta.

Short-lived herbs ca. 0.5 m high, with ascending branches at a ca. 30° angle; stems reddish-tinged, minutely puberulous; main internodes ca. 8 cm long. Leaves opposite proximally, alternate distally; petioles 0.3–1.3 cm long; blades herbaceous, rhomboid-ovate, mostly 2–5 cm long, 1.2–2.5 cm wide, base acute to obtuse, not acuminate, margins serrate with 7–13 teeth on each side, apex acute, adaxial surface pilosulous, abaxially sparsely pilosulous on veins, with many dark glandular dots; triplinervation from distal part of petiole, not marginal at base of blade. Inflorescences cymiform, with few shorter, lateral branches; peduncles 2–9 mm long, densely puberulous. Heads 5.5–6.0 mm high; involucral bracts 18–20 in 3–4 series, ovate-lanceolate to linear-lanceolate, 1–5 mm long, apices narrowly acute, margins narrowly scarious, pilosulous abaxially. Florets ca. 19; corollas violet, 2.5–3.0 mm long, basal tube ca. 0.8 mm long, throat ca. 1.5 mm long, with reddish resin in ducts, lobes ca. 0.3–0.4 mm long, with short hairs externally; style branches narrowly linear. Achenes 1.3–1.5 mm long, ribs rather persistently yellow, scabrid with spiculiform binary hairs; pappus ca. 2.5 mm long, bristles scarcely broader and almost contiguous at base.

Fleischmannia microstemoides is known only from the type, collected at low elevation east of the Andes in Pastaza. The species has a weak habit that superficially resembles *F. microstemon.* The leaves are not so thin and not acuminate at the base, the inflorescence is more strongly cymiform without the numerous lower lateral branches, the involucral bracts are more acute, and the corollas are larger.

Fleischmannia zakii H. Rob., sp. nov.
Fig. 8

Type.—Ecuador: Pcia. Pichincha: Carretera Quito - Lloa - Mondo, Hacienda "El Pedregal," 00°03′S, 78°40′W, 1650-1850 m, 10 Jul 1987, *Zak & Jaramillo 2158* (holotype US, isotype MO).

Ad *F. huigrensem* in bracteis involucri basilaribus elongatis sed in habitis volubilis et in foliis et bracteis involucri anguste acuminatis differt.

Scandent plants with branches spreading at a 70–80° angle at base, curving upward; stems greenish, minutely puberulous to glabrescent; internodes mostly 8–20 cm long. Leaves opposite; petioles 0.3–1.1 cm long; blades lanceolate, mostly 3.5–6.5 cm long, 0.9–1.5 cm wide, base shortly to narrowly acute, margins remotely serrulate, with 3–8 teeth on each side, apex narrowly acuminate, adaxial surface sparsely pilosulous, puberulous on veins, abaxially puberulous on veins, with glandular dots obscure or lacking; triplinervation from a little above base of blade. Inflorescences terminal, laxly subumbellate; peduncles mostly 1–3 cm long, finely puberulous. Heads 8–9 mm long; involucral bracts 18–20 in ca. 3 series, green, oblong-lanceolate, 3–7 mm long, very weakly bicostate, apices narrowly acuminate, margins very narrowly scarious, outer bracts puberulous abaxially, inner bracts glabrous. Florets 25–30; corollas lilac, 4.0–4.5 mm long, basal tube ca. 1 mm long, throat ca. 2.5 mm long, with colored resin in ducts, lobes ca. 0.7 mm long, many short hairs outside; style branches long-linear. Achenes ca. 1.5 mm long, with persistently yellow ribs, glabrous; pappus white, ca. 3 mm long, bristle bases contiguous, not broadened.

Fleischmannia zakii is known from only the type collection, obtained from 1650–1850 m elevation at the margins of fields in moist remnants of primary vegetation. The species is an individually distinctive, scandent plant with attentuate apices on the leaves and involucral bracts. Closest relation is to the more widely distributed Ecuadorian endemic, *F. huigrensis* (B. L. Rob.) R. M. King & H. Rob., which also lacks shorter outer bracts in the involucre. The

Fig. 7. *Fleischmannia microstemoides* H. Rob., holotype, *Holguer Lugo S. 4688* (US).

ECUADOR

ASTERACEE
Eupatorium
Fleischmannia zakii H.Rob.
Holotype
Prov. PICHINCHA: Carretera Quito-Lloa-Mindo, Hacienda "El Pedregal".
Area higrófila-lluviosa, suelo huraífero-rocoso. Vegetación primaria intervenida y borde de pastizal. Especies representativas de Piper, Cecropia, Melastomataceae, Cedrela, Alnus, etc.
00°03'S 78°40'W 1650-1850 m

Hierba terrestre-trepadora con capítulos lilas.

10 julio 1987
Vlastimil Zak & Jaime Jaramillo 2158
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 8. *Fleischmannia zakii* H. Rob., holotype, *Zak & Jaramillo 2158* (US).

species is named for the collector, Vlastimil Zak.

Peru

The species of Peru have proven difficult, partly because of inadequate collecting, partly because of the apparent disjunctions in some distributions, and partly because of obvious variations that occur within some species that are difficult to correlate. Still other undescribed species are to be expected as collecting continues.

One helpful fact has been the ease of resolution of the best known Peruvian member of the genus, *Fleischmannia marginata* (Poepp.) R. M. King & H. Rob. The species is distinct in its rather thickened leaf blades with smooth, glabrous adaxial surfaces as described by Poeppig (1845). The name has been used for material of many other species in Peru that are rejected from the concept at present. Many of the excluded specimens are the basis of new species described below. All material placed under the name *F. marginata* in the present study proves to be from one Departamento in Peru, Junín.

Other previously named species include two distinguished by their dense, reddish stem pubescence, *F. cookii* (B. L. Rob.) R. M. King & H. Rob. and *F. rhodotephra* (B. L. Rob.) R. M. King & H. Rob., the latter with cordate leaf bases. One, *F. mercedensis* (B. L. Rob.) R. M. King & H. Rob., is scandent; it is mentioned under the new species *F. davidsmithii*. *Fleischmannia ferreyrae* R. M. King & H. Rob. is a small subshrub with reduced distal leaves; it is compared under the Ecuadorian new species, *F. kingii*. *Fleischmannia lithophila* (B. L. Rob.) R. M. King & H. Rob. from Huánuco near Ancash is a coarse, mostly erect subshrub with large heads 9–10 mm long.

Of the previously named Peruvian species, *Fleischmannia fragilis* (B. L. Rob.) R. M. King & H. Rob., from Huánuco, has been the most difficult to define. It has been resolved in this study as a slender, decumbent to scrambling plant somewhat similar to the new species *F. altihuanucana*, but without the red stem hairs or minute stipitate glands on the peduncles and outer involucral bracts. A recent collection fitting this concept is *C. Ochoa 1562* from Cajamarca. Other specimens placed under the name prior to this study have not been reexamined and are doubtfully this species.

The seven new species from Peru encountered in this study are as follows:

Fleischmannia altihuanucana H. Rob., sp. nov.

Fig. 9

Type.—Peru: Depto. Huánuco: Pcia. Huánuco, 32 km from Huánuco on the Huánuco - La Union road, 9°53′S, 76°26′W, 2940–3100 m, 25 Jul 1982, *D. Smith Huapalla & Huapalla 2169* (holotype US, isotype MO).

Ad *F. rhodotephrem* et *F. cookii* in pilis caulinis rufescentibus simila sed in laminis foliorum non cordatis aut inflorescentibus laxioribus distincta.

Plants herbaceous to suffruticose, to 1.2 m high, weakly erect to prostrate at base, branches at a 60–70° angle; stems hirsutulous with distorted, reddish hairs. Leaves opposite; petioles 0.5–2.3 cm long; blades ovate, mostly 2.5–5.0 cm long, 1.2–3.0 cm wide, base broadly obtuse to subtruncate, margins crenate-serrate with usually 6–10 teeth on each side, apex acute to slightly acuminate, adaxial surface pilosulous with few glandular dots, abaxially pilosulous mostly on veins and veinlets, with many glandular dots; triplinervation with ascending veins from slight acumination at base of blade. Inflorescences loosely thyrsoid, with short, sparse lateral branches bearing few heads in small cymes; peduncles 2–9 mm long, puberulous and with some minute stipitate glands. Heads 7–9 mm long; involucral bracts ca. 18 in 3–4 series, outer bracts lanceolate, 2.5–3.5 mm long, inner oblong-linear to linear, 4.0–6.5 mm long, acute, outer bracts puberulous and with minute stipitate glands abaxially. Florets 15–19; corollas pink, 4.0–4.5 mm long, basal tube ca. 1 mm long, throat ca. 3 mm long, with colored resin in ducts, lobes ca. 0.5 mm long, many short hairs externally, style narrowly linear to filiform. Achenes ca. 2.2 mm long, ribs rather persistently yellow, few or no short binary hairs on ribs; pappus 4.5–5.0 mm long, bristles subcontiguous at base.

Common name: "Macha Macha."

Paratype.—Peru: Depto. Huánuco: Mito, 9000 ft., 8–22 Jul 1922, *Macbride & Featherstone 1508* (F, US).

Fleischmannia altihuanucana is known only from the two collections from west of the city of Huánuco at 2900–3100 m elev. Habitats are described as a dense thicket floor and a tall shrub field in valley bottoms. One habit description cites stems 2–4(–6) ft. long, weakly erect or often prostrate at base or even throughout trailing toward sun.

The new species may be closest to *Fleischmannia fragilis,* also from Mito, but that was described with stems at first glance appearing glabrous but being obscurely and minutely puberulous distally. The dense, reddish pubescence of the new species is more like *F. cookii* and *F. rhodotephrum,* both of which have denser inflorescences, and the latter of which has cordate leaf bases. The present species is further distinguished by the glandular dots of the leaves being unusually dense abaxially with a few occurring on the adaxial surface.

The species is named for its occurrence at high elevations in the Department of Huánuco.

Fleischmannia cajamarcensis H. Rob., sp. nov.

Fig. 10

Type.—Peru: Depto. Cajamarca: Pcia. San Miguel: Ushcundul, Niepos, borde de camino, suelos arcillosos y humedos, 2400 m, 29 Jun 1985, *Quiroz 1218* (holotype US, isotype HUT).

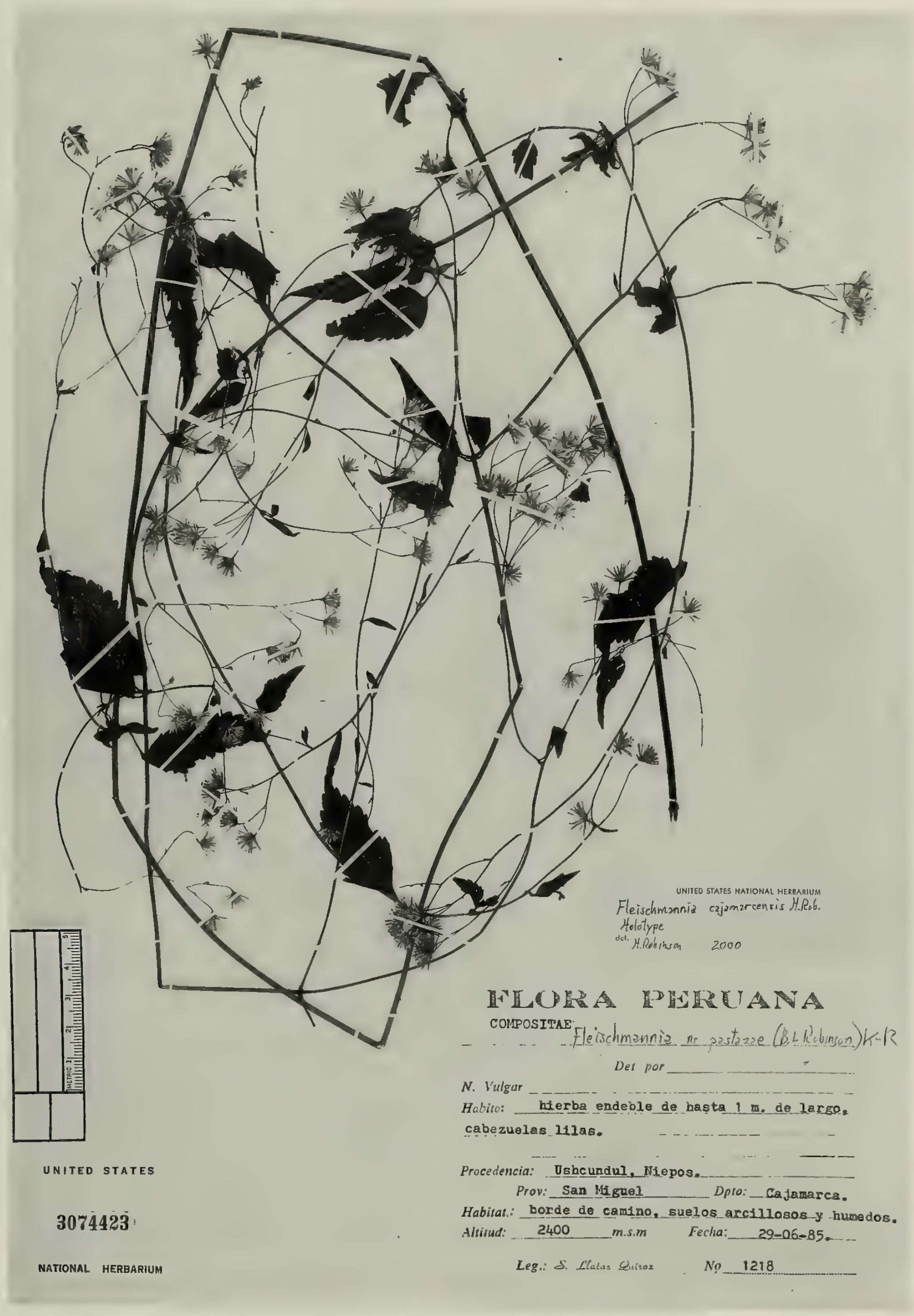
Ad *F. harlingii* in inflorescentiis laxe ascendidentiter ramosis simila sed in laminis foliorum membranaceis et base acutis et in capitulis et floribus minoribus et corollis lavandulis differt.

Plants weak subshrubs, to 1 m tall, branches slender, at a 45–60° angle; stems dark brown, glabrous, internodes often 10–18 cm long. Leaves opposite; petioles 0.5–1.5 cm long; blades membranaceous, narrowly ovate, mostly 2.5–5.5 cm long, 0.5–2.0 cm wide, base acute to obtuse, margins crenate-serrate, with 6–12 teeth on each side, apex narrowly acute to acuminate, adaxial surface pilose, abaxially pilose on veins, without evident glandular dots; triplinervation ascending from base of blade. Inflorescences laxly branched with ascending branches; peduncles mostly 0.7–2.5 mm long, glabrous or glabrescent. Heads ca. 6 mm long; involucral bracts 20–22 in 3–4 series, outer subulate, 1.5–2.5 mm long, often some loosely inserted near base of involucre, inner bracts narrowly oblong to linear, 3.5–6.0 mm long, apices apiculate to slightly erose, often lavender, glabrous abaxially. Florets ca. 19; corollas lavender, 2.8 mm long, basal tube ca. 0.5 mm long, throat ca. 1.7 mm long, no colored resin in ducts, lobes ca. 0.3 mm long, with short hairs externally; style branches linear with broader tips. Achenes ca. 2.2 mm long, ribs persistently yellow, setulose with fine binary hairs on ribs and upper sides; pappus ca. 3 mm long, bristles not broader below, subcontiguous.

Paratype.—Peru: Depto. Cajamarca: Pcia. Contumazá: La Pampa abajo de Guzmango, quebrada, 2500 m, 24 Jul 1977, *Sagástequi & Mostacero 9060* (HUT, US).

Fleischmannia cajamarcensis is known from two collections at 2400–2500 m in southwestern Cajamarca. Habitats are given as quebrada and suelas arcillosos y humedos, and habit is given as sufrútice and hierba endeble de hasta 1 m de largo. The lax inflorescence with ascending branches and the membraneous narrow leaves without evident glandular dots seem characteristic.

Fig. 9. *Fleischmannia altihuanucana* H. Rob., holotype, *Smith, Huapalla & Huapalla 2169* (US).



UNITED STATES NATIONAL HERBARIUM
Fleischmannia cajamarcensis H.Rob.
Holotype
del. H.Robinson 2000

FLORA PERUANA

COMPOSITAE Fleischmannia nr pastazae (B.L.Robinson) K-R

Det por

N. Vulgar

Habito: hierba endeble de hasta 1 m. de largo. cabezuelas lilas.

Procedencia: Ushcundul, Niepos.

Prov: San Miguel Dpto: Cajamarca.

Habitat.: borde de camino, suelos arcillosos y humedos.

Altitud: 2400 m.s.m Fecha: 29-06-85.

Leg.: S. Llatas Quiroz Nº 1218

Fig. 10. *Fleischmannia cajamarcensis* H. Rob., holotype, *Quirez 1218* (US).

Fleischmannia davidsmithii H. Rob., sp. nov.
Fig. 11

Type.—Peru: Depto. San Martín: Pcia. Rioja: Pedro Ruíz - Moyobamba road, km 390–394, Venceremos, 5°50′S, 77°45′W, 2040–1910 m, 1988?, *D. N. Smith 4533* (holotype US, isotype MO).

Ad *F. pratensem* in inflorescentiis corymbiformis densis simila sed in laminis foliorum supra base triplinervatis et in acheniis persistentiter flavo-costatis differt.

Plants subshrubs to 1.7 m tall, branching mostly at a 80–90° angle; stems puberulous, glabrescent, internodes to 14 cm long. Leaves opposite; petioles 0.3–1.5 cm long; blades narrowly ovate to lanceolate, mostly 3.0–5.5 cm long, 1.2–2.3 cm wide, base short-acute, margins with 5-12 coarse serrations, apex narrowly acuminate, adaxial surface pilosulous, abaxially minutely puberulous on veins, with obscure glandular dots; triplinervation from above base of blade. Inflorescences broadly corymbiform, 5–9 cm long and wide, with widely spreading branchlets bearing smaller, dense clusters of heads, branches often alternate or subalternate; peduncles 0.3–3.5 mm long, puberulous. Heads ca. 5 mm long; involucral bracts ca. 20 in ca. 4 series, outer ovate to oblong-ovate, 1.0–2.5 mm long, usually puberulous, inner bracts oblong, 4.0–4.5 mm long, obtuse, with few or no hairs abaxially. Florets 12–19; corollas white to pale violet, 2.5–3.0 mm long, basal tube ca. 0.9 mm long, throat ca. 1.5 mm long, colored resin not seen, lobes ca. 0.3 mm long, with many hairs; style branches linear. Achenes ca. 1.2 mm long, ribs persistently yellow, with few minute binary hairs; pappus ca. 2.5 mm long, bristles thin to base, nearly contiguous.

Paratypes.—Peru: Depto. Junín: Pichis trail, Porvenir, 1500–1900 m, 3, 4 Jul 1929, *Killip & A. C. Smith 25933* (US). Puno: Prov. Carabaya, Ollachea to San Gabon, "Ceja de la montaña", 1000–2000 m, 17-24 Jul 1978, *Dillon, Aronson, Herra & Berry 1118* (F, MO, USM, US).

Fleischmannia davidsmithii is here credited with a range from San Martin in the north to Puno in the south at elevations of 1000–2040 m. As with many species along the eastern side of the Andes, it seems to have an extensive range from north to south. The habitat data on the type specimen cites a disturbed edge of high montane rainforest, roadsides, and young second growth, "purma." Although not described as such, the habit with long internodes and widely spreading vegetative branches would suggest a scrambling or even scandent plant. The narrow leaves, with sharp teeth and triplinervation above the base of the blade, and the rounded inflorescences with crowded, small heads are distinctive. The species can be easily distinguished from the widespread *F. pratensis* by the triplinervation not at the base of the leaf blades and the persistently yellow ribs on the achenes. The new species may be closely related to the Peruvian *F. mercedensis,* a species described as a vine, but that species has a much looser inflorescence, minutely puberulous to subglabrous stems and leaves, and a triplinervation of the leaves at the base of the blades. The present species is named for the collector of the type specimen, David N. Smith.

Fleischmannia petiolata H. Rob., sp. nov.
Fig. 12

Type.—Peru: Depto. Amazonas: Pcia. Bongará: Shillac, north by trail from Pedro Ruíz, 5°49′S, 78°01′W, 2300 m, 31 Aug–2 Sep 1983, *D. N. Smith, Vasquez 4912* (holotype US, isotype MO).

A speciebus pluribus in petiolis elongatis et basibus laminarum duplo triplinervatis differt.

Plants clambering herbs or subshrubs to 1 m high, few branches at a ca. 90° angle; stems puberulous; internodes 8–14 cm long. Leaves opposite; petioles 1–6 cm long; blades ovate to broadly ovate, mostly 3.5–

Fig. 11. *Fleischmannia davidsmithii* H. Rob., holotype, *D. N. Smith 4533* (US).

9.0 cm long, 2–6 cm wide, base rounded to obtuse with slight acumination, margins sharply serrate to crenulate-serrate, usually with 5–15 teeth on each side, apex shortly narrowly acuminate, adaxial surface sparsely pilosulous, abaxially puberulous mostly on veins, with sparse and obscure glandular dots; main triplinervation distinctly above base, weaker triplinervation at base of blade, usually in acumination. Inflorescences loosely thyrsoid with branches bearing denser, smaller corymbiform clusters of heads; peduncles 0.5–4.0 mm long, puberulous. Heads ca. 6 mm high; involucral bracts 17–20 in 3-4 series, outer 1-2 mm long, obtuse to short-acute; inner bracts 4–5 mm long, oblong-linear, rounded at apex, with scarious margins, mostly glabrous abaxially. Florets 17–23; corollas lavender, 3.0–3.5 mm long, basal tube 0.5–1.0 mm long, throat ca. 2 mm long, with reddish resin in ducts, lobes ca. 0.5 mm long, with many short hairs externally; style branches linear. Achenes 1.3–1.5 mm long, black with ribs often slightly yellow, few or no scabriform or setuliform binary hairs; pappus 2.5–3.0 mm long, bristles contiguous at base.

Paratypes.—Peru: Depto. Huánuco: Pcia. Huánuco: cuesta de Carpish, entre Huánuco y Tingo María, 2700 m, 2 Aug 1945, *Vargas 156* (US, USM); Cayumba, entre Huánuco y Tingo María, expedición Huallaga, 800–900 m, 15 Jul 1948, *Ferreyra 4194* (US, USM). Pcia. Leonicio Prado: Distr. Hermilio Valdizan, cerca a la Divisoria, 1500–1600 m, 25 Jun 1976, *Schunke 9406* (F, MO, US, USM).

Fleischmannia petiolata is known from northern Amazonas and central Huánuco at elevations of 800–2700 m, but it has not yet been found from areas between. Habitats include "selva tropical alta," "selva subtropical," and "primary high montaine rainforest, moist." The habit is apparently clambering, as stated on the type specimen. The petioles are very slender and often exceptionally elongate. The leaf blades are distinctive in the double triplinervation, the basal one being weaker.

Fleischmannia quirozii H. Rob., sp. nov.
Fig. 13

Type.—Peru: Depto. Piura: Pcia. Huancabamba: La Beatita, 1200 m, 20 Apr 1986, *Quiroz 1868* (holotype US, isotype HUP).

A speciebus pluribus in floribus ca. 50 in capitulo et in pedunculis dense stipitato glanduliferis distincta.

Plants herbaceous, to 0.8 m tall, vegetative branches usually alternate, usually ascending at a 45–60° angle; stems puberulous to hirsutulous. Leaves mostly alternate or subopposite, less often opposite; petioles mostly 0.7–2.5 cm long; blades ovate, mostly 2-7 cm long, 1.5–4.7 cm wide, base broadly obtuse to subtruncate, margins serrulate to serrate with usually 7–9 teeth on each side, apex slightly acuminate, surfaces sparsely to densely pilosulous, abaxial surface with dark often obscure, glandular dots; triplinervation from small or large basal acumination of blade. Inflorescences multi-branched with rather few heads per branch; peduncles mostly 0.2–2.0 cm long, densely covered with small-tipped stipitate glands. Heads 7–8 mm long; involucral bracts 14–16 in ca. 4 series, somewhat reddish, often with minute, stipitate glands abaxially, outer few bracts subulate, 2–3 mm long, the inner ones oblong, to 6 mm long, apices short-acute, erose-margined. Florets ca. 50–56; corollas lavender to bluish, ca. 3.8 mm long, basal tube ca. 0.8 mm long, throat ca. 2.5 mm long, with little or no colored resin in ducts, lobes ca. 0.5 mm long, few or no hairs externally. Achenes 1.5–2.3 mm long, ribs yellow, with long setulae; pappus 3.0–3.5 mm long, bristles contiguous at base.

Paratypes.—Peru: Depto. Lambayeque: 26 km E of Olmos, steep roadside cliffs, almost exactly on border with Depto. Piura, 1000 m, 10 Jun 1978. *Gentry, Dillon, Aronson & Diaz 22593* (F, MO, US, USM). Prov Ferreñafe, Oxapampa (camino a Incahuasi),

Fig. 12. *Fleischmannia petiolata* H. Rob., holotype, *Smith & Vasquez 4912* (US).

4 Feb 1984, *Quiroz & Vázques 1956* (HUT, US).

Fleischmannia quirozii is a localized species along the border of Piura and Lambayeque at 1000–1200 m elevations. The type specimen is described as "Hierba annual, erguida de 0.80 m de porte, cabezuelas lilas-moradas, borde de caminos, laderas". Other specimens are cited from steep roadside cliffs and "borde de canales de regadío". The alternate branching, the large heads with ca. 50–56 florets, and the peduncles and involucre with many minute stipitate glands are distinctive. The specimen is named for the collector of two of the specimens, S. Llatas Quiroz.

Fleischmannia sagasteguii H. Rob., sp. nov.

Fig. 14

Type.—Peru: Depto. Lambayeque: Abra de Proculla, road from Olmos to Pucará, km 45 east of Olmos, 1950 m, 13 Jul 1986, *Plowman, Sagástegui, Mostacero, Mejía & Peláez 14283* (holotype US, isotypes F, HUT).

Ad *F. pratensem* in inflorescentiis aliquantum dense corymbiformibus simila sed in inflorescentiis densìoribus et capitulis robustioribus et in marginis acheniarum persistentiter flavis differt.

Plants herbaceous annuals, short-lived perennials or subshrubs, ca. 1 m high, branches spreading at a 45–75° angle; stems glabrescent, branches sparsely to densely puberulous. Leaves opposite; petioles 0.4–2.3 cm long, broad at base; blades ovate to triangular, mostly 2.5–6.5 cm long, 1.0–4.2 cm wide, bases truncate to broadly obtuse, margins coarsely serrate or crenate-serrate, with 7–15 teeth on each side, apex acute, adaxial surface sparsely to densely pilose, abaxially with few to many hairs usually mostly on veins, with yellowish glandular dots; triplinervation from base of blade. Inflorescences terminal on primary stems and long branches, in densly corymbiform clusters; peduncles 2–5 mm long, puberulous. Heads 6–7 mm long; involucral bracts ca. 20 in 3–4 series, outer surfaces sparsely to usually densely puberulous, outer lanceolate bracts 1.5–3.0 mm long, inner bracts oblong, ca. 5 mm long, apices obtuse. Florets ca. 20; corollas violet, 3.0–3.3 mm long, basal tube 0.5–0.7 mm long, throat 2.0–2.3 mm long, ducts sometimes with reddish resin, lobes ca. 0.5 mm long, with many hairs externally; style branches linear, slightly broadened distally. Achenes 1.5–2.0 mm long, with persistently yellow ribs, setulose with binary hairs along ribs; pappus 2.0–2.5 mm long, bristles narrow at base, slightly separated.

Paratypes.—Peru: Depto. Cajamarca: Pcia. Contumazá: Alrededores de Trinidad, 1950 m, 6 Jul 1977. *Sagástegui, Alvitez & Mostacero 8940* (HUT, US). Depto. Lambayeque: ca. 70 km östl. Olmos, 20°S, 2035 m, 26 Dec 1970, *Ellenberg 3695* (US). Lambayeque, Huaratara, 2000 m, 5 Jul 1986, *Quiroz 1969* (HUP, US). Depto. Piura: Pcia. Huancabamba: Abra de Porculla, entre Olmos y Jaén, 2100–2200 m, 28 Jun 1959, *Ferreyra 13736* (US, USM). El Lúcumo (Palambla - Yumbe), 1350 m, 13 Sep 1981, *Lopez, Sagástegui, Lopez & Mostacero s.n.* (HUT, US).

Fleischmannia sagasteguii occurs mostly in the Departments of Lambayeque and Piura at elevations of 1920–2200 m, with one somewhat distinctive specimen seen from southwestern Cajamarca. Habitats are cited as dry forest along presently dry rocky quebrada, "quebrada boscosa," "monte bajo," "Teilimmergr. mässig xeromorpher montaner Wald mit mesomorphem Unterwuchs," and "cercos, borde de caminos, laderas, monte perennes." Habit is cited as "herba anual, erguida o postrada, de hasta 1.2 m de largo," or as "sufrútice" in the Cajamarca specimen. The involucral bracts are usually very pubescent but are nearly glabrous in the Cajamarca specimen. The tight, often isolated clusters of heads seem distinctive. The species is named for the well-known botanist at the Universidad Nacional de Trujillo and a collector of the

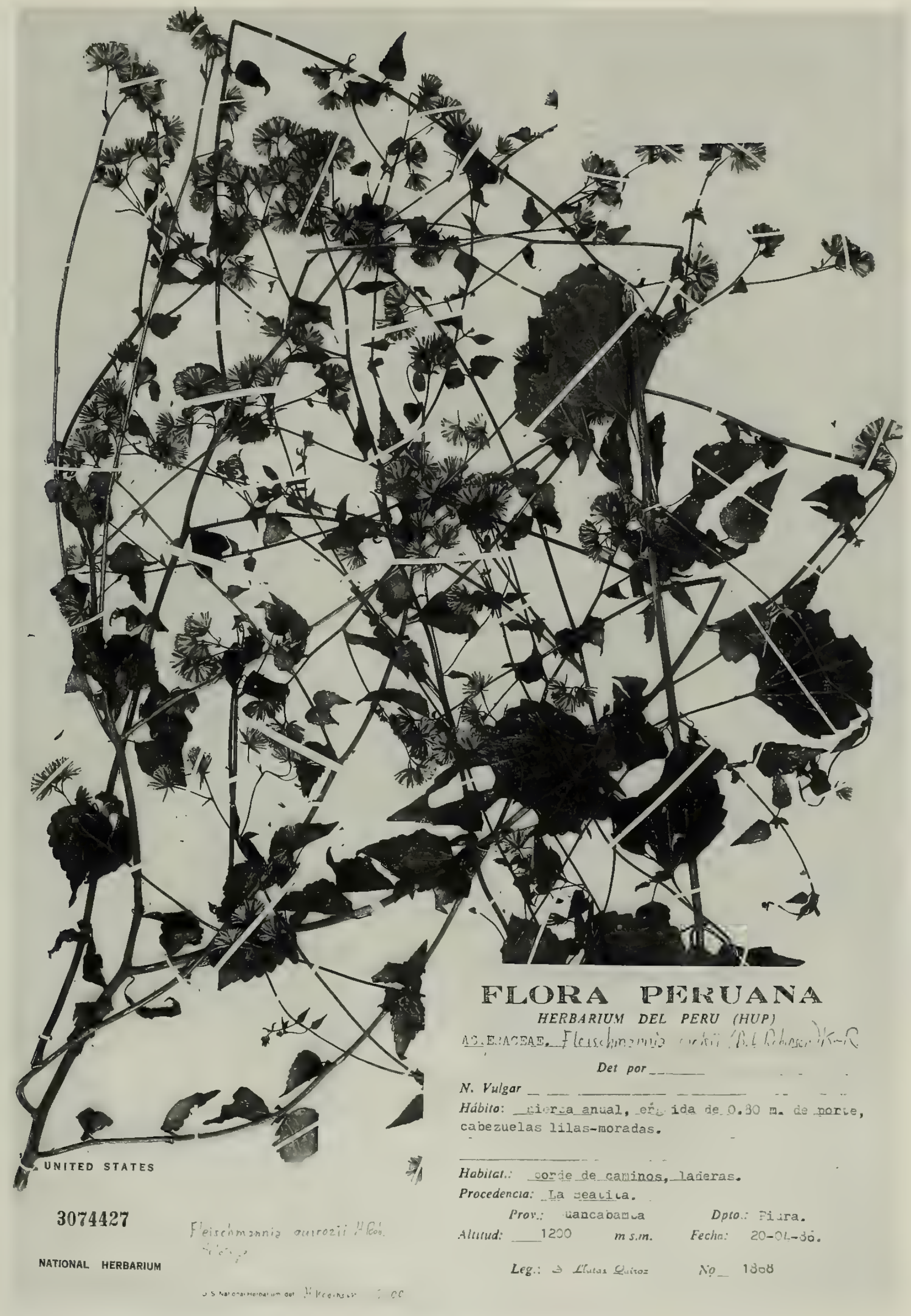


Fig. 13. *Fleischmannia quirozii* H. Rob., holotype, *Quiroz 1868* (US).

Fleischmannia sagastequii H.Rob
Holotype

U S National Herbarium, det. H. Robinson 2000

PLANTS OF PERU COMP.

No. 14283
Fleischmannia cockii (B L Robinson) K&R.

DEPT. LAMBAYEQUE. Prov. Lambayeque: Abra de Porculla. Road from Olmos to Pucará, km. 45 east of Olmos. Alt. 1920 m. Dry forest along presently dry rocky quebrada.

Hierba de hasta 1 m. de alto creciendo en el fundo de quebrada seca, en sombre. Flores lilas pálidas.

13 July 1986

Coll. T. Plowman, A. Sagástegui A., J. Mostacero L., F. R. Mejía & F. Peláez
FIELD MUSEUM OF NATURAL HISTORY
HERBARIUM TRUXILLENSE (HUT)

Fig. 14. *Fleischmannia sagasteguii* H. Rob., holotype, *Plowman, Sagástegui, Mostacero, Mejía & Peláez 14283* (US).

Fig. 15. *Fleischmannia vargasii* H. Rob., holotype, *Gentry, Revilla, Castaneda & Daly 19418* (US).

type and two paratypes, Abundio Sagástegui Alva.

Fleischmannia vargasii H. Rob., sp. nov.
Fig. 15

Type.—Peru: Depto. Cuzco: shrubby slope above Machu Picchu, along old Inca trail, 2600 m, 17 Apr 1977, *Gentry, Revilla, Castaneda & Daly 19418* (holotype US, isotypes F, US, USM).

A speciebus pluribus in inflorescentiis thyrsoideis et incapitulis minutis et in bracteis involucri pallidis gradatis et omnino obtusis differt.

Plants herbaceous, scrambling, to 0.8 m high, branching at a 80–90° angle; stems hirtellous, greenish to brownish. Leaves opposite; petioles mostly 0.5–2.5 cm long; blades ovate, mostly 2.5–6.5 cm long, 2.0–4.5 cm wide, base rounded to subtruncate, margins crenate-serrate, with 5–10 teeth on each side, apex short-acuminate, adaxial surface densely pilosulous to velutinous, abaxially densely pilosulous mostly on veins, with dense glandular dots; triplinervation from base or basal acumination of blade. Inflorescences terminal, usually on long, thyrsoid lateral branches, with small corymbiform clusters of rather crowded heads; peduncles 1–4 mm long, hispidulous. Heads mostly ca. 4 mm long; involucral bracts ca. 20, in ca. 4 series, pale greenish to pale brownish, gradate, ovate to oblong, 0.5–3.0 mm long, all obtuse to rounded, margins broadly scarious, mostly glabrous abaxially. Florets 12–19; corollas white, 2.0–2.2 mm long, basal tube ca. 0.2 mm long, throat 1.3 mm long, without colored resin in ducts, lobes ca. 0.3 mm long, with many short hairs externally; style branches linear. Achenes 1.7–2.0 mm long, with persistently yellow ribs, scabrous with few small spiculiform binary hairs on ribs; pappus ca. 1.8 mm long, bristles scarcely broadened at base, subcontiguous.

Paratypes.—Peru: Depto. Cuzco: Pcia. Convencíon, Samagaro?, 900 m, 18 May 1963, *Vargas 14473* (CUZ, US). Rosario Mayo, 1200 m, 12 May 1968, *Vargas 20689* (CUZ, US).

Fleischmannia vargasii is known only from the Department of Cuzco at 900-2600 m in elevation. The species is particularly distinctive in the small size of the heads and the orderly progression of short to long, blunt, pale bracts in the involucre. The leaf tips show considerable variation from short-acute to long-acuminate.

The species is named for the collector of two of the specimens, C. Vargas C. of Cuzco.

Acknowledgments

The extensive efforts of the technician, Marjorie Knowles are acknowledged. The photographs were prepared by John Steiner of the photography laboratory of the National Museum of Natural History.

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114(2):557–559. 2001.

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Applications published in the Bulletin of Zoological Nomenclature

The following Applications were published on 21 December 2000 in Vol. 57, Part 4 of the *Bulletin of Zoological Nomenclature.* Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case No.

3156 *Chiton lepidus* Reuss, 1860 (currently *Lepidochitona lepida*; Mollusca, Polyplacophora): proposed conservation of the specific name.

3096 *Dichrorampha* Guenée, 1845 (Insecta; Lepidoptera): proposed precedence over *Amaurosetia* Stephens, 1835.

3162 *Ceratichthys micropogon* Cope, 1865 (currently *Nocomis micropogon*; Osteichthyes, Cypriniformes): proposed conservation of usage of the specific name by the designation of a neotype.

3163 *Holacanthus ciliaris bermudensis* Goode, 1876 (currently *Holacanthus bermudensis*; Osteichthyes, Perciformes): proposed conservation of usage of the subspecific name by the designation of a neotype.

APPLICATIONS PUBLISHED IN THE BULLETIN OF ZOOLOGICAL NOMENCLATURE

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Case No

3166 *Campanularia noliformis* McCrady, 1859 (currently *Clytia noliformis*; Cnidaria, Hydrozoa): proposed conservation of the specific name by the designation of a neotype.
3146 *Valvata minuta* Draparnaud, 1805 (currently *Hauffenia, Neohoratia* or *Islamia minuta*; Mollusca, Gastropoda): proposed replacement of the lectotype by a neotype.
3123 DOLICHOPODINI Brunner von Wattenwyl, 1888 (Insecta, Grylloptera): proposed emendation of spelling to DOLICHOPODAINI, so removing the homonymy with DOLICHOPODIDAE Latreille, 1809 (Insecta, Diptera).
3136 *Crotaphytus vestigium* Smith & Tanner, 1972 (Reptilia, Squamata): proposed conservation of the specific name.
3041 *Cynodon* Spix in Spix & Agassiz, 1829 and *Rhaphiodon* Agassiz in Spix & Agassiz, 1829 (Osteichthyes, Characiformes): proposed conservation, and proposed designation of *C. gibbus* and *R. vulpinus* Spix & Agassiz, 1829 as the respective type species of *Cynodon* and *Rhapiodon.*
3167 *Schistochlamys* Reichenbach, 1850 and *Neothraupis* Hellmayr, 1936 (Aves, Passeriformes): proposed conservation

Opinions published in the Bulletin of Zoological Nomenclature

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Opinion No.

1963. *Blennocampa* Hartig, 1837, *Cryptocampus* Hartig, 1837, *Taxonus* Hartig, 1837, *Ametastegia* A. Costa, 1882, *Endelomyia* Ashmead, 1898, *Monsoma* MacGillivray, 1908, *Gemmura* E.L. Smith, 1968, BLENNOCAMPINI Konow, 1890 and CALIROINI Benson, 1938 (Insecta, Hymenoptera): conserved by setting aside the type species designations by Gimmerthal (1847) and recognition of those by Rohwer (1911) . . .
1964. *Apis proava* Menge, 1856 (currently *Electrapis proava*; Insecta, Hymenoptera): conserved by the designation of a neotype . . .

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Opinion No.

1955. *Strombidion caudatum* Fromentel, 1876 (currently *Strobilidium caudatum*; Ciliophora, Oligotrichida): specific name placed on the Official List . . .
1956. *Eudendrium arbuscula* Wright, 1859 (Cnidaria, Hydrozoa): specific name conserved . . .
1957. *Sphaerius* Waltl, 1838 (Insecta, Coleoptera): conserved; and SPHAERIIDAE ERICHSON, 1845 (Coleoptera): spelling emended to SPHAERIUSIDAE, so removing the homonymy with SPHAERIIDAE Deshayes, 1854 (1820) (Mollusca, Bivalvia) . . .
1958. *Macrophya* Dahlbom, 1835 (Insecta, Hymenoptera): conserved by the designation of *Tenthredo montana* Scopoli, 1763 as the type species; and *Tenthredo rustica* Linnaeus, 1758: usage of the specific name conserved by the replacement of the syntypes with a neotype . . .
1959. *Terebratula* Müller, 1776 (Brachiopoda): *Anomia terebratula* Linnaeus, 1758 designated as the type species . . .
1960. *Crotalus ruber* Cope, 1892 (Reptilia, Serpentes): specific name given precedence over that of *Crotalus exsul* Garman, 1884 . . .
1961. *Coluber infernalis* Blainville, 1835 and *Eutaenia sirtalis tetrataenia* Cope in Yarrow, 1875 (currently *Thamnophis sirtalis infernalis* and *T. s. tetrataenia*; Reptilia, Serpentes): subspecific names conserved by the designation of a neotype for *T. s. infernalis* . . .
1962. *Arctocephalus* F. Cuvier, 1826 and *Callorhinus* Gray, 1859 (Mammalia, Pinnipedia): conserved by the designation of *Phoca pusilla* Schreber, 1775 as the type species of *Arctocephalus*; and *Otaria* Péron, 1816 and *Eumetopias* Gill, 1866: conserved by the designation of *Phoca leonina* Molina, 1782 as the type species of *Otaria* . . .

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