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PROCEEDINGS

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Cretaceous anuran and dinosaur footprints from the Patuxent Formation of Virginia

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Abstract.—Footprints of an anuran (gen. et sp. indet.), a theropod dinosaur (*Megalosauropus* sp.), and an ornithopod dinosaur (*Amblydactylus* sp.) have been recovered from the Lower Cretaceous Patuxent Formation in Stafford County, Virginia. These footprints are the first record of terrestrial vertebrates from Cretaceous strata in Virginia, and their discovery suggests that the scarcity of bones and teeth in the Patuxent probably is an artifact of preservation. The anuran trackway provides the oldest known direct evidence for hopping locomotion among these amphibians.

The Patuxent Formation has yielded an abundant fossil macroflora from Maryland and Virginia (Fontaine 1889; Ward et al. 1905; Berry 1908, 1910a, 1910b, 1910c, 1911a, 1911b, 1911c, 1911d; Clark & Miller 1912; Brenner 1967; Wolfe 1972; Doyle & Hickey 1975; Skog 1982, 1988, 1992; Hickey 1986), as well as a diverse palynoflora (Brenner 1963, Hughes & Moody 1966, Doyle 1977, Doyle & Robbins 1977). In sharp contrast, the only vertebrate material reported from this unit is a fish skeleton, found somewhere in the James River valley of Virginia (Berry 1911a). Therefore, it is significant that footprints of an anuran and two kinds of dinosaur have been found north of Fredericksburg, Virginia, in Stafford County (Fig. 1). These prints provide our first glimpse of the Cretaceous vertebrate fauna that once existed in Virginia. The Lower Cretaceous Arundel Formation, which overlies the Patuxent Formation in Maryland but not in Virginia (Fig. 2), has produced a diverse but fragmentary vertebrate fauna that includes turtles, crocodiles, and dinosaurs (Lull 1911a, 1911b; Gilmore 1921; Ostrom 1970; Galton & Jensen 1979; Kranz 1989; Weishampel 1990; Martin & Brett-Surman 1992). The diversity of this fauna suggests that a diverse fauna also may have existed while the slightly older Patuxent sediments were accumulating. Until the discovery of the footprints described here, however, no direct evidence for such a fauna was available.

Location, age, and geologic setting.—The footprints described here were found by Jon Bachman in strata of the Lower Cretaceous Patuxent Formation in a roadcut on the east side of U.S. Route 1, located 0.25 mi south of Potomac Creek in Stafford County, Virginia (Fig. 1). In its outcrop belt, the Patuxent Formation is approximately 200 to 300 ft thick (Clark & Miller 1912). The unit dips gently and thickens to the east, becoming about 575 ft thick twenty-five mi east-southeast of Fredericksburg, near Oak Grove (Reinhardt et al. 1980). In the Fredericksburg region, pre-Mesozoic crystalline rocks directly underlie the Patuxent Formation with profound unconformity. These rocks crop out along the floor of Potomac Creek well to the west of U.S. Route 1. Because the footprint-bearing outcrop is located toward the eastern margin of the Patuxent outcrop belt, the footprints probably come from the upper half of that formation. However, faults are known from the general vicinity of the footprint-bearing outcrop (Mixon & Newell 1977), so the

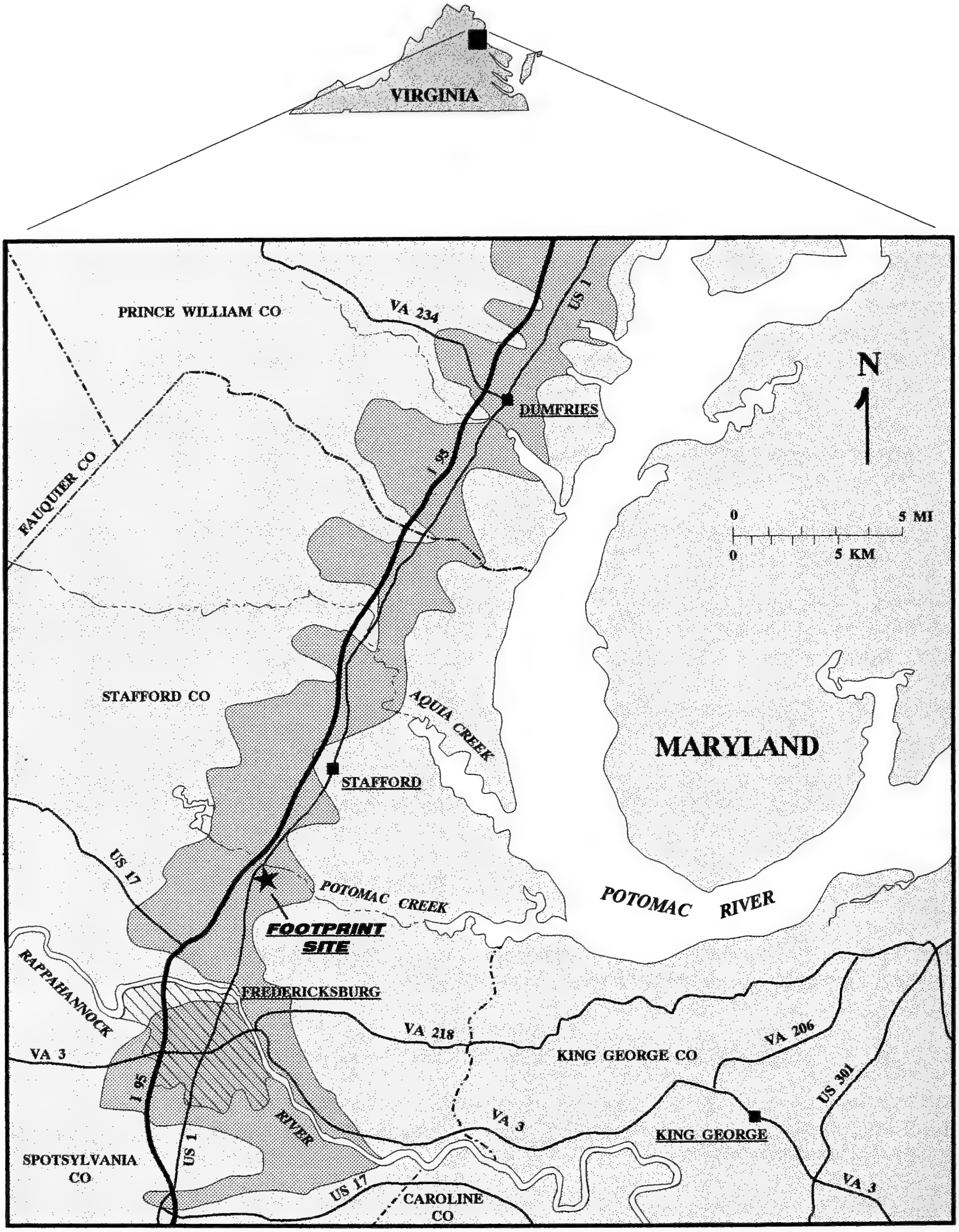

Fig. 1. Map showing Bachman locality (star) where footprints have been found in the Lower Cretaceous Patuxent Formation north of Fredericksburg, Virginia (oblique rule). Outcrop belt of Lower Cretaceous Patuxent Formation is shown in dark gray. Younger Tertiary and Quaternary sediments crop out to the east of this belt, while older, pre-Mesozoic igneous and metamorphic rocks crop out to the west (both areas shown in light gray). The Lower Cretaceous strata dip gently toward the east and thicken in that direction.

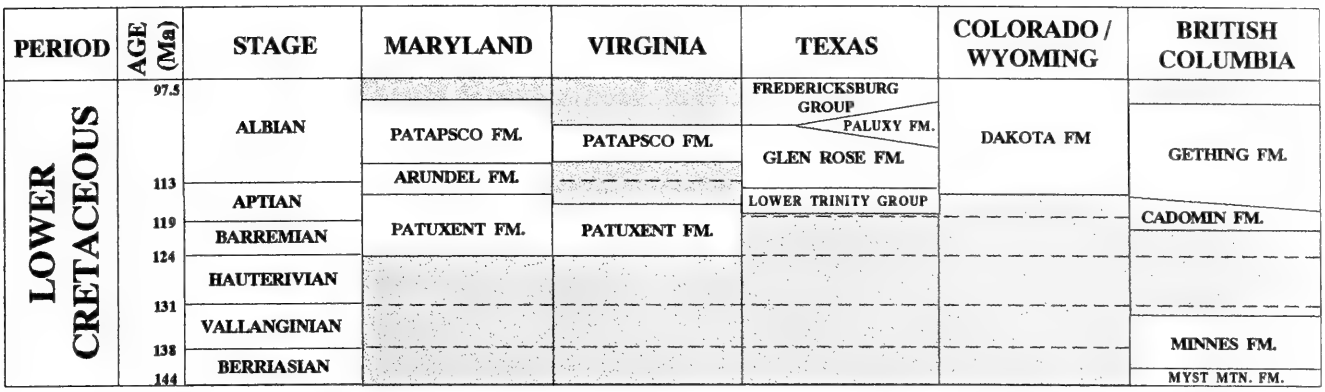

Fig. 2. Comparison of the Lower Cretaceous geologic columns preserved in Maryland, Virginia, Texas, Colorado/Wyoming, and British Columbia. Time intervals represented by preserved strata are shown; missing time intervals are indicated by gray areas.

stratigraphic position of this outcrop could be lower than it appears to be.

The Patuxent, based on palynomorph studies (Brenner 1963, Doyle & Robbins 1977, Reinhardt et al. 1980), is Barremian to Aptian (124 to 115 Ma) in age. The relatively high horizon of the footprint-bearing bed suggests that an Aptian age (119 to 115 Ma) is more likely than Barremian. The Aptian part of the Patuxent represents a portion of the Lower Cretaceous column that is sporadically but widely preserved in North America (Fig. 2). Thus, a number of Aptian units (the Arundel Formation of Maryland, the Glen Rose Formation of Texas, the basal Dakota Formation of Colorado and Wyoming, and the Cadomin and basal Gething Formations of British Columbia) are close in age to the Patuxent, and their footprints and skeletal remains are especially relevant for comparison to the Patuxent footprints described here.

In its outcrop belt, the Patuxent Formation has yielded only terrestrial fossil remains (Clark & Miller 1912, Berry 1911a), and its sedimentary fabric indicates that most of the unit accumulated in a fluvial braided-stream environment (Glaser 1969). However, about thirty miles east-southeast of the Bachman locality near Oak Grove, glauconite has been reported in the Patuxent in its subcrop belt. Because glauconite forms under marine conditions, the presence of this mineral indicates that marine incursions across the Coastal Plain from the east came within thirty miles of the footprint-bearing locality during Patuxent time (Reinhardt et al., 1980). These regional stratigraphic relationships indicate that the depositional environment of the Patuxent shifted southeastward from fluvial braided-stream through delta plain to marginal-marine delta front environments (Reinhardt et al. 1980). Although the footprint-bearing part of the Bachman locality is dominated by fine-grained sediments (see Table 1), other outcrops in the immediate vicinity tend to be dominated by cross-bedded to massive medium- to coarse-grained sands and sandstones that often are pebbly. This local association of lithologies indicates that the strata at the Bachman locality were formed either in a temporary slack-water area within the lower reaches of a fluvial braided-stream system, or else it was part of a deltaic environment that was briefly established across the lower reaches of a fluvial braided-stream system while its gradient was lowered due to a marine incursion from the east.

The frog footprints were impressed on a clayey silt layer that dried out enough not to be disrupted by deposition of an inch-thick (2.5 cm-thick) layer of ripple-cross-laminated sandy and clayey silt containing scattered stem and leaf debris. The top of this one inch-thick layer in turn was in the process of drying when the two types of dinosaurs came by and left their footprints. After this layer dried enough to become

Table 1.—Section of Patuxent Formation on U.S. Route 1, 0.25 mile south of Potomac Creek.

Bed	Description	Thickness
8	Covered, sandy residuum overgrown with pines	8.5 ft
7	Sandstone, fine- to medium-grained, pale-yellowish-orange (10YR8/6) to very-pale-orange (10YR8/2), clayey and silty, contains scattered clayballs, fines upward	1.8
6	Siltstone, clayey, light-brownish-gray (5YR5/1), thinly laminated, contains leaf impressions (mostly conifers)	0.2
5	Sandstone, medium- to coarse-grained, pale-yellowish-orange (10YR8/6) to very-pale-orange (10YR8/2), poorly sorted, crossbedded, base has 6 inch amplitude southeast-trending swales cut into bed below; fines upward to very fine- to fine-grained and silty	1.5 to 2.0
4	Sandstone, dominantly fine-grained but very fine- to medium, silty, yellowish-gray (5YR8/1), contains mudballs, carbon chips scattered on bedding surfaces, stem fragments and impressions scattered throughout, faintly laminated but mostly massive, symmetrical ripples and interference ripples on laminar surfaces, dinosaur footprints within this interval	0.5 to 1.0
3	Siltstone, very fine sandy, micaceous, very pale-orange (10YR8/2), abundant leaf impressions (mostly ferns), and stem fragments, well bedded with ⅛ to ¼ in.-thick impersistent laminae; some laminae contain symmetrical ripple marks; upper surface planar, anuran prints on top of this unit	2.5
2	Sandstone, fine- to medium-grained, poorly bedded, very pale-yellowish-brown (10YR7/2), scattered stem fragments present, planar bedded with 0.5 to 2.0 in.-thick laminae	1.5
1	Sandstone, medium- to coarse-grained, pale-yellowish-orange (10YR8/6) to very pale-orange (10YR8/2), scattered mudballs (up to 2 in. diameter) and quartz pebbles (up to 4 in. diameter), subrounded to rounded, prominently crossbedded	10.0
Total thickness		27.0 ft

firm, it was in turn covered by a bed of silty, poorly sorted fine- to medium-grained sand that contained abundant mudballs. This crudely graded layer ranges from 1.25 to 2.5 in. (3 to 6 cm) in thickness. The distribution of these layers appears to be quite local, as would be expected in a lower fluvial braided-stream or upper deltaic environment. There are no indications that the local environment was paludal to lacustrine, as has been surmised for much of the Arundel Formation (Glaser 1969). Although the anuran suggests proximity to permanent fresh water, the presence of well-formed footprints of any kind indicates that the local environment was damp but subaerial at the times the prints were formed. The flora of the Patuxent is strikingly similar to that of the modern warm-temperate rain forests of New Zealand, which are dominated by broad-leafed conifers and ferns (Brenner 1963), and this implies that a similar climate existed in Virginia during deposition of the Patuxent.

Much of the Patuxent is unlithified, but some horizons in the Stafford County area are semilithified to lithified. Between 1790 and 1840, the lithified strata were quarried and used as a building stone known as "Aquia Creek sandstone" or "Virginia freestone." Parts of the White House, Capitol, Treasury Building, and National Portrait Gallery were built of this material (Withington, 1975). The strata in the footprint-bearing outcrop are only in a semilithified state, and thus unsuitable for use as building stone. Even so, their modest coherence greatly simplified collection and

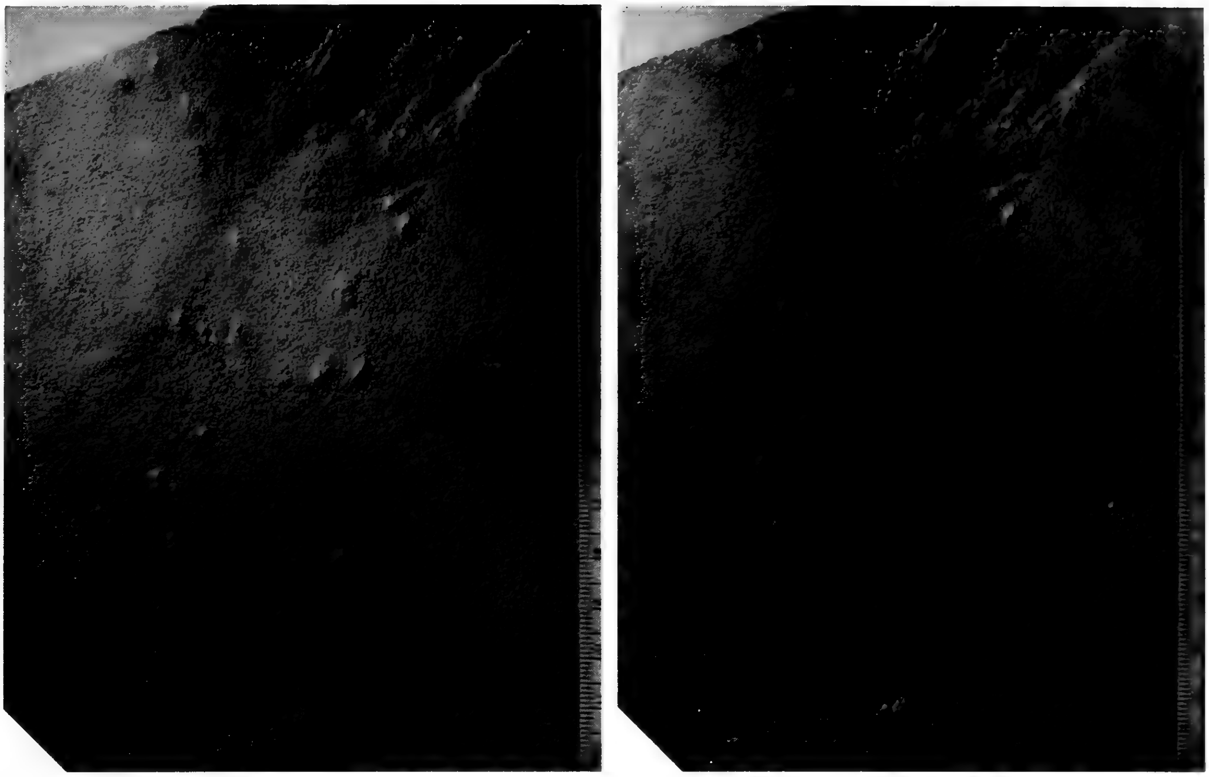

Fig. 3. Stereophotos of part of an anuran trackway preserved on a counterpart slab (USNM 475487) from the Lower Cretaceous Patuxent Formation of Virginia. Scale is in centimeters.

preservation of the footprints described here.

Systematics.—Specimens described in this paper have been donated to the collections of the United States National Museum (USNM). Their taxonomic placement is summarized as follows:

Class Amphibia
Order Anura
Gen. et sp. indet.

Two contiguous slabs (USNM 475487 and USNM 475488) from the Bachman locality preserve a single long trail of a small quadrupedal animal. The preserved impressions represent the counterpart filling of the original trackway. All but one of the tracks on one slab are shown in Fig. 3, and the entire trackway is represented in Fig. 4. Generally the tracks are poorly preserved, in part due to the small size of the animal that made them. Even so, the trackway pattern is distinctive. The animal moved with left and right rear feet spread widely apart, and it possessed front feet that appear to be notably smaller and less widely spread than the rear feet. Its gait placed left and right feet side-by-side during locomotion, rather than in the obliquely-alternating pattern that is normal for most tetrapod vertebrates during locomotion. This pattern indicates a hopping mode of progression. Although much of the trackway is indistinct, one pair of rear and front feet are fairly well preserved (Figs. 5, 6). These prints reveal the presence of three robust toes on each rear foot, with the middle toe elongated only slightly beyond the other two. The front feet are less distinct, but they appear to be elongate and rotated outward about 30° from the line of travel. As preserved, this trackway corresponds to no known animal. The relatively faint preservation of the entire trackway, however, strongly suggests that at least some of the trackmaker's toes may not have impressed into the substrate.

When our Cretaceous trackway is compared to tracks made by a modern frog (*Rana clamitans*) and a modern toad (*Bufo woodhousei*), the Cretaceous trackway can

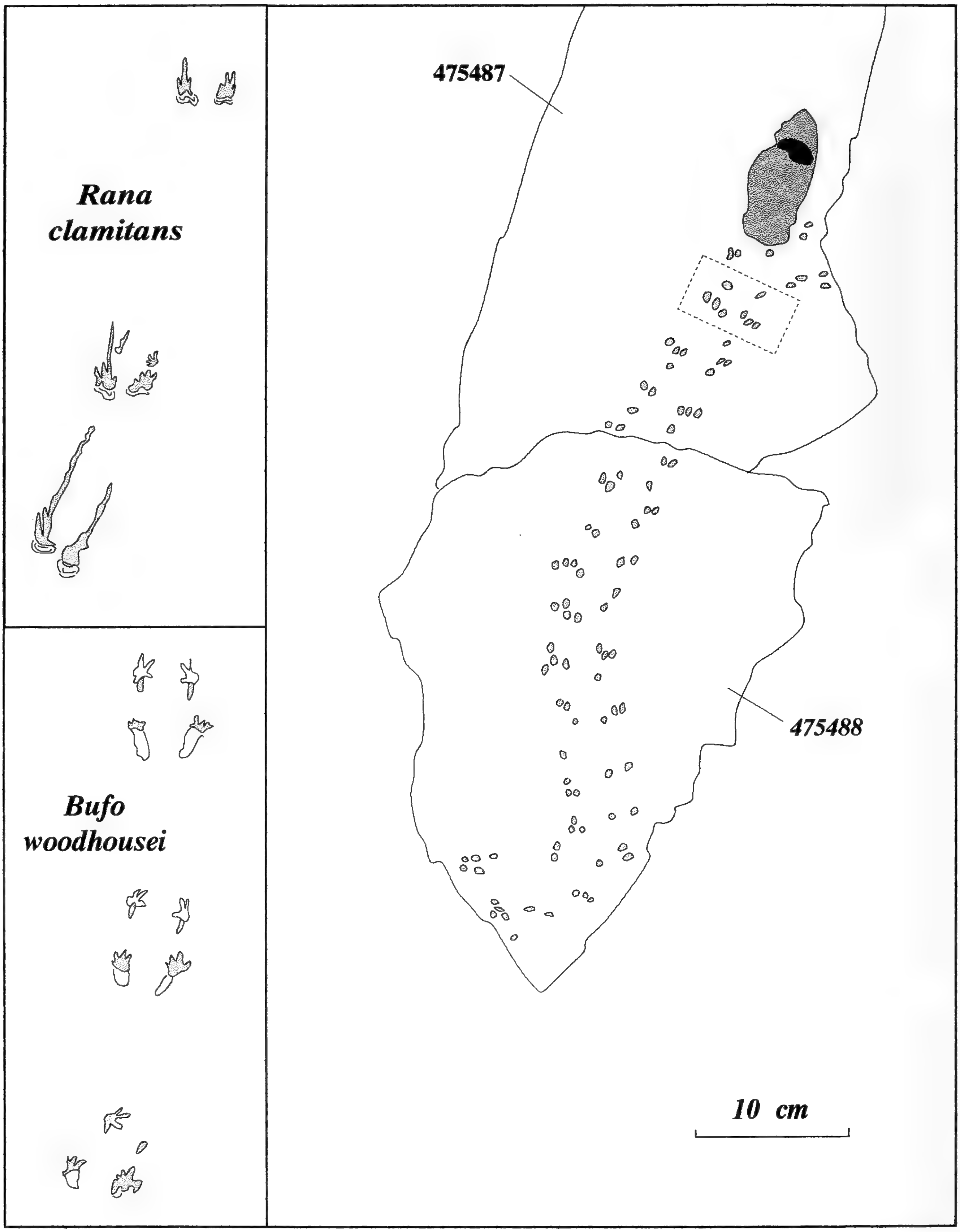

Fig. 4. Comparison of Patuxent anuran trackway (right) with footprints made in plaster by a modern frog (*Rana clamitans*, upper left) and a modern toad (*Bufo woodhousei*, lower left). Tracks are light gray, except for *Bufo woodhousei* where light gray areas are portions of tracks that are deeply impressed and unshaded areas are portions of tracks only very lightly impressed. Dark gray area in upper right is an area of mineralization around a woody stem or branch (black). Trackway at right is shown as a set of positive prints and thus is mirror-reversed to Fig. 3. Dashed rectangle encloses footprints shown in Figs. 5 and 6. All prints drawn to same scale.

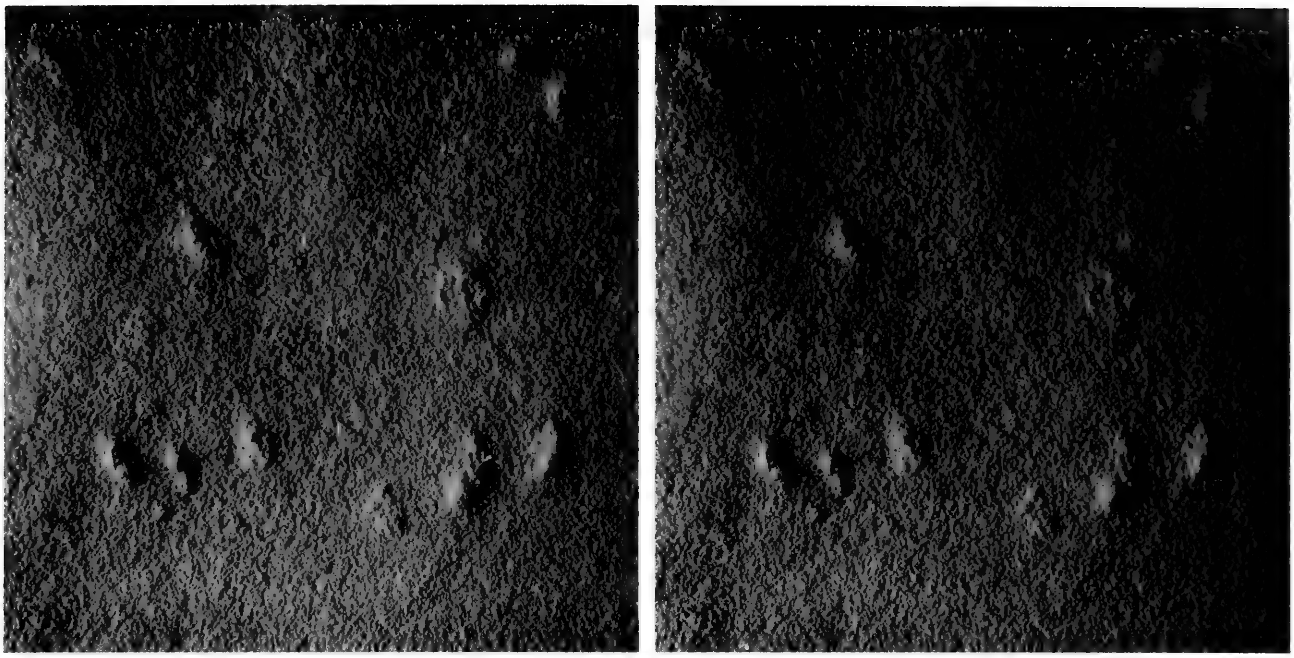

Fig. 5. Closeup stereophotos of the third set of counterpart track fillings in the anuran trackway illustrated in Fig. 3, which is also the track set marked in Fig. 4 by the dashed rectangle.

be seen to be plausible for an anuran hopping across a substrate that was barely soft enough to record the animal's passage. Although anurans have four toes on their front feet and five toes on their rear feet, tracks made for us by modern frogs and toads hopping across wet plaster (Fig. 4) indicate that usually only the central three toes (II–IV) of the pes leave clear marks. This indicates that modern anurans primarily use pedal digits II–IV to power their hops and also implies that they use pedal digits I and V primarily for balance. Similarly, the frog only occasionally produced distinct manus prints, and the toad produced manus prints that were lightly impressed except for digit I, which was much more deeply impressed than any of the other digits. From these observations, we conclude that our Cretaceous trackway probably was made by an anuran that left only an imperfect representation of its feet. The Cretaceous anuran typically left only impressions of pedal digits II–IV, and its manus either did not leave visible marks or left impressions only of digit I. In this interpretation, the impressions of manual digit I are rotated 150° inward, which would be normal for an anuran, rather than 30° outward as would be indicated if these marks represented the impression of the entire diminutive front foot of some very enigmatic animal.

The only characteristic of this trackway that is exceptional for an anuran is the distance between hops, which proportionally is much shorter than in modern frogs and toads (Fig. 4). Given the great antiquity of this trackway, however, there is no compelling reason to expect that its maker should have been nearly so efficient at hopping as are modern frogs or toads. Because the trackmaker maintained a steady (albeit plodding) gait, in that regard it was distinctly more like a toad than a frog. Toads can afford to be deliberate in their gait, because they possess poisonous skin glands that make them nearly immune to predation. Frogs, in contrast, must rely on their powerful hops and erratic movements to avoid attack. Therefore, the deliberate and plodding gait demonstrated by this trackway strongly suggests that its maker, although probably too ancient to be a true toad, probably possessed skin glands that produced secretions to protect it from attack. Members of the living family Discoglossidae, known as far back in the fossil record as the Jurassic, produce distasteful skin secre-

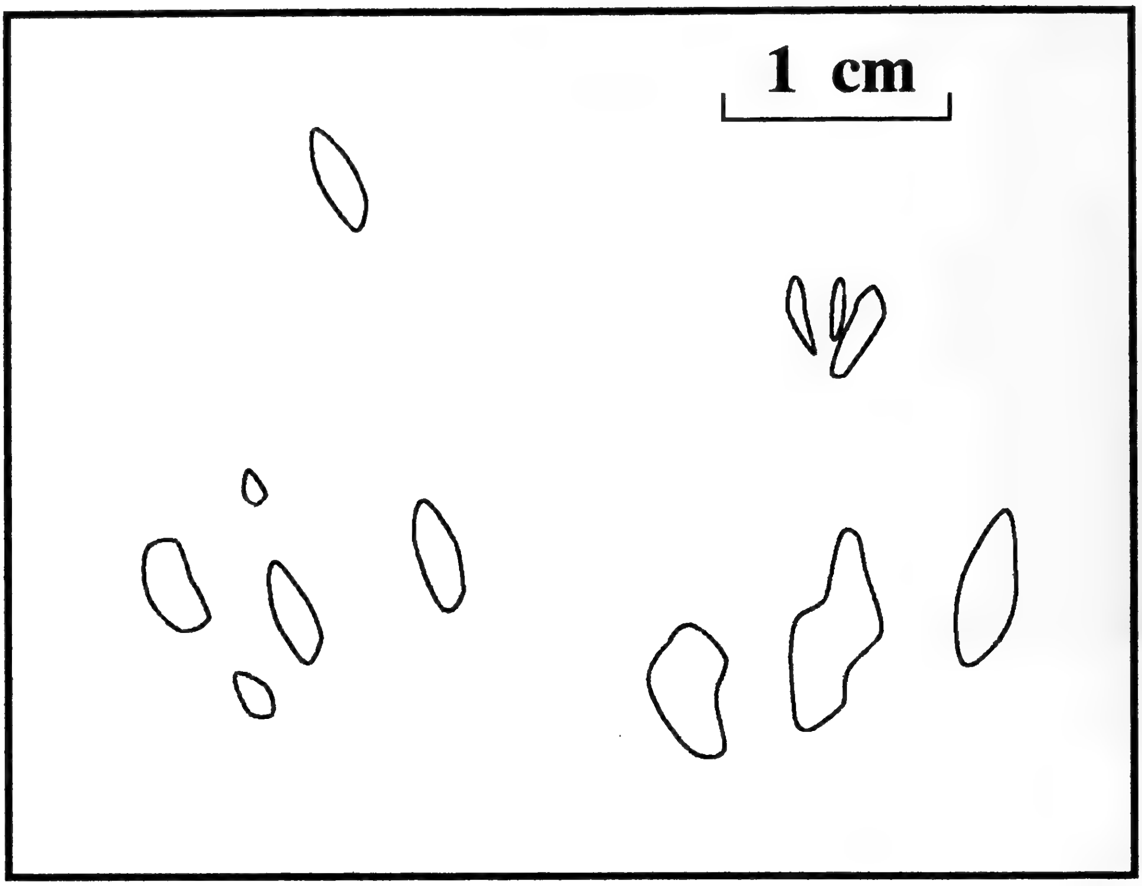

Fig. 6. Interpretation of the stereophotos of counterpart anuran footprint fillings shown in Fig. 5. Footprints are shown as counterparts for easier comparison with Fig. 5.

tions (Zweifel 1992). Therefore, it is reasonable to suggest that at least some anurans developed this type of protection by the Early Cretaceous.

Anuran trackways have not been reported in the ichnotaxonomic literature (Haubold 1971). Therefore, by definition, this trackway represents an undescribed genus and species. Unfortunately, the rather poor detail of this trackway allows diagnosis of it only to the ordinal level of taxonomy. For this reason, it is not suitable for use as a type for a new ichnotaxon. Yet even at the ordinal level of identification, this trackway is still of considerable interest. First, it is the oldest direct evidence for the existence of anurans in Virginia or anywhere else in the Eastern United States. The recent skeletal description of a functionally modern frog (*Prosalirus bitis*) from the Lower Jurassic of Utah (Shubin & Jenkins 1995) indicates that anurans were present in western North America well before the Early Cretaceous, and four living families are known to have been present by the Early Cretaceous in South America (Ascaphidae), Europe (Discoglossidae, Paleobatrachidae), and Asia (Pipidae) (Benton 1987, Carroll 1988). From these occurrences, it could be inferred that anurans were present in eastern North America in the Early Cretaceous, but none of this skeletal material provides direct proof of their presence. Second, the Patuxent specimen is attributable to an anuran specifically because of its hopping mode of locomotion. Thus, even though a hopping capability has been attributed to *Prosalirus* on anatomical grounds, our specimen provides the oldest direct evidence for sustained hopping locomotion in frogs.

Class Reptilia
Order Theropoda
Megalosauropus sp.

Several tridactyl footprints (USNM 475489, USNM 475490, and USNM

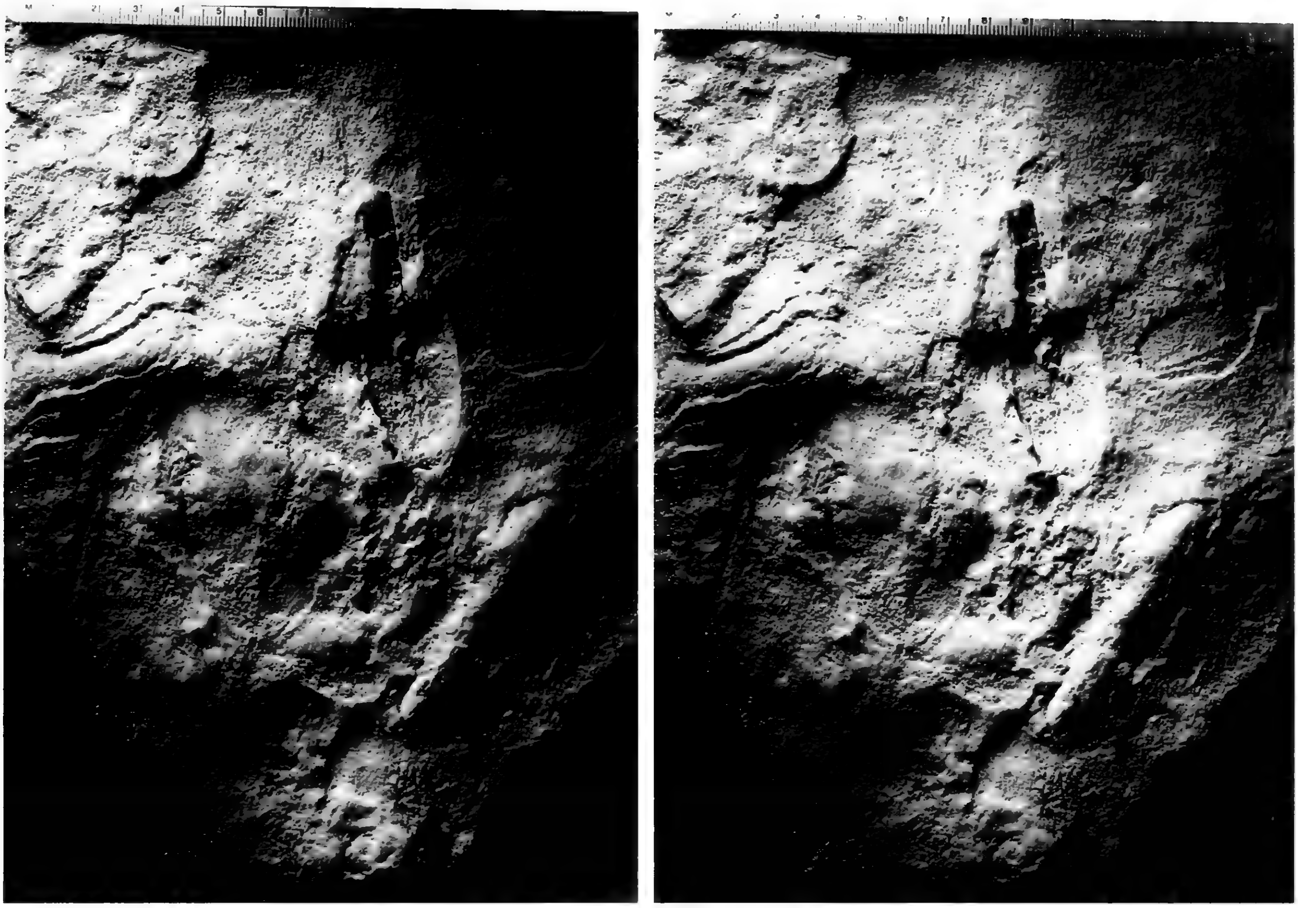

Fig. 7. Stereophotos of a counterpart filling of a footprint of *Megalosauropus* (USNM 475489) from the Lower Cretaceous Patuxent Formation of Virginia. Scale is in centimeters.

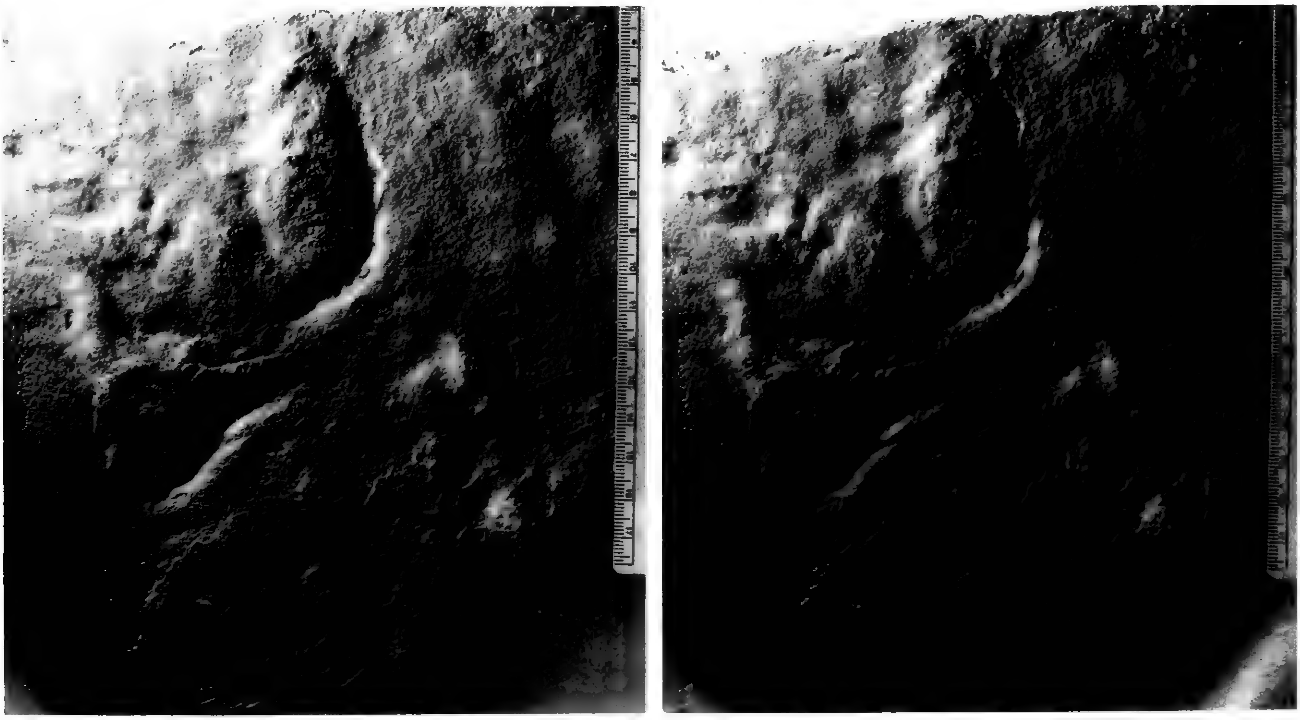

Fig. 8. Stereophotos of a counterpart filling of a footprint of *Megalosauropus* (USNM 475490) from the Lower Cretaceous Patuxent Formation of Virginia. Scale is in centimeters.

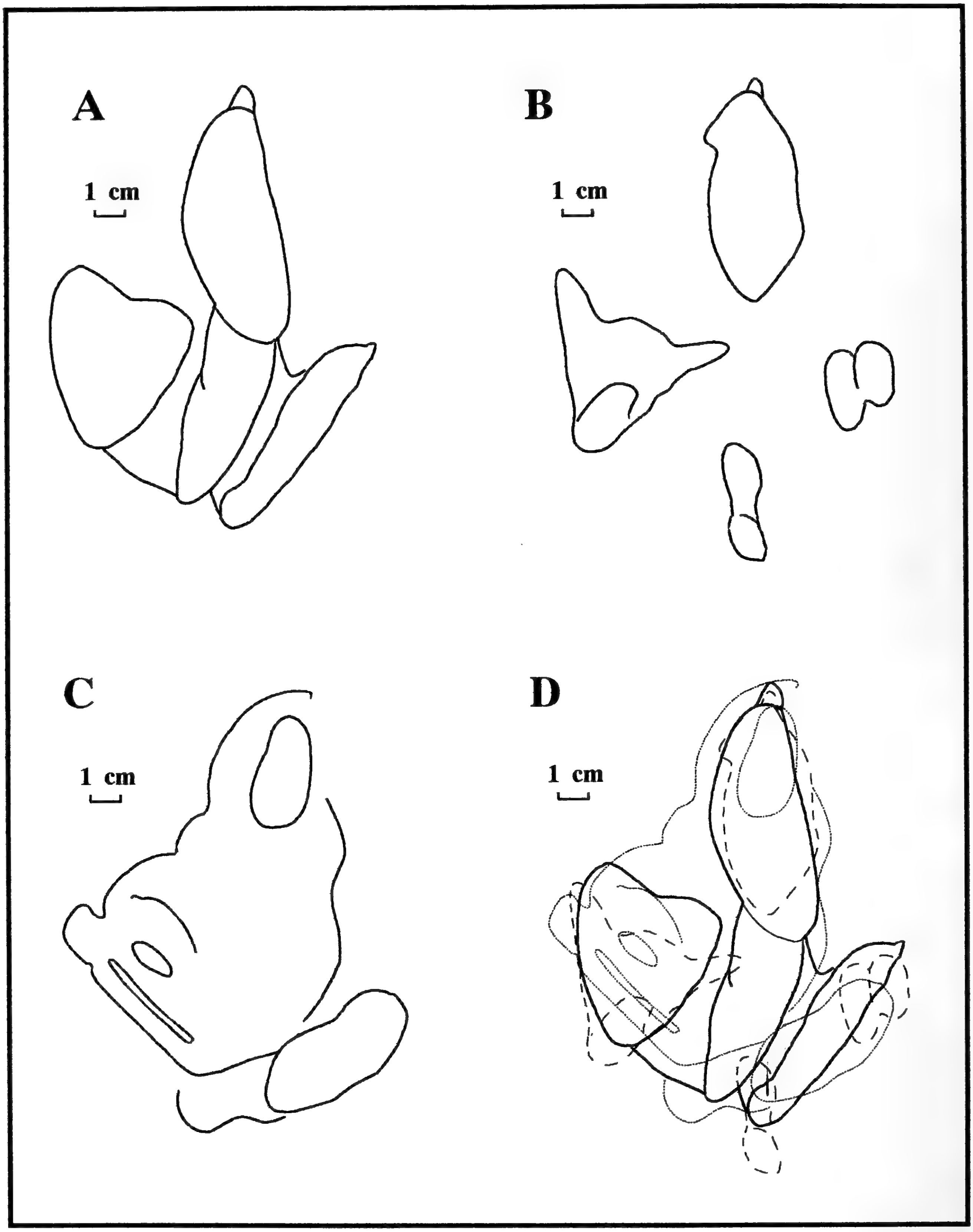

Fig. 9. A. Interpretation of footprint of *Megalosauropus* derived from the counterpart left footprint filling shown in Fig. 7. B. Interpretation of footprint of *Megalosauropus* derived from the counterpart left footprint filling shown in Fig. 8. C. Interpretation of right footprint of *Megalosauropus* (USNM 475491, not figured). D. Composite of footprint interpretations shown in Fig. 8A–C. Because the counterparts are of left feet and the positive is of a right foot, symmetries match without mirror-symmetry adjustment.

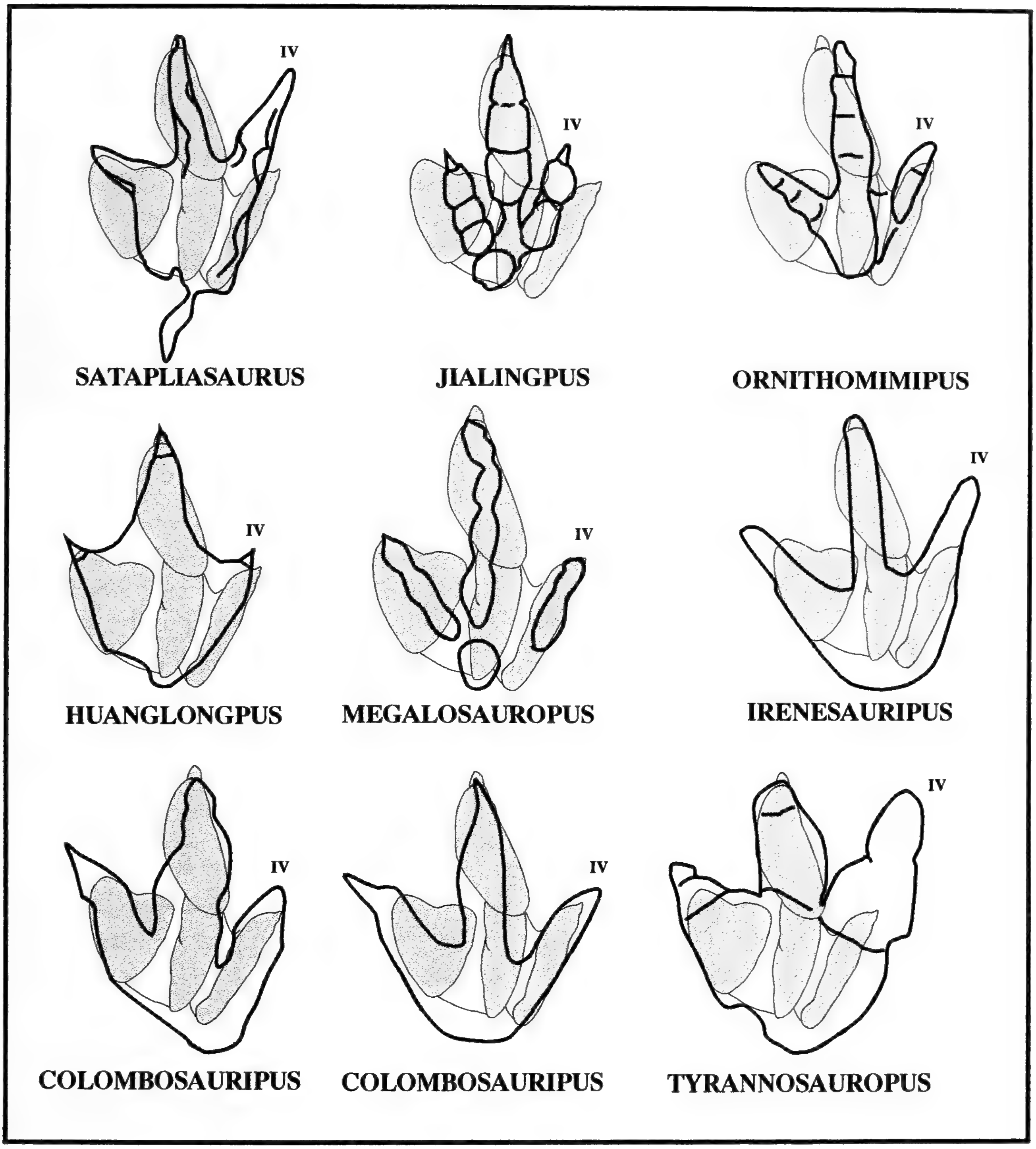

Fig. 10. Comparison of footprint interpretation in Fig. 9A with eight genera (nine species) of theropod ichnotaxa described previously. Described footprints redrawn from Haubold (1971) and Yang and Yang (1987).

475491) are characterized by a relatively narrow divarication between digits II and IV and an elongate middle toe. These prints can be readily referred to the Theropoda. Two of these specimens (Fig. 7, Fig. 8), representing counterpart fillings of tracks, are illustrated. Both of these, as well as a third poorly preserved positive print, are interpreted by outline drawings in Fig. 9A–C. These drawings were made by placing clear plastic film over each track, tracing its observable characteristics, and then scanning the tracings into a graphics program. The exact form of each track is different in detail, but when all of the outline drawings are superimposed at the same scale (Fig. 9D) it can be seen that they were made by feet that were identical in size and basic

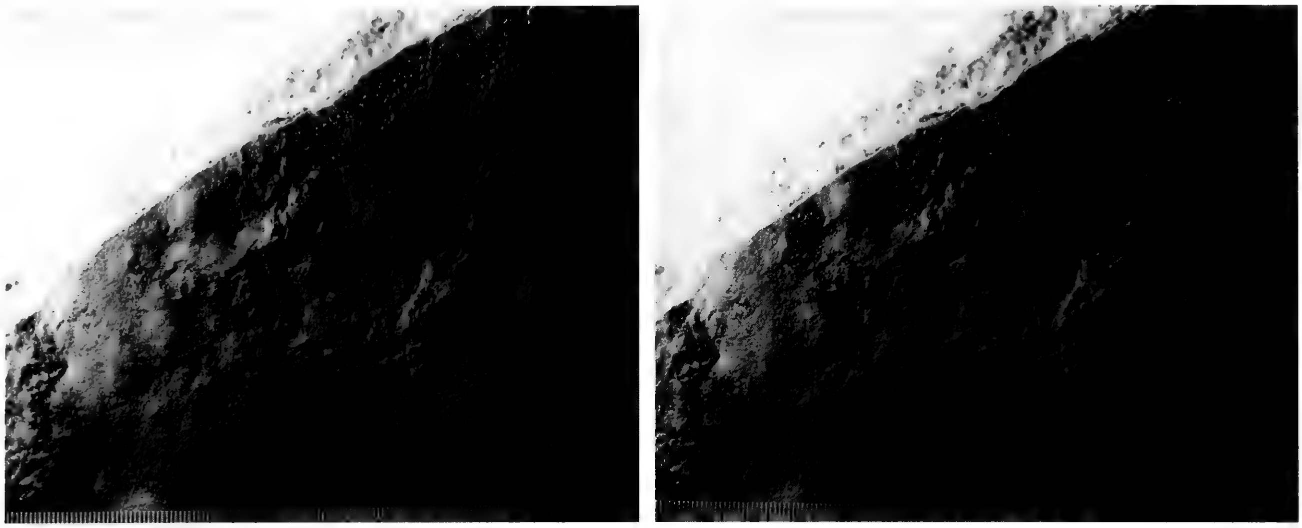

Fig. 11. Stereophotos of a counterpart filling of a left footprint of *Amblydactylus* (USNM 475492) from the Lower Cretaceous Patuxent Formation of Virginia. Scale is in centimeters.

pattern. As all three of these footprints came from a single horizon and locality, we strongly suspect that they were all made by the same taxon of animal and quite possibly by a single individual. Thus, differences among these three tracks here are ascribed to differences in substrate and/or differences in locomotor pattern.

The fundamental foot pattern of all of these tracks clearly is that of a theropod dinosaur, and nine theropod footprint taxa have been described that either are about the same age as our tracks or show anatomical similarity to our specimens (Fig. 10). Relative toe lengths are significantly different between our specimens and *Satapliosaurus*, *Irenesauripus*, *Colombosauripus*, and *Tyrannosauropus*, so there is no reason to assign our tracks to any of these taxa. The digit divarication of our specimens differs significantly from *Jialingpus*, and the digits in *Ornithomimipus* are much less robust and more slender.

Of all of these described forms, *Huanglongpus* and *Megalosauropus* are most similar to our specimens. Indeed, *Megalosauropus*, our specimens, and *Huanglongpus* could be interpreted as merely variants of a single foot pattern on firm, moderately firm, and soft substrates respectively. As *Megalosauropus* is the earlier described taxon, and Haubold (1971) has referred "*Eubrontes*" *titanopelobatidus* Shuler (1917) from the Glen Rose Formation of Texas to this genus, we consider it appropriate to refer our specimens to *Megalosauropus*. Our specimens are only about half as long as the type material of *Megalosauropus* (18 cm vs. 32.5 cm), and this could reflect a species level difference between our material and previously described material. However, on the basis of only three specimens, quite possibly from a single individual, it is equally possible that our specimens represent an immature individual of one of the two described species. Because our material is sparse and imperfectly preserved, we see no point in attempting a species designation at this time.

Although the foot structure indicated by *Megalosauropus* immediately suggests that it was made by a theropod dinosaur, the precise type of theropod is less readily determined. As the name implies, *Megalosauropus* initially was assumed to represent a megalosaurid or allosaurid carnosaur. But the relatively modest size of known specimens assigned to this taxon and the relatively elongate digit III are not what would be expected from the foot of a carnosaur, which should have made a footprint like *Colombosauripus*. Similarly, the foot of an ornithomimid should have made a track like *Ornithomimipus*, while the foot of a troo-

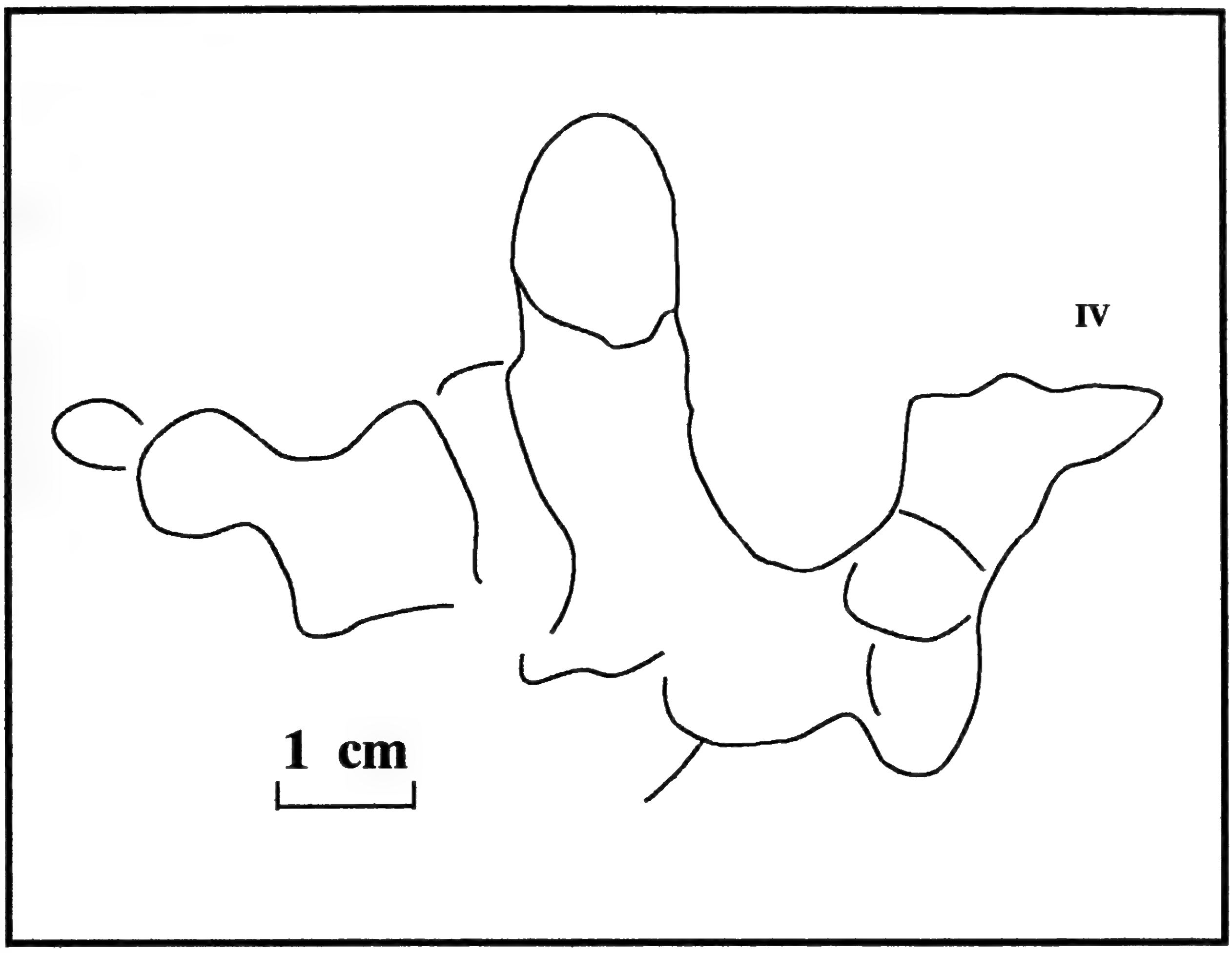

Fig. 12. Interpretation of footprint of *Amblydactylus* derived from the counterpart left footprint filling shown in Fig. 11.

dontid should have made a track like *Irenesauripus*. The foot of a dromaesaurid is unlike any footprint presently described in the literature. Therefore, on the basis of the foot structure of known Early Cretaceous theropods, it seems most likely that *Megalosauropus* footprints were made by a coelurosaur or ceratosaur.

On the basis of common allometric proportions among coelurosaurs and ceratosaurs, we can determine that the animal that produced our footprints was about 9 ft (2.7 m) long and stood about 3 ft (0.9 m) high at its hips. The track maker of *Megalosauropus broomensis* was about twice this size. This range of sizes is more typical of ceratosaurs (including abelisaurids) than coelurosaurs. It is also similar to the proportions of animals, described from fragmentary osteological remains from the Arundel Formation of Maryland, that have been named *Coelurus gracilis* (Gilmore 1920), "*Allosaurus*" *medius* (Marsh 1888), and *Creosaurus potens* (Lull 1911b). *Coelurus gracilis* most recently has been placed in the Coelurosauria as a nomen dubium by Norman (1990). Molner (1990) has recently suggested that "*Allosaurus*" *medius* and *Creosaurus potens* are synonymous with each other and referred them both to *Dryptosaurus*, which he placed in Theropoda as incertae sedis. Any or all of these poorly known taxa conceivably could have made *Megalosauropus* footprints of the type described here.

Order Ornithopoda
Amblydactylus sp.

A fourth tridactyl dinosaurian footprint was recovered from the Bachman locality that can be ascribed to a different type of

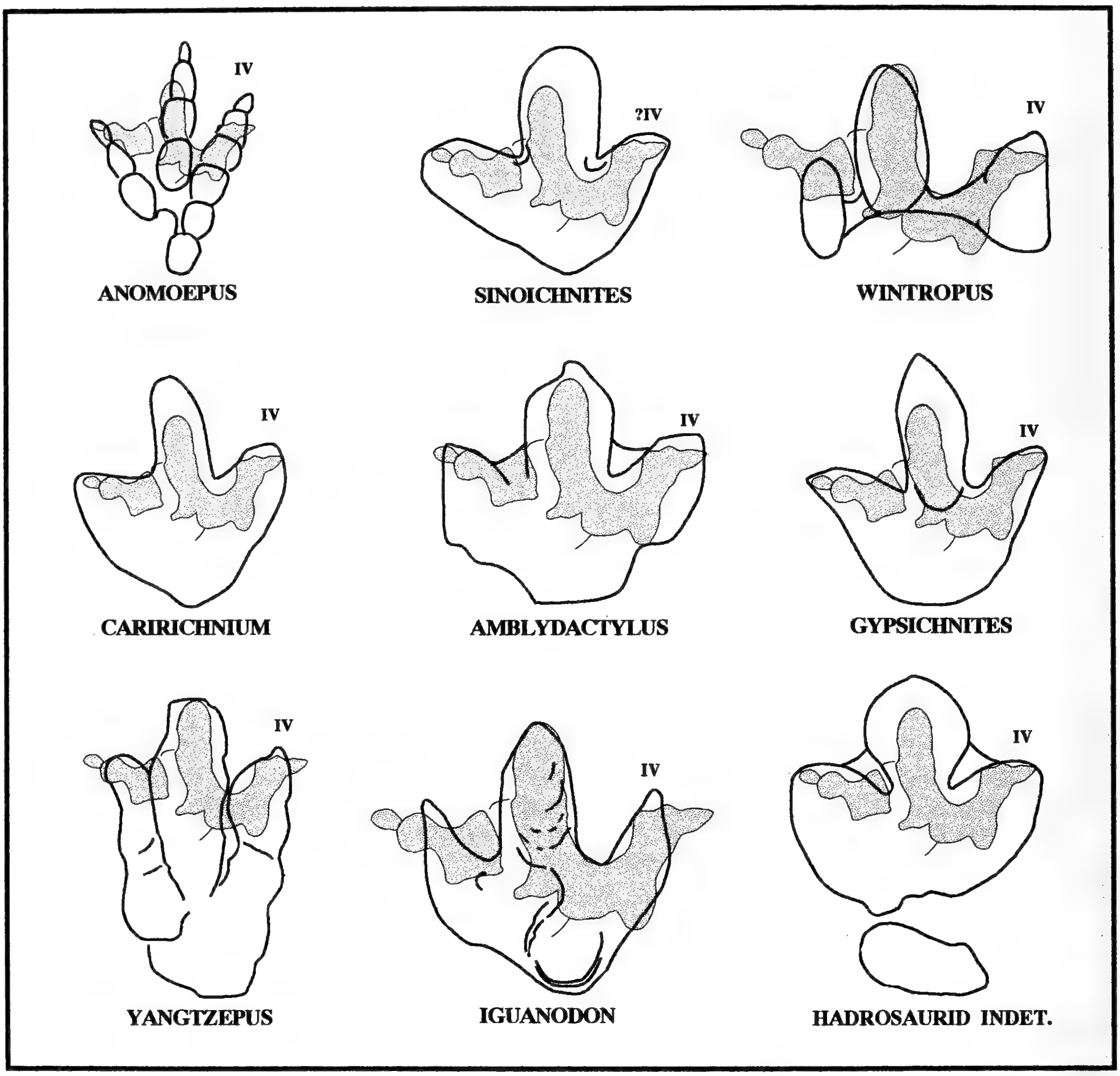

Fig. 13. Comparison of footprint interpretation in Fig. 12 with nine genera of ornithischian ichnotaxa described previously. Described footprints redrawn from Haubold (1971), Currie (1989), and Yang and Yang (1987).

animal than the previously described specimens. This counterpart filling of a footprint (USNM 475492, Fig. 11, Fig. 12) is smaller in absolute size, relatively much broader, and has a relatively much shorter medial toe than that present in *Megalosauropus*. When this print is compared to other described tridactyl dinosaur footprints, all reasonable comparisons are with nine ichnotaxa of ornithopods (Fig. 13). Within this group, the great divarication of digits II and IV and the extreme shortness of digit III compare closely only to footprints assigned to the ichnogenus *Amblydactylus*. Digit III on our specimen is less robust than on the example of *Amblydactylus* shown in Fig. 13, but not all specimens presently assigned to *Amblydactylus* have a robust digit III (for example, see Currie 1989:297). For this reason, and also because *Amblydactylus* has been described previously from Lower Cretaceous strata of similar age in the western United States and Canada, we assign our specimen to that genus with some confidence. There is only one described species, *Amblydactylus gethingi.* Our specimen is unusually small for that species, so we could either have a footprint of an immature individual or a specimen referable to a new species smaller than *A. gethingi.* In the absence of any other *Amblydactylus* material from the eastern United States, however, we cannot distinguish between these two possible explanations. Therefore, it is premature to attempt any positive species assignment within *Amblydactylus* based on this single footprint.

The extremely blunt-toed appearance of *Amblydactylus* immediately suggests that it represents an iguanodontid ornithopod. However, the small size of our specimen is very atypical for that family, unless it represents a juvenile of a normally much larger species. If our specimen represents an adult or nearly adult animal, the track maker more probably was a hypsolophodontid, tenontosaurid, dryosaurid, or camptosaurid ornithopod. The only skeletal ornithopod material identified from the overlying Arundel Formation has been referred to *Tenontosaurus* sp. (Weishampel 1990). Although *Tenontosaurus* originally was classified as an iguanodontid (Ostrom 1970), it more recently has been referred to the Hypsilophodontidae (Dodson 1980). Its foot structure has not yet been analyzed in detail, so detailed comparison between *Tenontosaurus* and *Amblydactylus* is not yet possible. However, known *Tenontosaurus* skeletal material represents animals 5 to 25 ft (1.5 to 7.5 m) in length (Dodson 1980). These are all larger than the track maker at our site which, on the assumption that it was an ornithopod, was only about 3 ft (1 m) long and had a hip height of about 1 ft (0.4 m).

Summary.—Footprints from an outcrop of the Lower Cretaceous Patuxent Formation provide the first direct evidence for land animals from that unit. Three types of animals are represented: an anuran (gen. et sp. indet.), a theropod dinosaur (*Megalosauropus*), and an ornithopod dinosaur (*Amblydactylus*). The discovery of these footprints establishes for the first time that diverse kinds of terrestrial vertebrates were present in Virginia during the Cretaceous Period. Their presence suggests that the scarcity of skeletal animal remains in the Patuxent is the result of depositional or postdepositional diagenetic processes that selectively destroyed bone, and not due to any scarcity of land animals among the Early Cretaceous Patuxent landscape.

Acknowledgments

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Literature Cited

Benton, M. J. 1987. Mass extinctions among families of nonmarine tetrapods: the data.—Memoires de la Societe Geologique de France, N.S. 150:21–32.

Berry, E. W. 1908. Geologic relations of the Cretaceous floras of Virginia and North Carolina.—Bulletin of the Geological Society of America 20:655–659.

———. 1910a. The epidermal characters of *Frenelopsis ramosissima.*—Botanical Gazette 1(1,2):305–309.

———. 1910b. A revision of the fossil plants of the genus *Nageiopsis* of Fontaine.—Proceedings of the United States National Museum 38(1738): 185–193.

———. 1910c. A revision of the fossil plants of the genera *Acrostichopteris, Taeniopteris, Nilsonia,* and *Sapindopsis* from the Potomac Group.—Proceedings of the United States National Museum 38(1769):625–644.

———. 1911a. Lower Cretaceous. Maryland Geological Survey, Johns Hopkins Press, Baltimore, Maryland, 622 pp.

———. 1911b. A revision of several genera of gymnospermous plants from the Potomac Group in Maryland and Virginia.—Proceedings of the United States National Museum 40(1821):289–318.

———. 1911c. A Lower Cretaceous species of Schizaeaceae from eastern North America.—Annals of Botany 25:193–198.

———. 1911d. A revision of the fossil ferns from the Potomac Group which have been referred to the genera *Cladophlebis* and *Thyrsopteris.*—Proceedings of the United States National Museum 41:307–332.

Brenner, G. J. 1963. The spores and pollen of the Potomac Group of Maryland.—Maryland Department of Geology, Mines, and Water Resources Bulletin 27:1–215.

———. 1967. The gymnospermous affinity of *Eucommiidites* Erdtman, 1948. Review of Palaeobotany and Palynology 5:123–127.

Carroll, R. L. 1988. Vertebrate paleontology and evolution. W.H. Freeman and Co., New York, 698 pp.

Clark, W. B., & B. L. Miller. 1912. Physiography and geology of the coastal plain province of Virginia, with chapters on the Lower Cretaceous, by Edward W. Berry, and the economic geology, by Thomas Leonard Watson.—Virginia Geological Survey Bulletin 4:1–274.

Currie, P. J. 1989. Dinosaur footprints of western Canada. Pp. 293–300 *in* D. D. Gillette and M. G. Lockley, eds., Dinosaur tracks and traces. Cambridge University Press, New York, 454 pp.

Dodson, P. 1980. Comparative osteology of the American ornithopods *Camptosaurus* and *Tenontosaurus.*—Memoires de la Societe Geologique de France 139:81–85.

Doyle, J. A. 1977. Spores and pollen; the Potomac Group (Cretaceous) angiosperm sequence. Pp. 339-363 *in* E. G. Kauffman and J. E. Hazel, eds., Concepts and methods of biostratigraphy. Dowden, Hutchison, and Ross, Stroudsburg, Pennsylvania, 658 pp.

———, & L. J. Hickey. 1975. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pp. 139-206 *in* C. B. Beck, ed., Origin and early evolution of angiosperms. Columbia University Press, New York, 341 pp.

———, & E. I. Robbins. 1977. Angiosperm pollen zonation of the continental Cretaceous of the Atlantic Coastal Plain and its application to deep wells in the Salisbury embayment. *In* Proceedings of the Eighth Annual Meeting of the American Association of Stratigraphers and Palynologists.—Palynology 1:43–78.

Fontaine, W. M. 1889. The Potomac or younger Mesozoic flora.—United States Geological Survey Monograph 15:1–375.

Galton, P. M., & J. A. Jensen. 1979. Remains of ornithopod dinosaurs from the Lower Cretaceous of North America.—Brigham Young University Geological Studies 25:1–10.

Glaser, J. D. 1969. Petrology and origin of Potomac and Magothy (Cretaceous) sediments, middle Atlantic Coastal Plain.—Maryland Geological Survey Report of Investigations 11:1–102.

Gilmore, C. W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus.*—Bulletin of the United States National Museum 110:1–154.

———. 1921. The fauna of the Arundel Formation of Maryland.—Proceedings of the United States National Museum 59:581–594.

Haubold, H. 1971. Ichnia Amphibiorum et Reptiliorum fossilium. Pp. 1-124 *in* O. Kuhn, ed., Handbuch der Palaoherpetologie, part 18, Gustav Fischer Verlag, Stuttgart.

Hickey, L. J. 1986. Summary and implications of the fossil plant record of the Potomac Group. *In* R. A. Gastaldo and T. W. Broadhead, eds., Land plants; notes for a short course.—Department of Geology, Auburn University,. Auburn, Alabama, Studies in Geology 15:162–181.

Hughes, N. F., & S. J. Moody. 1966. Descriptions of schizaeaceous spores taken from Early Cretaceous macrofossils.—Palaeontology 9(2):274–289.

Kranz, P. M. 1989. Dinosaurs in Maryland.—Maryland Geological Survey Educational Series No. 6, 34 pp.

Lull, R. S. 1911a. The Reptilia of the Arundel Formation. Pp. 173-178 *in* Lower Cretaceous Volume, Maryland Geological Survey, 622 pp.

———. 1911b. Systematic Paleontology of the Lower Cretaceous deposits of Maryland: Vertebrata. Pp. 183-211 *in* Lower Cretaceous Volume, Maryland Geological Survey, 622 pp.

Marsh, O. C. 1888. Notice of a new genus of Sauropoda and other new dinosaurs from the Potomac Formation.—American Journal of Science (Series 3) 35:89–94.

Martin, C. S., & M. K. Brett-Surman. 1992. A preliminary report on new dinosaur material from the Arundel Formation (Lower Cretaceous) of Maryland.—Journal of Vertebrate Paleontology 12(3 supplement):41A–42A.

Mixon, R. B., & W. L. Newell. 1977. Stafford fault system: structures documenting Cretaceous and Tertiary deformation along the Fall Line in northeastern Virginia.—Geology 5:437–440.

Molnar, R. E. 1990. Problematic Theropoda: "Carnosaurs." Pp. 306-317 *in* D. B. Weishampel, P. Dodson, and H. Osmolska, eds., The Dinosauria. University of California Press, Berkeley, California, 733 pp.

Norman, D. B. 1990. Problematic Theropoda: "Coelurosaurs." Pp. 280-305 *in* D. B. Weishampel, P. Dodson, & H. Osmolska, eds., The Dinosauria.

University of California Press, Berkeley, California, 733 pp.

Ostrom, J. H. 1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana.—Peabody Museum of Natural History Bulletin 35:1–234.

Reinhardt, J., R. A. Christopher, & J. P. Owens. 1980. Lower Cretaceous stratigraphy of the core. *In* Geology of the Oak Grove Core.—Virginia Division of Mineral Resources Publication 20(3): 31–52.

Shubin, N. H., & F. A. Jenkins, Jr. 1995. An Early Jurassic jumping frog.—Nature 377(6544):49–52.

Shuler, E. W. 1917. Dinosaur tracks in the Glen Rose limestone, near Glen Rose, Texas.—American Journal of Science (Ser. 4) 44:294–298.

Skog, J. E. 1982. *Pelletixia amelguita*, a new species of fossil fern in the Potomac Group (Lower Cretaceous).—American Fern Journal 72:115–121.

———. 1988. Reassignment of *Aspidium heterophyllum* to a new genus in the family Maloniaceae.—American Journal of Botany 75(8):1120–1129.

———. 1992. The Lower Cretaceous ferns in the genus *Anemia* (Schizaeaceae), Potomac Group of Virginia, and relationships within the genus.—Review of Palaeobotany and Palynology 70(4): 279–295.

Ward, L. F., W. M. Fontaine, A. Bibbins, & G. R. Wieland. 1905. Status of the Mesozoic floras of the United States.—United States Geological Survey Monograph 48:1–616.

Weishampel, D. B. 1990. Dinosaurian Distribution. Pp. 63-139 *in* D. B. Weishampel, P. Dodson, and H. Osmolska, eds., The Dinosauria. University of California Press, Berkeley, California, 733 pp.

Withington, C. F. 1975. Building stones of our nation's capital.—United States Geological Survey INF-74-35, 44 pp.

Wolfe, J. A. 1972. Phyletic significance of Lower Cretaceous dicotyledonous leaves from the Patuxent Formation, Virginia.—American Journal of Botany 59(6, part 2):664.

Yang, X. L., & Y. D. Yang. 1987. Dinosaur footprints from Mesozoic of Sichuan basin. Sichuan Scientific and Technical Publishing House, Chengdo, China, 30 pp.

Zweifel, R. G. 1992. Frogs and toads. Pp. 76-105 *in* H. G. Cogger and R. G. Zweifel, eds., Reptiles and amphibians. Weldon Owen Incorporated, San Francisco, California, 240 pp.

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A new species of the genus *Platymantis* (Amphibia: Ranidae) from Luzon Island, Philippines

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Abstract.—A new species, *Platymantis mimulus*, is described from Mt. Maquiling, southeastern Luzon Island, Philippines. This population was previously confused with juveniles of *Platymantis dorsalis* because of their very similar appearance, based on general morphological characters. However, the diminutive size of this species (19–24.5 mm snout-vent length for males and 22–27.5 mm for females) and its call distinguish it from *P. dorsalis* (26–35 mm snout–vent length for males and 33–43 mm for females) from Luzon Island.

Platymantis dorsalis and *Platymantis corrugatus* are the names that have long been applied to Philippine populations of common forest-floor *Platymantis*. They fit the following diagnosis: moderate in size, about 27 to 50 mm SVL at maturity; blunt or rounded terminal phalanges; small finger disks, not or not much wider than subtending phlanges (*dorsalis*) or blunt finger tips without disks (*corrugatus*); and distinctive patterns of dorsal ornamentation involving either short or long ridges and tubercles. Two other species, *Platymantis levigatus* with similar terminal phlanges but with moderate finger disks and smooth skin was described from Tablas Island (Brown & Alcala 1974), and *Platymantis spelaeus*, fitting the above diagnosis in terms of the finger disks and terminal phalanges but differing in its larger size and lack of ridges or tubercles in the dorsal ornamentation, was described in 1982 from Negros Island (Brown & Alcala 1982). These species are the *dorsalis* Group of Philippine *Platymantis* (Brown, Brown & Alcala 1997).

Recently, two of us (Alcala & Diesmos), while collecting on Mt. Maquiling, southeastern Luzon Island, noted that several small, *dorsalis*-like frogs were actually calling males and that the call differed from that of typical *dorsalis*. The diminutive size of this species differentiates it not only from *dorsalis* but also from the other three species noted above. A reexamination of more than 100 specimens assigned to *P. dorsalis* that were collected by E. H. Taylor on Mt. Maquiling in 1920 and 1921 (Taylor 1922a) and assigned by him to *P. meyeri* (= *dorsalis*), includes, among those treated as juveniles, a number of examples of this new, small species. At the time he noted that the large series possibly included more than one species. Inger (1954) also assigned all of the small-disked populations to *dorsalis* or *corrugatus*.

Materials and Methods

Holotypes of *Platymantis dorsalis*, *corrugatus*, *meyeri*, *levigatus*, and *spelaeus* as well as extensive early collections from some mountains on Luzon that have been referred to *dorsalis* were examined (Appendix A). Repositories for the types are British Museum of Natural History (BMNH), Museum National de Histoire Naturelle (MNHN), and California Academy of Sci-

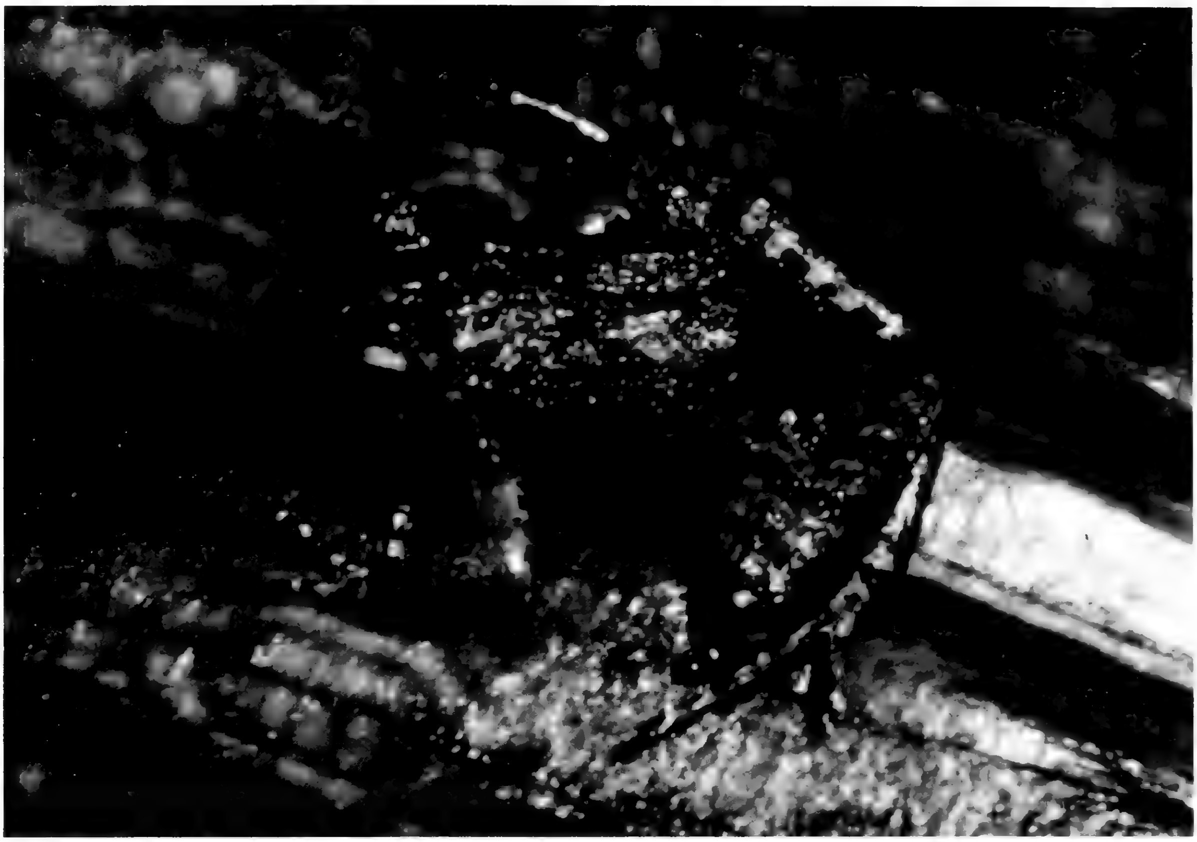

Fig. 1. *Platymantis mimulus* (CAS 201191, a paratype). Dorsal view showing characteristic ornamentation.

ences (CAS). The other specimens are at the CAS and the Philippine National Museum (PNM).

Morphometric characters: snout–vent length (SVL), head length (HL), head breadth (HW), snout length (SnL), diameter of eye (ED), diameter of tympanum (TD), tibia length (TiL), third finger length from proximal edge of basal tubercle (3FL) were measured to the nearest 0.1 mm using a Helios dial caliper. Other non-metric, morphological characters include: webbing of fingers and toes, skin ornamentation, shape of snout, color pattern, vomerine teeth, tubercles of hands and feet, and shape of terminal phalanges. Advertisement calls were recorded for both *dorsalis* and *mimulus*. They were analyzed, using a Kay Electrics SonaGraph (Model #550) and SIGNAL Sound Analysis System software.

Platymantis mimulus, new species
Fig. 1

Platymantis meyeri (part) Taylor, 1922b, p. 129

Holotype.—CAS 196362, an adult male, Mt. Maquiling, Los Banos, Laguna Province, Luzon Island, at an elevation of about 400 m, collected by A. C. Alcala, 30 Jul 1994.

Paratypes.—CAS 196359–61, 196363, 201176–77, 201189–94, 201483; PNM 5061 (same general locality as holotype), collected 1994–1996; CAS 61002–04, 61006–08, 61010, 61012, 61016–22, 61024, 61029–30, 61032, 61037, 61040–42, 61225–26, 61229–30, 61232, 61235–38, 61244–45, 61247–49, 61251–57, 61259–63, 61266–68, PNM 5060 Mt. Maquiling, Laguna Province, Luzon Island, collected by E. H. Taylor in 1920–21.

Diagnosis.—Differs from other Philippine species of small-disked *Platymantis* in the following combination of characters: small size, 19.0–27.5 mm SVL for 40 mature specimens (Table 1); finger disks about same size as those of toes, not or scarcely broader than digits proximal to disks; terminal phalanges blunt or rounded; and a few tubercles and some short, irregular folds on anterior dorsum.

Table 1.—SVL (mm) of adults for Philippine small-disked species of *Platymantis* (*n* = number).

Species	Male	Female
corrugatus	27.2–38.2 *n* = 23	35.3–47.7 *n* = 20
Holotype		44.7 (sex unknown)
dorsalis	26.7–35.0 *n* = 22	33.0–42.9 *n* = 13
Holotype		36.6
levigatus	29.5–30.3 *n* = 4	34.3–38.5 *n* = 3
Holotype		38.5
mimulus	19.0–24.5 *n* = 26	22.0–27.5 *n* = 14
Holotype	23.3	
spelaeus	41.5–46.9 *n* = 6	52.8–60.5 *n* = 11
Holotype		60.5

Description of holotype.—A mature male, measurements in mm: SVL 23.3, HL 8.1, HW 8.8, SnL 3.0, ED 2.6, TD 1.2, TiL 11.5, 3FL 3.3; dorsum grayish brown with some darker blotches; dorsum with a few scattered tubercles and some short ridges anteriorly; venter nearly smooth.

Description.—SVL 19.0–24.5 mm for 26 adult males and 22.0–27.5 mm for 14 mature females; HW 1.06–1.19 of HL and 0.37–0.43 of SVL; snout rounded; upper jaw only slightly protruding; SnL 0.32–0.42 of HL and 0.28–0.38 of HW; ED 0.72–0.94 of SnL and 0.25–0.30 of HW; tympanum exposed, TD 0.50–0.88 of ED; canthus rounded; lores moderately oblique, concave; vomerine teeth strongly protruding, patches widely separated; fingers not webbed; fingers with small, grooved disks; first, second and fourth fingers nearly equal in length; 3FL 1.00–1.24 of SnL and 0.13–0.16 of SVL; subarticular tubercles large, strongly protruding but not pointed; one row of large supernumerary tubercles; inner and middle metacarpal tubercles large, oval; outer small, elongate; hind limbs long, TiL 0.49–0.62 of SVL and HW 0.67–0.77 of TiL; toes webbed at base: first, second, and third to base of subarticular tubercle, to distal edge of basal subarticular tubercle on fifth and short of basal tubercle on fourth; disks of toes about equal to or slightly larger than those of fingers; subarticular tubercles as for fingers; inner metatarsal tubercle elongate; outer round, strongly protruding; plantar area smooth; tubercle at heel absent; dorsum, head, snout, eyelids, and limbs with a few to numerous tubercles; short, low, often irregularly shaped ridges on posterior head and anterior parts of dorsum; posterior belly and thighs with small granules; throat and chin smooth.

Color (in preservative).—Dorsal background tan to grayish-tan, with dense brown to blackish-brown blotching anteriorly and on head, occasionally a pale, vertebral stripe; venter creamy, densely blotched and flecked with brown anteriorly and on throat and chin, only lightly on belly; lips with dark bars; hind limbs and lower fore limbs with transverse light and dark bars; upper fore limbs uniform creamy or flecked with brown for recently preserved; color is faded to light brownish-tan with varied patterns of pale blotches for those in preservative for many years.

Color (in life).—Dorsal background pale brownish with variable darker blotches; lips and limbs with dark bars.

Reproduction.—Gravid females of *Platymantis mimulus* have 10–14 large, unpigmented eggs in the ovaries. No information is available on egg deposition site or development, but presumably the mode is direct development as is characteristic for other known species of the genus. Advertisement calls were heard and recorded. Other species such as *Platymantis montanus*, *P. dorsalis*, and *Philautus surdus* were also heard and recorded at the same time.

Etymology.—The name *mimulus* (noun in apposition) meaning "little mimic" refers to size at maturity and appearance when compared with individuals of the sympatric species, *Platymantis dorsalis*.

Comparisons.—The very small size of this species readily differentiates it from all previously described Philippine species with small, digital disks (Table 1). The oth-

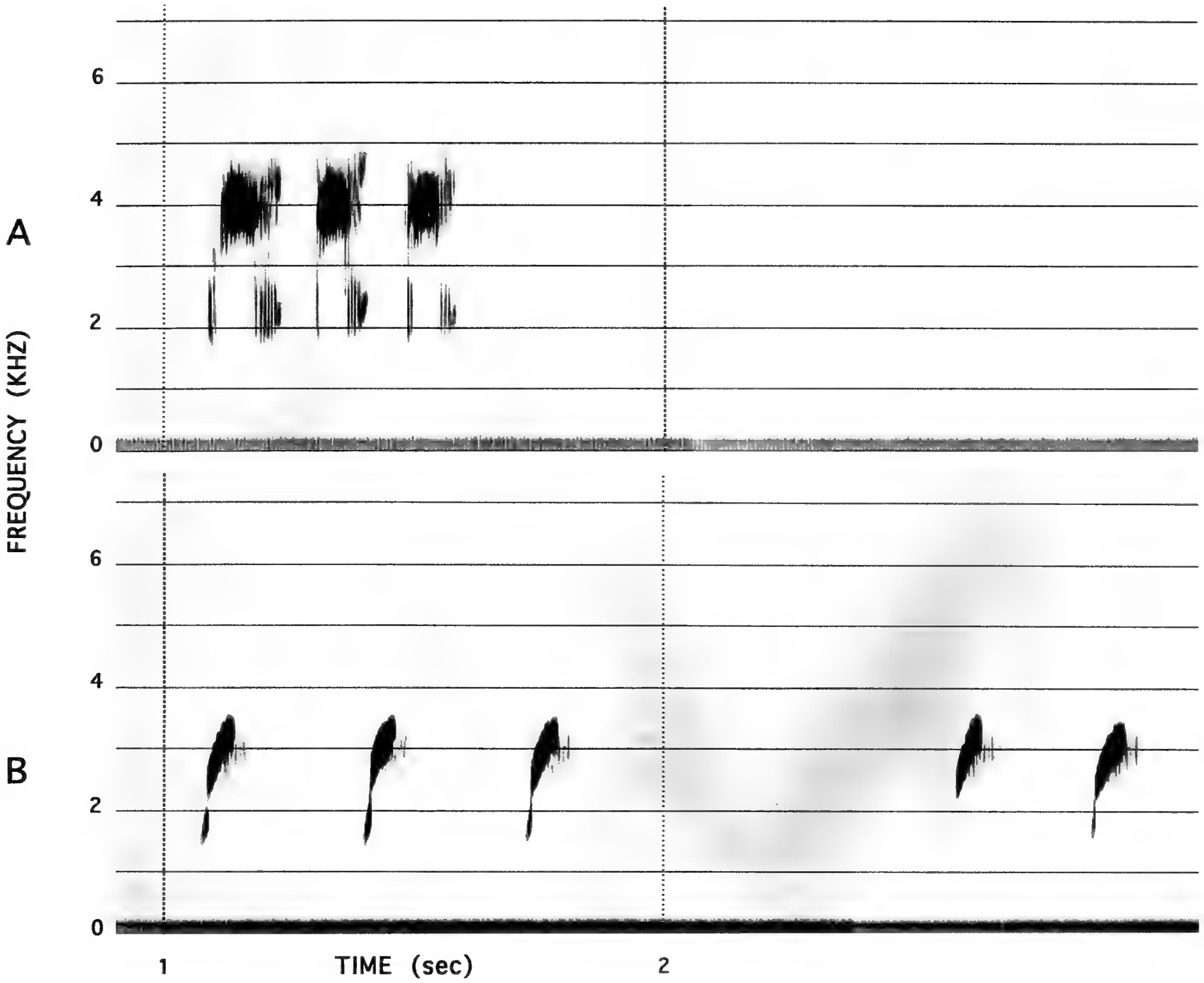

Fig. 2. Audiospectrograms of advertisement calls of (A) *Platymantis dorsalis* (CAS 201561) and (B) *Platymantis mimulus* (CAS 201191) both from Mt. Maquiling, Luzon Island.

er species similarly small in size for mature specimens (most notably *subterrestris*, *montanus*, and *polilloensis*) have large finger disks and broad "T"-shaped, terminal phalanges. In terms of the finger and toe disks, finger length, subarticular tubercles, and ornamentation of the dorsum and limbs, *mimulus* and *dorsalis* are very similar. Adults of *mimulus* have heretofore been confused with juveniles of *dorsalis* (Taylor 1922b).

Platymantis mimulus differs morphologically from *dorsalis* primarily in its much smaller size at maturity and minor differences in ornamentation of the dorsum. Their very similar general appearance contributed to the confusion of *mimulus* with juveniles of *dorsalis*. This is supported by the fact that the only significant, proportional difference, among those examined, is a slight difference in head shape (SnL/HW for *mimulus*: mean = 33.300, *SD* = 2.849, *n* = 20; for *dorsalis*: mean = 35.850, *n* = 20; *t* = 3.010, *df* = 38, P = 0.005).

These two species also have very different advertisement calls. The call of *Platymantis dorsalis* sounds like whet-whet (produced by whistling). The first part starts at about 1400 to 1500 Hz but is the dominent frequency between 2200 and 3600 Hz (Fig. 2A). The duration of each call ranges from about 0.056 to 0.075 seconds, and the intervals between calls from about 0.22 to 0.80 seconds for those recorded.

The call of *Platymantis mimulus* sounds like osek-sek-sek. The dominant frequency is 3300 or 3400 to 4500 or 4600 Hzl, sweeping up at the beginning from about 2000 Hz and at the end dropping back to the same level (Fig. 2B). The duration of each call is about 0.13 to 0.15 seconds. The intervals between calls, for those recorded, ranged from 0.20 to about 1.5 seconds.

Habitat.—*Platymantis mimulus* is recorded from original lowland forest and man-made forest (mostly exotic Mahogany species) on Mt. Maquiling at 200 to 650 m. It is a ground dwelling, forest species, as is *P. dorsalis*. Taylor (1922b) notes that young frogs of *dorsalis* (including his examples of *mimulus*) are usually found along streams, whereas adults of *dorsalis* are usually further away in the forest. Our recent samples of *mimulus* are mostly from the forest floor and thick grasses at the forest edge, one is from under a rotting log and one from inside a curled leaf on a shrub about 30–40 cm above ground.

Range.—Known thus far only from Mt. Maquiling in southern Luzon Island.

Discussion

The discovery of this diminutive *Platymantis* on Mt. Maquiling, Luzon Island, that has long been identified with juveniles of *P. dorsalis* indicates the need to reexamine other populations from throughout the islands that have been assigned to *P. dorsalis*. Field studies as well as reexamination of existing samples in numerous museums may be necessary in the effort to identify other mimics of *dorsalis*.

Other examples possibly already exist based on our evidence of populations of diminutive, dorsalis-like frogs on Mt. San Cristobal and Mt. Banahao at Lucban, Luzon. However, because of the small size of these samples (six males and two females and eight males respectively) and the need for verification of some field observations, we hold in abeyance our taxonomic assignment of these populations. Their calls appear different from the calls of either *P. mimulus* or *P. dorsalis*. However, we still need a recording of the voices for analysis and comparison and larger samples for information on intra-population variation.

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Literature Cited

Brown, W. C., & A. C. Alcala. 1974. New frogs of the genus *Platymantis* (Ranidae) from the Philippines.—Occasional Papers of the California Academy of Sciences No. 113:1–12.

———, & ———. 1982. A new cave *Platymantis* (Amphibia: Ranidae) from the Philippine Islands.—Proceedings of the Biological Society of Washington 95:386–391.

———, R. M. Brown, & A. C. Alcala. 1997. Species of the *hazelae* Group of *Platymantis* (Amphibia: Ranidae) from the Philippines, with Descriptions of Two New Species.—Proceedings of the California Academy of Sciences (in press).

Duméril, A. 1853. Mémoire sur les Batraciens Anoures, de la famille des Hylae-formes ou Rainettes, conprenant la description d'un genre nouveau et de onze espèces nouvelles.—Annales des Sciences Naturelles (3)19:135–179.

Guenther, A. 1873. Notes on some reptiles and batrachians obtained by Dr. Adolph Bernhard Meyer in Celebes and the Philippine Islands.—Proceedings of the Zoological Society, London 1873:165–172.

Inger, R. F. 1954. Systematics and zoogeography of the Philippine amphibia.—Fieldiana: Zoology 33:183–531.

Taylor, E. H. 1922a. Additions to the herpetofauna of the Philippine Islands.—I. Philippine Journal of Science 21:161–206.

———. 1922b. The herpetological fauna of Mt. Maquiling.—Philippine Agriculturist 11:127–139.

Appendix A
Specimens Examined

Cornufer dorsalis A. Duméril, 1853. Philippines (Java is an error): MNHN 4880 (holotype) and Mt. Isarog, Camarines Sur Province, Luzon Island: FMNH 251648, 251656, 251653, 251660, 251662–63, 251665, CAS 200414–416; Mt. Maquiling, Laguna Province, Luzon Island: CAS 61005, 61009, 61011, 61013, 61015, 61027–28, 61030–31, 61033, 61227, 61231, 61233–34, 61239–40, 61242–43, 61264–65, 196358, 196365–67, 200417–18, 200420–27; Mt. Banahao, Quezon Province, Luzon Island: CAS 61180, 201013–14, 201186–88.

Hylodes corrugatus A. Duméril, 1853. Philippines (Java is an error.): MNHN 4884 (holotype).

Platymantis meyeri Günther, 1873. Laguna del Bay, Luzon Island, Philippines: BMNH 1947.2.5–5 (holotype).

Platymantis levigatus Brown and Alcala, 1974. Tablas Island, Philippines: CAS 136097 (holotype) and CAS 136098 (same locality).

Platymantis spelaeus Brown and Alcala, 1982. southern Negros Oriental, Philippines: CAS 153469 (holotype) and CAS 153470–83, (same locality).

Platymantis mimulus new species. Mt. Maquiling, Luzon Island, Philippines: (See account of this species.)

Platymantis sp. Mt. San Cristobal and Mt. Banahao at Lucban (Mt Banahao massive), Luzon Island, Philippines: CAS 201009–11, 201178–85, 201197–200.

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A new species of chaenopsid fish, *Emblemariopsis ruetzleri*, from the western Caribbean off Belize (Blennioidei), with notes on its life history

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Abstract.—A new species of *Emblemariopsis* is described from the shallow waters around Carrie Bow Cay, Belize. *Emblemariopsis ruetzleri* differs from other species of the genus in having a combination of 14 pectoral-fin rays and a low supraorbital cirrus, whereas the other two species with 14 pectoral-fin rays (*E. pricei* and *E. randalli*) have no supraorbital cirri. Sexually mature males of the new species are dark headed and live in holes in coral (usually dead coral), whereas females and immature males are pale and surface dwelling. The new species is diminutive, with an average size of 14.5 mm SL for the 35 dark-headed and sexually mature territorial males collected from holes (largest specimen 19.4 mm SL).

While studying the life history of the sea fan blenny, *Emblemariopsis pricei* Greenfield (1975), at the Smithsonian Institution's marine laboratory at Carrie Bow Cay (Ellen Cay) on the Belize Barrier Reef, we routinely collected dark-headed territorial male specimens of *Emblemariopsis* that we found living in holes in coral. Nearly all of the dark-headed males collected from holes in living coral proved to be the territorial, sexually mature males of *E. pricei*; females, nonbreeding males, and immatures of *E. pricei* are found on sea fans and coral surfaces (Tyler & Tyler 1997).

Nearly all of the dark-headed males collected from holes in dead coral differed from *E. pricei* by being somewhat less darkly pigmented in preservation (but not in life as seen with only the front of the head protruding from the hole), by having a low, simple supraorbital cirrus, and by being smaller in average size. This smaller species, which has 14 pectoral-fin rays like *E. pricei* (and *E. randalli* Cervigon, 1965), is an undescribed species. Although dark-headed males of the new species usually are found in holes in dead coral (rarely in live coral), the two females captured to date are pale and inhabit the algal turf in the same dead coral habitat where holes containing mature males are found. The only known pale, immature male was found on the surface of a live coral, near dead coral containing a hole with a dark-headed male.

We describe below this diminutive species whose life history and shelter specificity we continue to investigate.

Methods

Abbreviations: ANSP = Academy of Natural Sciences of Philadelphia; CBC = Carrie Bow Cay, Belize; SL = standard length; USNM = United States National Museum specimens at the National Museum of Natural History, Smithsonian Institution.

All specimens were collected using a weak solution of quinaldine sulfate (1 gram per 500 ml water). Those from holes were trapped in clear plastic tubes placed upright over the opening of the holes immediately after the solution was squirted into them, driving out the partially narcotized and disoriented specimens. Those collected on the surface had been partially narcotized by the solution dispensed around them before being caught in plastic tubes or plastic bags.

Emblemariopsis ruetzleri, new species

Diagnosis.—The new species differs from all other species of *Emblemariopsis* by having a combination of 14 pectoral-fin rays and a supraorbital cirrus (low and simple).

The two other species of *Emblemariopsis* with 14 pectoral-fin rays (*E. randalli* and *E. pricei*; see Tyler & Tyler 1997 for meristics and other differences between these two species) do not have supraorbital cirri. Of the seven species of *Emblemariopsis* with 13 pectoral-fin rays, a supraorbital cirrus is either absent (*E. bahamensis* Stephens, *E. bottomei* Stephens, *E. diaphana* Longley) or present (*E. leptocirris* Stephens, *E. occidentalis* Stephens, *E. signifera* (Ginsberg), *E. tayrona* (Acero)) (see Stephens 1963, 1970, for meristics of the first six species and Acero 1987, for the last).

Type locality.—All 38 specimens are from the reefs around Carrie Bow Cay (or Ellen Cay on some hydrographic charts), Belize (see below for details), on the Belize Barrier Reef, 16°48.15′N, 88°04.91′W, 18 km off the nearest point on the mainland (Sittee Point, south of Dangriga), 1–8 m depth.

Type specimens.—The 35 dark-headed, sexually mature, hole-dwelling males range from 11.9–19.4 mm SL, average 14.5 mm SL; the single pale, immature, surface-dwelling male is 14.6 mm SL; and the two females are 12.3–13.4 mm SL.

Holotype: USNM 337496, 14.4 mm SL, dark-headed male from hole in dead coral, spur and groove formation just east of CBC, 5 m, 1 Mar 1995, J. and D. Tyler, A. Sundberg.

Paratypes: Dark-headed males from holes in coral: USNM 337497, 1, 11.9 mm SL, from hole in dead coral, same data as holotype (notes on color in life). USNM 337509, 1, 19.4 mm SL (cleared and stained), from hole in dead coral, patch reef about 800 m southwest of CBC, 8 m, 12 Mar 1994, J. and D. Tyler, A. Sundberg. USNM 337510, 2, 13.5–14.3 mm SL (cleared and stained), from holes in dead coral, spur and groove formation just east of CBC, 7 m, 7 Mar 1995, J. and D. Tyler, A. Sundberg. USNM 325490, 1, 13.6 mm SL, from hole in living *Porites astreoides*, surge channel in forereef along east side of CBC, 2.5 m, 19 Mar 1991, R. and K. Clarke (the only hole-dwelling male from living coral). USNM 325491, 2, 13.4–16.0 mm SL, from holes in dead *Acropora palmata*, back of reef crest along east side of CBC, 1 m, 21 Mar 1991, R. and K. Clarke. USNM 337499, 5, 12.9–15.7 mm SL, from holes in different but close-by large heads of dead coral (four from the sides of the head and one from the top) marked with ribbons for subsequent observations after removal of original occupants, patch reef just northwest of CBC, 1.5 m, 3 Mar 1995, J. and D. Tyler. USNM 337498, 1, 15.2 mm SL, replacement from one of the holes from which individuals were removed on 3 Mar 1995 (see preceding entry), patch reef just northwest of CBC, 1.5 m, 7 Mar 1995, J. and D. Tyler. USNM 337500, 1, 12.6 mm SL, from hole in dead coral marked with ribbon for subsequent observations after removal of original occupant (no replacements seen during next seven days of observations), patch reef just northwest of CBC, 1 m, 28 Feb 1995, J. and D. Tyler (notes on color in life). USNM 337501, 1, 13.6 mm SL, from hole in dead coral rubble, patch reef at Curlew Cay, southeast of CBC, 5 m, 2 Mar 1995, J. and D. Tyler, A. Sundberg (notes on color in life). USNM 337502, 1, 12.1 mm SL, from hole in dead part of otherwise living *Montastrea* sp., patch reef about 800 m southwest of CBC, 8 m, 3 Mar 1995, J. and D. Tyler, A. Sundberg. USNM 337503, 1, 17.6 mm SL, from hole in dead part of otherwise living *Diplo-*

ria sp., spur and groove formation just east of CBC, 5 m, 15 Mar 1995, J. and D. Tyler, A. Sundberg. USNM 337504, 2, 13.6–15.0 mm SL, from holes in dead coral (openings of 2.7 and 3.0 mm diameter; burrow with the 3.0 mm opening collected), patch reef just northwest of CBC, 1 m, 13 Mar 1994, J. and D. Tyler. USNM 337505, 1, 12.5 mm SL, from hole in dead part of otherwise living *Montastrea* sp., patch reef about 1000 m southwest of CBC, 8 m, 6 Mar 1994, J. and D. Tyler, A. Sundberg. USNM 337506, 4, 14.2–17.0 mm SL, from holes in dead coral, patch reef just northwest of CBC, 1 m, 12 Mar 1994, J. and D. Tyler. USNM 337507, 2, 12.9–13.0 mm SL, from holes in dead coral (both openings 2.5 mm diameter), spur and groove formation just east of CBC, 8 m, 13 Mar 1994, J. and D. Tyler, A. Sundberg. USNM 337508, 1, 15.3 mm SL, from hole in dead *Acropora palmata* (opening of 5.3 mm diameter; burrow collected), patch reef just northwest of CBC, 1 m, 6 Mar 1994, J. and D. Tyler. USNM 341534, 1, 16.6 mm SL, from hole in dead part of otherwise living *Montastrea* sp., patch reef just northwest of CBC, 1 m, 16 Mar 1996, J. and D. Tyler (see below for a pale male collected nearby on the surface, USNM 341535). USNM 341536, 1, 15.2 mm SL, from hole in dead part of otherwise living *Montastrea* sp., cut in back reef just east of south end of CBC, 1 m, 21 Mar 1996, J. and D. Tyler (notes on color in life). USNM 341537, 1, 13.8 mm SL, from hole in dead part of otherwise living *Montastrea* sp., patch reef just northwest of CBC, 1 m, 24 Mar 1996, J. and D. Tyler (see below for a female collected at the same time nearby on the surface, with the same catalogue number). ANSP 173572, 1, 15.6 mm SL, from hole in dead part of otherwise living *Montastrea* sp., patch reef just off south end of CBC, 1 m, 6 Mar 1994, J. and D. Tyler, R.E. Clark (notes and photograph in laboratory of color in life). ANSP 173573, 1, 13.1 mm SL, from hole in dead coral rubble, spur and groove formation just east of CBC, 3 m, 12 Mar 1994, R. and K. Clarke. ANSP 173574, 2, 13.4–15.3 mm SL, from holes in dead *Acropora palmata*, spur and groove formation just east of CBC, 5 m, 15 Mar 1994, J. and D. Tyler.

Pale male from surface of coral: USNM 341535, 1, 14.6 mm SL, from surface of living part of *Montastrea* sp., within 20 cm of hole in dead part of coral from which a dark-headed male was collected just moments before (see USNM 341534, above), patch reef just northwest of CBC, 1 m, 16 Mar 1996, J. and D. Tyler.

Females: USNM 325489, 1, 12.3 mm SL, from surface of algal-turf covered coral boulder, back of reef crest along east side of CBC, 1 m, 18 Mar 1991, R. and K. Clarke. USNM 341537, 1, 13.4 mm SL, from surface of algal-turf area in dead region of a mostly living *Montastrea* sp., within 10 cm of hole in dead part of coral from which a dark-headed male was collected just moments before (see above under same catalogue number), patch reef just northwest of CBC, 1 m, 24 Mar 1996, J. and D. Tyler.

Description.—See Table 1 for meristics and Table 2 for measurements.

Snout short, slightly less than diameter of orbit. Supraorbital cirrus short, simple; cirrus length usually less than one-half pupil diameter (and about equal to length of nasal cirrus), sometimes about one-half pupil diameter, and about equal to pupil in largest specimen. Anterior nasal opening tubular, with a simple cirrus projecting from rear edge; cirrus length about equal to length of tubular part. Depth of head about 6–7 times in SL. Depth of body at anal-fin origin about 7–8 times in SL. Anterior two or three dorsal-fin spines moderately elongate, second spine usually longest (but often the first longest), greatest spine-length about 2 times in head length; interradial membrane more deeply incised in the two females and the pale surface-dwelling male than in the dark-headed hole-dwelling males. Pelvic fins shorter than pectoral fins; pelvic rays extending beyond incised membranes, third ray about one-third to two-thirds (usually

Table 1.—Meristics of *Emblemariopsis ruetzleri* new species.

Dorsal-fin spines		Dorsal-fin rays				Anal-fin rays*		
XX	XXI	10	11	12	13	19	20	21
21	7	1	23	3	1	7	23	2

Pectoral-fin rays†			Caudal vertebrae‡		
13	14	15	25	26	27
7	56	3	1	16	1

* All specimens with two anal-fin spines.

† Two specimens with 13 rays on both sides; three specimens with 13 rays on one side and 14 on the other; one specimen with 15 rays on both sides; one specimen with 14 rays on one side and 15 on the other.

‡ The number of abdominal vertebrae was not clearly visible on radiographs, but all three cleared and stained specimens have 11 abdominal vertebrae, and we presume that there are usually a total of 37 veterbrae.

one-half) length of second ray; pelvic spine short and only visible in cleared and stained specimens.

Dorsal fin usually XX,11; anal fin usually II,20; pectoral fin usually 14 on both sides; pelvic fin I,3 (spine inconspicuous); caudal fin with 13 segmented unbranched rays and 2-4 procurrent rays above and below.

About 15–20 teeth in upper jaw, with fifth, sixth, and sometimes seventh from front enlarged on both sides. About 17–19 teeth in lower jaw, the fifth to eighth or ninth from front enlarged on both sides. About 7–8 large palatine teeth, in a crescent. About 7–8 moderate-size vomerine teeth. Gill rakers two above and six below the angle (from a cleared and stained specimen).

There being no standardized terminology for the cephalic sensory pore system widely accepted for blennies, we prefer to illustrate the major features in the diagnostically important orbital and temporal regions (Fig. 1) rather than to verbally describe them. We follow the terminology used for *Emblemariopsis* and related genera by Stephens (1970) in simply noting that there is a sin-

Table 2.—Measurements of *Emblemariopsis ruetzleri* new species, in percent of standard length (SL).

	Dark-headed males from holes in coral					
Character	Number of specimens	Range in values in percent of SL	Average value	Value for holotype	Pale male from coral surface (one specimen)	Pale female from algal turf (one specimen)*
Head length	19†	23.3–27.8	25.8	25.7	24.7	26.1
Head depth	18	13.7–16.3	14.7	13.9	13.7	14.9
Snout length	16	4.6–6.1	5.3	5.9	5.5	6.0
Orbit diameter	15	6.1–7.3	6.6	6.9	6.8	7.1
Interorbital width	15	2.6–3.6	2.9	2.8	3.1	3.0
Body depth	15	10.4–15.0	12.8	11.8	11.6	13.1
Pelvic-fin spine length	3‡	1.5–2.1	1.8	—	—	—
First pelvic-fin ray length	12	9.0–11.3	10.5	10.4	9.2	9.0
Second pelvic-fin ray length	12	12.8–15.4	14.3	14.6	13.7	13.4
Third pelvic-fin ray length	11	7.2–9.2	8.4	8.7	7.5	7.5
Pectoral-fin length	12	18.4–21.6	19.8	20.1	21.2	26.1
Spiny dorsal-fin height	17	10.8–14.0	12.6	12.5	14.4	15.7

* A second female specimen is too poorly preserved and twisted for most measurements to be meaningful, but it has a relatively high spiny dorsal fin at 15.4% SL and a long pectoral fin of 26.0% SL like the female in the table.

† RANGE 12.1–19.4 mm SL.

‡ Cleared and stained specimens, 13.5–19.4 mm SL.

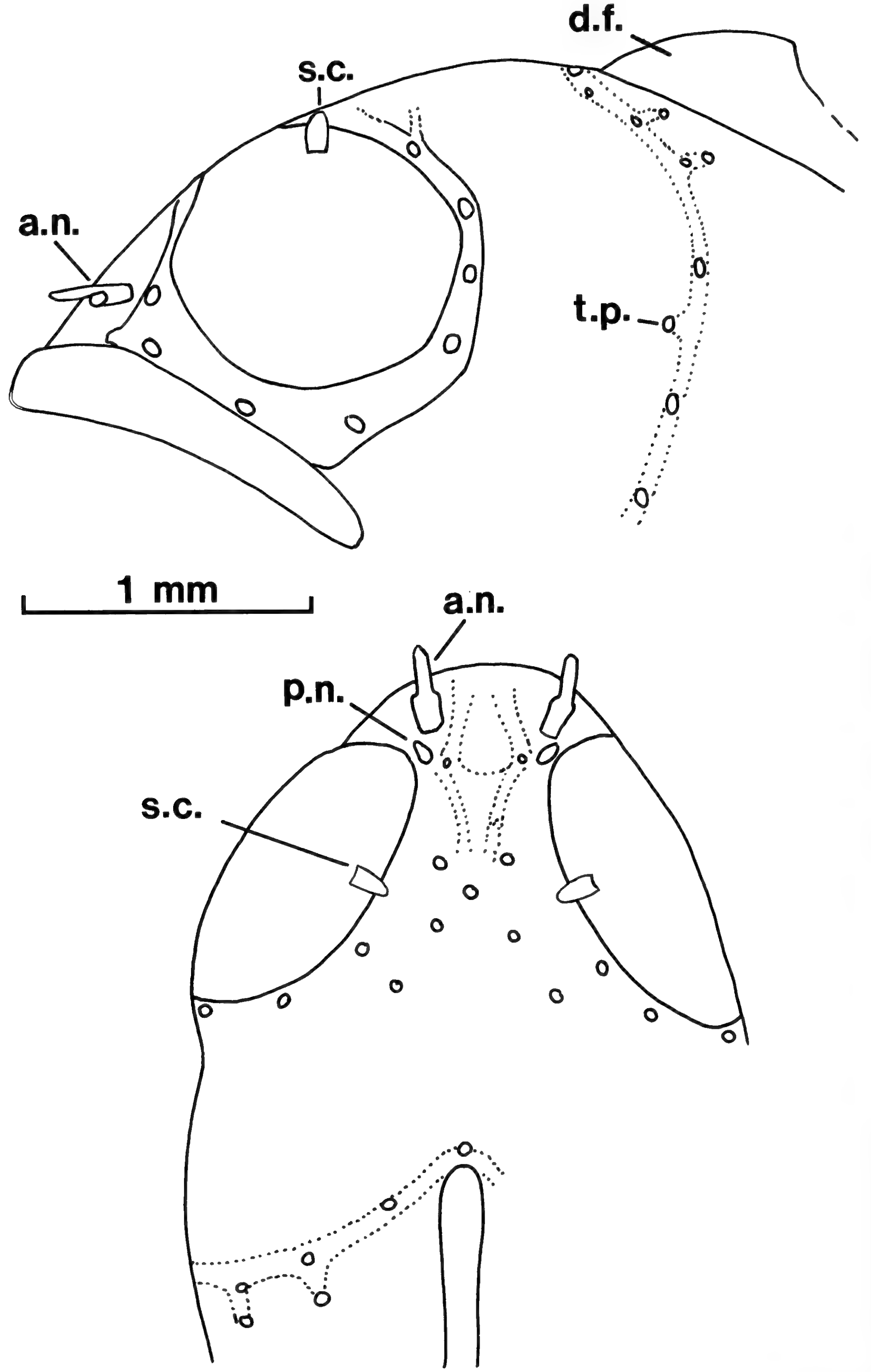

Fig. 1. Cephalic sensory pore system in *Emblemariopsis ruetzleri*, based mostly on USNM 337505, 12.5 mm SL: above, pores of the infraorbital and the preopercular-temporal series; below, pores in the interorbital area and the more posterodorsal ones of the infraorbital series and those of the preopercular-temporal series evident in dorsal view. Scale line applies to both dorsal and lateral views. Abbreviations: a.n. = anterior nostril; p.n. = posterior nostril; d.f. = dorsal fin; t.p. = temporal pore; s.c. = supraorbital cirrus. There are no postorbital pores.

Fig. 2. Living dark-headed male of *Emblemariopsis ruetzleri* from a hole in a dead part of an otherwise living head of *Montastrea* sp., ANSP 173572, 15.6 mm SL, 35 mm photograph of specimen under anesthesia in the lab, showing a typical amount of melanophore development for mature males; patch reef just off south end of Carrie Bow Cay, Belize, 1 m.

gle temporal pore (Fig. 1, lateral view) and that postorbital pores are absent.

Coloration of dark-headed, hole-dwelling males in life (Fig. 2): The following description is based on notes from five males (see list of type specimens) collected on separate occasions. Each specimen was kept alive under light anesthesia with quinaldine for several hours in the laboratory before preservation. These males have low anal mounds, prominent genital papillae, and elongate, relatively plump testes.

The head of living males is uniformly jet black when observed protruding from holes in coral. However, immediately upon emergence from the hole after application of quinaldine and capture in a clear plastic test tube, the head notably lightens and small dark spots predominate over a yellowish green background. The rest of the body is relatively transparent except for dark spotting on the spinous dorsal fin, scattered black and white markings on the bases of the dorsal and anal fins, yellowish green suffusions over parts of the body, and a prominent internal pattern of dark and light bars on the upper abdomen and along the vertebral column and pterygiophores.

The entire head is covered with numerous small black spots; those on the preopercular region of the cheek tend to be larger than those on the snout and the opercle, and two larger black spots are especially prominent on the lower jaw. All of these black spots (whose expansion in undisturbed specimens presumably leads to the jet black head seen protruding from the hole of the burrow) are underlain by a yellowish to gold-green coloration, with some patchy areas of chalky white. There are also a few discrete chalky white markings in the following locations: one is along the lower rear of the orbit; one is just above and behind this mark; and several other smaller ones are scattered around the cheek region, including one or two that seem to outline cephalic lateral-line pores. The black pupil is surrounded by a narrow ring of golden yellow, outside of which the rest of the eye is creamy with gold-brown suffusions, bluish to purplish to yellow-green iridescence, and irregular streakings of black. The supraorbital cirrus is creamy with black spots or streakings; the nasal cirrus is sometimes dark spotted. As seen dorsally on the head, there is a large, roundish area in the occipital region from the rear of the eyes to the origin of the spinous dorsal fin that has a creamy basal color overlain by golden yellow, with numerous small spots of grayish blue to greenish iridescence and even smaller and fewer black dots.

The black spotting of the head broadly continues posteriorly onto the lateral side of the body to the level of the pectoral-fin base; dorsal to the pectoral-fin base the region of spotting tapers posteriorly variously to the base of about the eighth to the last dorsal-fin spine. There is a relatively unpigmented region between this tapered region of spotting and the upper edge of the rear half of the abdominal cavity.

The fleshy base of the pectoral fin has black spots about as large as those on the preopercular region. The basal one-fifth to one-third of the pectoral-fin rays has chalky white markings overlain with much smaller black spots; sometimes there is one large irregular white mark and/or sometimes several more rounded ones. [illegible] more distal regions of the pectoral-fin rays are pale. The rest of the thoracic area toward the isthmus and the lower half of the abdomen behind the pectoral-fin base are covered by small black spots.

The dorsal half of the abdominal cavity from behind the pectoral-fin base has a distinctive pattern of internal coloration. There is a chalky white band that is transected in the middle by a vertical saddle-shaped bar of blackish to dark yellow-green pigment (color partially dependent on both the condition of the living specimen and the angle of observation), with the dark saddle being wider dorsally than ventrally. Ventral to this chalky, saddled, upper region of the abdominal cavity, the lower abdomen is slightly yellowish with small black external spots. There is a dark spot at the front of the anal region and a white spot just behind it.

The membranes between the first three dorsal-fin spines are chalky white with black spots and, especially basally, black reticulations. There are scattered black spots covering most or parts of the otherwise pale interradial membranes posterior to the third dorsal-fin spine variously to the eighth to last dorsal-fin spine. The density of the spotting and its posterior extent is a function of the degree of overall body darkness. Posterior to the darkened part of the spinous dorsal fin, the interradial membranes are usually without many melanophores and become more uniformly pale. In the paler parts of the dorsal fin, each spine or soft ray has specks or slightly larger dots of black along much of the length of the element or immediately alongside it but not broadly on the interradial membrane; there also are a few white spots along some of these fin elements. At the base of each dorsal-fin element is a discrete spot of either black or white, with the two colors usually alternating with one another on the bases of successive elements.

The anal fin has essentially no pigmentation on the interradial membranes, but there are black specks along most of the fin rays. At the base of each anal-fin spine and ray is a discrete spot of either black or white, alternating on successive elements just as in the dorsal fin (with the base of the first ray following the two spines usually with the first black spot).

The caudal fin is pale except for two white elongate marks, one along the bases of several rays in the upper lobe and one along the bases of several rays in the lower lobe, and several smaller white spots of variable occurrence more distally on the fin.

Besides the external pigmentation patterns described above, there is little other surface pigmentation on the body. The transparent body is, however, distinctly patterned by internal markings associated with the vertebrae and pterygiophores, as well as by those of the abdominal cavity. There are rusty pink patches of internal color on the top of the head and the top of the iris.

The vertebral column has prominent dark markings that alternate with shorter white marks to form a continuous series along the top of the centra. The dark markings range in color from blackish to dark golden green (depending on specimen condition and angle of observation), and the white markings are creamy. The white markings span the tops of two centra and have no ventral extensions. The dark markings usually span three or four centra, and, at their anterior and posterior ends, they have ventral extensions along the front of the centra that continue down the haemal spines. These dark markings extend only partially down the length of the haemal spines in the region just behind the level of the anus, but they extend most of the way down the lengths of more posterior haemal spines. The net

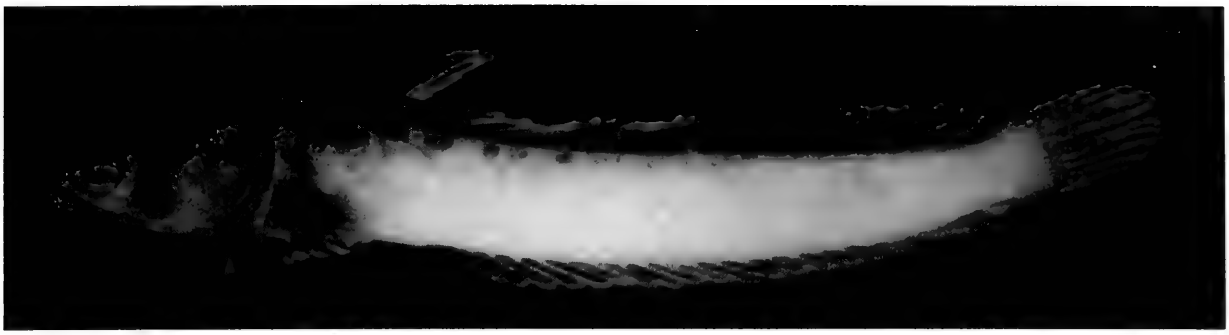

Fig. 3. Preserved holotype of *Emblemariopsis ruetzleri* from a hole in a dead coral of unidentified species, USNM 337496, 14.4 mm SL; spur and groove formation just east of Carrie Bow Cay, Belize, 5 m.

effect is of short white horizontal markings separating longer dark horizontal markings along the top of the vertebral column, with dark ventral extensions onto every other or every third or fourth haemal spine.

Coloration of preserved dark-headed males (Figs. 3, 4): With preservation, the transparent body becomes increasingly opaque, and nearly all of the internal coloration of the vertebral column, pterygiophores, and abdominal cavity is obscured; the surface melanophores form nearly all that remains of the pattern seen in life. Of the internal coloration, only rusty or pink

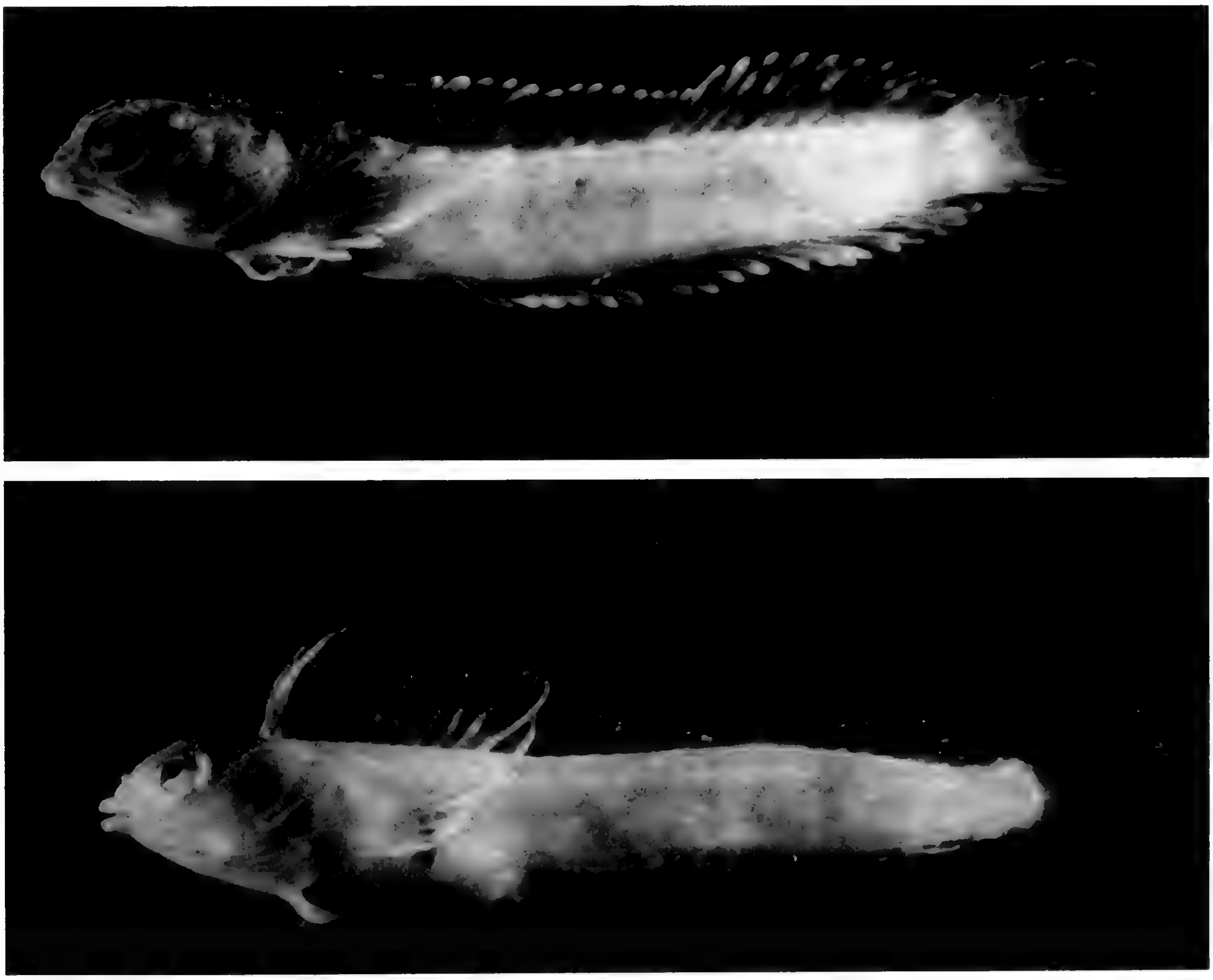

Fig. 4. Preserved specimens of a 13.8 mm SL dark-headed male (above) and a 13.4 mm SL female of *Emblemariopsis ruetzleri* collected within moments of one another, the male from a hole in a dead part of an otherwise living head of *Montastrea* sp. and the female from the surface of the algal turf within 10 cm of that hole, both specimens USNM 341537; patch reef just northwest of Carrie Bow Cay, Belize, 1 m.

Fig. 5. Preserved pale male of *Emblemariopsis ruetzleri* from the surface of the living part of a mostly living head of *Montastrea* sp. (collected within moments of a dark-headed male from a hole 20 cm away in a dead part of the coral head), USNM 341535, 14.6 mm SL; patch reef just northwest of Carrie Bow Cay, Belize, 1 m.

patches on the top of the head and the top half of the iris usually are evident. All of the chalky white and greenish yellow to grayish blue iridescent undertones of live specimens are lost after months in preservative, except that sometimes there are remnants of the chalky markings on the cheek and pectoral-fin base. The pattern of dark melanophores on the surface remains as described above in living specimens, with the darkest males having closely spaced spots of dark pigment over most of the head and anterior half of the body, on the entire course of the spinous dorsal fin, and along the bases of every few dorsal- and anal-fin rays.

Coloration of live and preserved females and an immature male (Figs. 4, 5): When alive, females (two specimens collected, with high anal mounds and no genital papillae) and immature males (one specimen collected, with low anal mound, genital papilla low and not protruding, and testes thin) have transparent bodies that show all of the internal markings described above for dark-headed males. However, the only external coloration evident in life comprises some small black and white alternating spots along the bases of the dorsal-/and anal-fin elements (as above for dark-headed males) and some coloration between the first two or three dorsal-fin spines (details not specified in our notes). In preservative, the opaque body obscures all of the internal markings on the vertebral column, pterygiophores, and abdominal cavity. Some rusty pink coloration is found on the head in the roundish occipital area, top half of the eye, and sometimes in the opercular region. External melanophores (sometimes rusty in color rather than black) evident in preserved specimens are as follows: dark spots along the bases of some of the dorsal-fin and anal-fin elements; lightly scattered spots along the course of the dorsal- and anal-fin elements laterally but not on the interradial membranes; irregular bands of speckling in the interradial membrane between the first two or three dorsal-fin spines (mostly as an irregular band just internal to the distal edge of the membrane, with some chalky color also present between the second and third spines in the larger female); and a few spots along the upper jaw and on the underside of the lower jaw.

Sexual dimorphism.—In addition to mature dark-headed males of *E. ruetzleri* differing from pale females and immature males in coloration, there is dimorphism in the length of the pectoral fin and in the height of the elevated anterior part of the spinous dorsal fin. In both female specimens, the pectoral fin (26.0–26.1% SL) is longer and the anterior spinous dorsal-fin rays (15.4–15.7% SL) are higher than in mature males (18.4–21.6% SL for the pectoral fin and 10.8–14.0% SL for the dorsal fin). In the single immature pale male specimen, the pectoral-fin length (21.2% SL) is similar to the high end of the range of mature males, and the elevation of the anterior elements of the spinous dorsal fin is only slightly greater than that of mature males.

In mature dark-headed males the interradial membrane of the anterior region of the dorsal fin is not greatly indented between the spines, but in both of the female specimens and in the immature male specimen the interradial membrane is deeply incised (to about one-half of its greatest depth) between the third and fourth dorsal spines. This difference between mature males and females in the depth of the indentation between the third and fourth spines also is evident in *Emblemariopsis occidentalis* (see figures in Böhlke & Chaplin 1968:548, incorrectly identified as *Pseudemblemaria signifera*, as shown by Stevens 1970).

Characters supporting generic allocation.—Although Acero (1987) recommended synonymizing *Emblemariopsis* with *Coralliozetus*, we follow the ongoing cladistic-based revisions of various chaenopsids by Hastings (e.g., 1992, 1997) and Hastings & Springer (1994) in recognizing the distinctiveness of *Emblemariopsis* within a *Coralliozetus*-like clade.

The most recent revision of the taxonomy of the species of *Emblemariopsis* and related genera is that of Stephens (1970). *Emblemariopsis ruetzleri* has all of the diagnostic features given by Stephens for that genus (Stephens 1970:283; based on seven species, *E. bahamensis*, *E. bottomei*, *E. diaphana*, *E. leptocirris*, *E. occidentalis*, *E. signifera*, *E. randalli*, i.e., all but *E. pricei*, *E. ruetzleri*, and *E. tayrona*). These features are as follows (condition of *E. ruetzleri* given in parenthesis if there is variation in the generic character): no spinous projections on the frontal or parietal; nasals separate; snout short; pelvics shorter than pectorals; pelvic fin with membranes deeply incised between first two rays and last pelvic ray short; one or two temporal pores (one in *E. ruetzleri*); no postorbital pores; dorsal fin not sail-like; dorsal fin XIX–XXII, 10–14 (usually XX, 11 in *E. ruetzleri*), anal fin II, 19–23 (usually II, 20 in *E. ruetzleri*); pectoral rays 12–14 (usually 14 in *E. ruetzleri*); no anterior flap on first dorsal spine; first three dorsal spines closely spaced; 5–9 moderate- to large-size teeth on palatine (7–8 large-size teeth in *E. ruetzleri*); 6–12 small- to moderate-size teeth on vomer (7–8 moderate-size teeth in *E. ruetzleri*); supraorbital cirrus either present and short or absent (short in *E. ruetzleri*); nasal cirrus simple or absent (simple in *E. ruetzleri*); sexual dimorphism well developed or absent (dimorphism in coloration, pectoral-fin length, and height of spinous dorsal fin in *E. ruetzleri*).

In conjunction with the description and phylogenetic relationships of a new genus of Chaenopsidae, Hastings (1992: table 1), mentioned five derived characteristics that in combination are unique to the three species of *Emblemariopsis* that he studied (*E. diaphana*, *E. signifera*, *E. tayrona*). *Emblemariopsis ruetzleri* has all five of these derived features: females with pelvic-fin rays prolonged, the membranes not extending to the tips; males same as preceding; mesopterygoid absent; nasals with ridges; and third pelvic-fin ray reduced, its length about one-half that of second ray but longer than pelvic spine.

Hastings (1992) also listed another four derived features, each of which is found in one or two but not all three of the species he examined: supraorbital cirrus present (primitive, the condition in *E. ruetzleri*) or absent; fleshy flap anteriorly on first dorsal-fin spine present (primitive) or absent (as in *E. ruetzleri*); dorsal fin of males relatively low (primitive, the condition in *E. ruetzleri*) or elevated; and third basibranchial ossified (primitive) or unossified (unossified in the two smaller cleared and stained specimens of *E. ruetzleri*, 13.5 and 14.3 mm SL, but ossified in the largest specimen, 19.4 mm SL).

In a manuscript nearing completion, P. Hastings (pers. comm.) describes a synapomorphy of the four species of *Emblemariopsis* he has examined (the three species given in Hastings 1992, plus *E. lepto-*

cirris): the neural spine of the penultimate vertebra is truncate and much shorter than the preceding neural spines and the single epural is expanded proximally and occupies the position of the neural spine. *Emblemariopsis ruetzleri* has a shortened penultimate neural spine and expanded epural (as does *E. pricei*; Fig. 6), which gives us further assurance of the proper generic allocation of the new species.

Habitat and natural history notes.—Mature males are dark-headed and inhabit holes in coral, usually dead coral, whereas females are pale and are found on the surface of the algal turf overlying dead coral and near the hole-dwelling males; the single immature, pale male collected during the study was on the surface of a live part of a coral that also had a dead section containing a dark-headed male in a hole.

Two burrows of *E. ruetzleri* were collected along with their male residents. The internal surface of both burrows was smooth and brownish black, and each was the empty coiled shell of a vermetid gastropod. M. G. Harasewych (pers. comm.) tentatively identified these two shells, on the basis of their structure and locality, as those of *Dendropoma*, perhaps *D. irregularis*. We have not collected any other chaenopsid at Carrie Bow Cay inside a vermetid shell.

Both burrows contained both eyed and eyeless eggs that were being incubated by the resident male. Moreover, both burrows had at least two different developmental stages of eyed and eyeless eggs, indicating several different clutches. One of the burrows was so intact that almost the full complement of eggs could be counted; there were about 32 eyeless and 58 eyed eggs, a total of about 90 (±3). This burrow had an opening diameter of 5.3 mm and a similar diameter deep inside the coil where the eggs (both eyed and eyeless) were attached. The other burrow was broken in the region where eggs were attached, and a partial count of those remaining yielded about 60 eggs. This burrow had an opening diameter of 3.0 mm and was about 3.7 mm diameter lower inside the coil in the region of the eggs. The eggs in both burrows were between 0.6–0.7 mm in diameter.

The smaller of the two female specimens collected during this study, 12.3 mm SL, is not fully ripe. The right side ovary has 13 developing eggs of about 0.25–0.3 mm diameter and many much smaller egg primordia. The larger female, 13.4 mm SL, is fully ripe, with nine eggs of 0.55–0.6 mm diameter on the right side and only a few much smaller eggs. We presume, therefore, that there are a total of about 18 eggs available for laying by this mature female. This is further confirmation that burrows with about 90 incubating eggs must be the result of multiple deposits.

To determine whether vacant holes in dead coral were as keenly competed for by *E. ruetzleri* as are those in live coral by *E. pricei* (Tyler & Tyler 1997), we removed a dark-headed male (USNM 337500) of *E. ruetzleri* from a hole in a shallow patch reef just off the northwest side of Carrie Bow Cay on 28 Feb 1995, marked the location with a ribbon, and returned to it daily to see if a replacement had entered the empty hole. No replacement individual was present during the seven days of subsequent monitoring.

Additionally, on 3 Mar 1995 we collected five dark-headed males of *E. ruetzleri* (USNM 337499, mature males, 12.9–15.7 mm SL) on a shallow patch reef on the northwest side of Carrie Bow Cay, and marked their holes with ribbons. The five collected specimens were kept alive in the laboratory. They had blanched only moderately when collected and thereafter in the aquaria, and had good retention of darkness in preservative. We next observed the marked holes on 7 Mar and found that four of them were empty whereas one had a dark-headed replacement that we removed. The replacement was a 15.2 mm male (USNM 337498) that blanched considerably when collected. It had a minimal speckling of melanophores on the head and body, and it is now one of the least dark

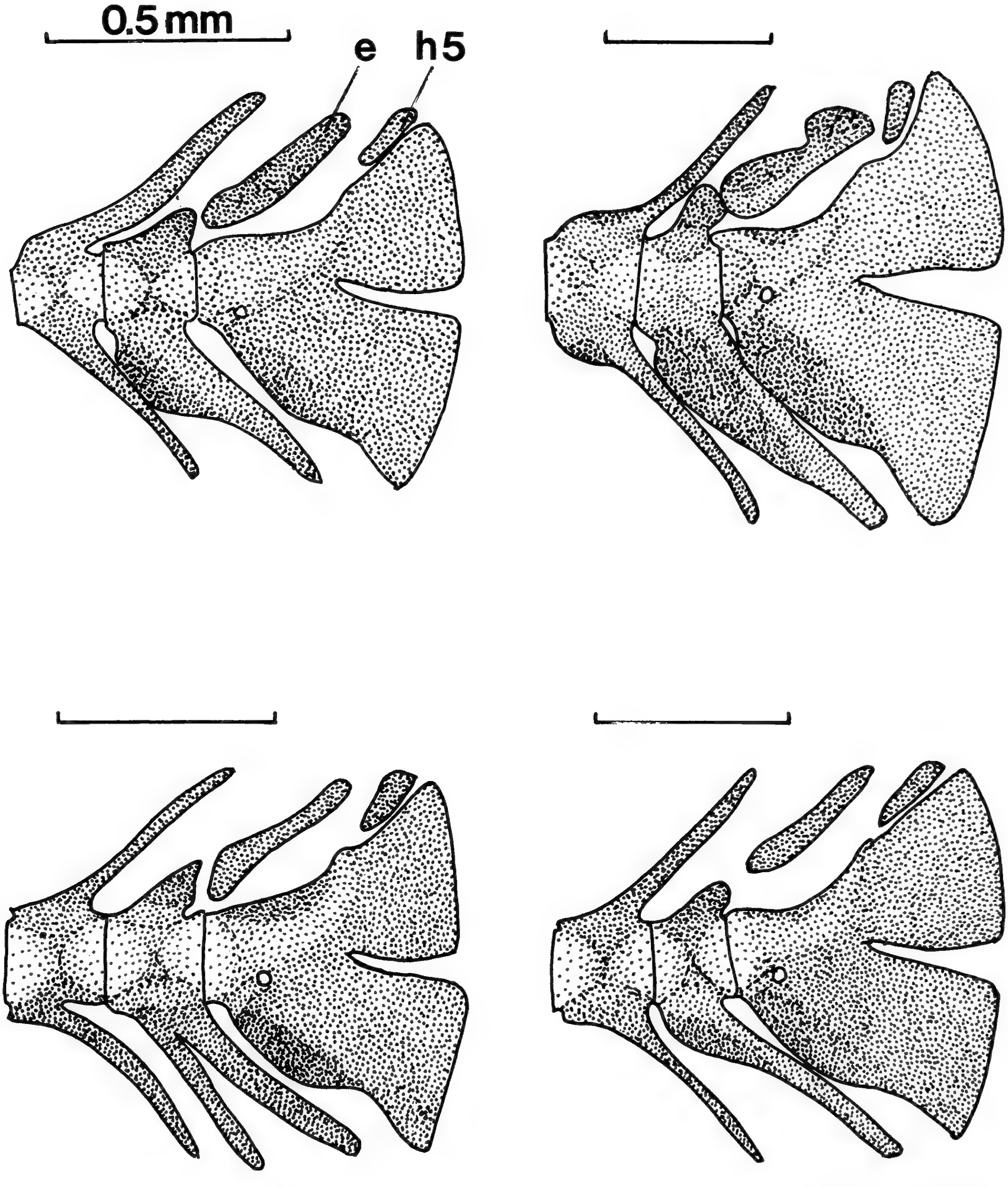

Fig. 6. Caudal skeletons in two specimens of, above, *Emblemariopsis ruetzleri*, USNM 337510, 13.5 mm SL to left and USNM 337507, 19.4 mm SL to right, and, below, two specimens of *E. pricei*, both USNM 325446, 13.6 mm SL to left and 16.5 mm SL to right, to show the derived condition in both species of the short neural spine of the penultimate centrum, typical of most species of the genus. The caudal skeleton has a single epural, hypural 5 free, and hypurals 1–4 consolidated. Abbreviations: h5 = fifth hypural; e = epural.

males in preservative. We conclude that, in marked contrast to *E. pricei*, holes in coral appropriate for habitation of mature males may not be in short supply for *E. ruetzleri*.

We presume that *E. ruetzleri* feeds on microplankton in the water column based on finding the remains of small or larval crustaceans in the stomach contents of several specimens.

We found the holes occupied by *E. ruetzleri* on both the relatively horizontal (top) and vertical (side) surfaces of dead corals, but we did not find a predominance of one orientation versus the other.

Etymology.—We take pleasure in naming this new species in honor of Dr. Klaus Ruetzler, Curator of Invertebrate Zoology at the National Museum of Natural History, who has so effectively directed the Smithsonian's Caribbean Coral Reef Ecosystem (CCRE) Program and its marine laboratory at Carrie Bow Cay, Belize, since its inception in 1972; he has given generously of his time and talents for all those years in providing research opportunities for many Smithsonian scientists and their colleagues throughout the world.

Discussion

Emblemariopsis ruetzleri and *E. pricei* are the only species of chaenopsids with strikingly dark-headed males living in holes in large coral mounds that are relatively common around Carrie Bow Cay.

The hole-dwelling males of both of these species are found in similar habitats around the reef crest, on patch reefs in the lagoon, and in the spur and groove zone around Carrie Bow Cay (to at least 8 m depth for *E. ruetzleri*, and deeper for *E. pricei*). Mature males of *E. ruetzleri*, however, are almost always found in holes in dead coral (only one of 35 dark-headed males in a hole in living coral), whereas those of *E. pricei* are almost always found in holes in live coral.

Most of the burrows that have been collected of breeding males of *E. pricei* are in the empty, partially tubular, and partially irregularly eroded tubes of serpulid worms (*Spirobranchus*) embedded in coral, but the two burrows that have been collected of breeding males of *E. ruetzleri* were both in empty, coiled, smooth-surfaced tubes of vermetid gastropods embedded in coral.

Another chaenopsid present around Carrie Bow Cay, the sailfin blenny *Emblemaria pandionis* Evermann & Marsh, is found in irregular cavities formed by many different kinds of invertebrates (worms, bivalves, snapping shrimps) and by erosion, in a great variety of sizes and shapes of dead coral rubble. In a few cases these cavities are probably the old corroded remains of vermetid gastropods (Smith & Tyler, in litt.). However, the cavities occupied by *E. pandionis* are of various shapes and are rough surfaced in loose rubble, in comparison to those of the complete coiled smooth tubes in large coral heads or boulders occupied by *Emblemariopsis ruetzleri*. Some chaenopsids in the eastern Pacific are known to have their shelter burrows in vacated mollusk tubes, including *Emblemaria hypacanthus* (Jenkins & Evermann) in *Turbo* gastropod shells (Hastings 1991) and *Acanthemblemaria crockeri* Beebe & Tee-Van in, among other kinds, *Lithophaga* boring bivalve cavities (Hastings 1988).

Another ecological difference between the two common species of *Emblemariopsis* at Carrie Bow Cay is the habitat of females, nonbreeding males, and immatures. Those of *E. pricei* are found mostly on the surface of soft-coral sea fans (*Gorgonia ventalina* Linnaeus) and clumps of live elkhorn coral (*Acropora palmata* (Lamarck)), whereas females of *E. ruetzleri* are on the surface of the algal turf on the same kinds of coral heads and boulders as the holes of the breeding males, and the immature males are also surface dwelling (on live coral near dead sections of coral for the single immature specimen collected).

The new species is one of the many chaenopsids living at least some of its life history in holes in dead coral around Carrie Bow Cay. All five species of *Acanthemblemaria* found there have both males and females in holes in dead coral (Clarke 1994), in contrast to *E. ruetzleri* having only dark-headed breeding males in such holes. Hole-dwelling males of the two common species of *Emblemariopsis* around Carrie Bow Cay are easily distinguished from the five species of *Acanthemblemaria* there because the heads of the species of the latter genus have spiny or rugose upper surfaces and are never as darkly and uniformly black as those of the two species of *Emblemariopsis*.

There are several other chaenopsids besides *Emblemariopsis ruetzleri* and *E. pricei* in which mature males utilize different habitats than females and immature males. In the sailfin blenny, *Emblemaria pandionis*, at Carrie Bow Cay, mature males are resident in holes in coral rubble, but females and immature males move about much more freely along the sandy bottom and frequently change their rubble shelter sites (Smith & Tyler, in litt.). In the Gulf of California sailfin blenny, *Emblemaria hypacanthus*, Hastings (1991) has shown that in areas of low predation risk, males are closely tied to their shelters whereas females move about more freely in the open, but that in areas of high predation both sexes spend most of their time in shelters. Hastings (1986) also has shown that most males of *Coralliozetus angelica* (Böhlke & Mead) in the Gulf of California are resident in barnacle shells, but females spend much time foraging in the open.

With sexually active males ranging in size from 11.9 to 19.4 mm SL ($\bar{X}$ = 14.5 mm SL for 35 individuals), *E. ruetzleri* is a relatively small species. A few other species of *Emblemariopsis* apparently are also relatively small, such as *E. leptocirris* and *E. occidentalis*, which have maximum known sizes of about 21 mm SL. Others are only slightly larger, such as *E. bahamensis*, *E. diaphana*, *E. signifera*, and *E. tayrona*, which reach between 23–25 mm SL (Stephens 1963, 1970; Acero 1987). The largest members of the genus are *E. randalli*, *E. bottomei*, and *E. pricei*, which have maximum sizes of 28–30 mm SL (Cervigon 1965, Stephens 1963, Tyler & Tyler 1997).

Emblemariopsis ruetzleri is about as diminutive as the smallest species of *Acanthemblemaria* at Carrie Bow Cay, *A. paula* Johnson & Brothers, which has a maximum size of about 18 mm SL and is sexually active as small as 11 mm SL (Johnson & Brothers 1989).

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Literature Cited

Acero, A. 1987. The chaenopsine blennies of the southwestern Caribbean (Pisces, Clinidae, Chaenopsinae). III. The genera *Chaenopsis* and *Coralliozetus*.—Boletin Ecotropica, Fundacion Universidad de Bogota Jorge Tedeo Lozano 16: 1–21.

Böhlke, J. E., & C. C. G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Academy of Natural Sciences of Philadelphia, 771 pp.

Cervigon, F. 1965. *Emblemariopsis randalli* nov. sp., una nueva especie de Chaenopsidae de las costas de Venezuela.—Novedades Cientificas, Contribuciones Ocasionales del Museo do Historia Natural La Salle, Serie Zoológica 33:1–4.

Clarke, R. D. 1994. Habitat partitioning by chaenopsid blennies in Belize and the Virgin Islands.—Copeia 1994(2):398–405.

Greenfield, D. W. 1975. *Emblemariopsis pricei*, a new species of chaenopsid blenny from Belize.—Copeia 1975(4):713–715.

Hastings, P. A. 1986. Habitat selection, sex ratio and sexual selection in *Coralliozetus angelica* (Blennioidea: Chaenopsidae). Pp. 785–793 *in* T.

Uyeno, R. Arai, T. Taniuchi, and K. Matsuura, eds., Indo-Pacific fish biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyological Society of Japan, 985 pp.

———. 1988. Correlates of male reproductive success in the browncheek blenny, *Acanthemblemaria crockeri* (Blennioidea: Chaenopsidae).—Behavioral Ecology and Sociobiology 22:95–102.

———. 1991. Flexible responses to predators in a marine fish.—Ethology Ecology & Evolution 3: 177–184.

———. 1992. Phylogenetic relationships of *Tanyemblemaria alleni*, a new genus and species of chaenopsid (Pisces: Blennioidei) from the Gulf of Panama.—Bulletin of Marine Science 51(2): 147–160.

———. 1997. Phylogenetic relationships of the *Coralliozetus* clade of chaenopsid blennies, with description of a new genus (Teleostei, Blennioidei).—Bulletin of Marine Science (in press).

———, & V. G. Springer. 1994. Review of *Stathmonotus*, with redefinition and phylogenetic analysis of the Chaenopsidae (Teleostei: Blennioidei).—Smithsonian Contributions to Zoology 558:1–48.

Johnson, G. D., & E. B. Brothers. 1989. *Acanthemblemaria paula*, a new diminutive chaenopsid (Pisces: Blennioidei) from Belize, with comments on life history.—Proceedings of the Biological Society of Washington 102:1018–1030.

Stephens, J. S. 1963. A revised classification of the blennioid fishes of the American family Chaenopsidae.—University of California Publications in Zoology 68:1–165.

———. 1970. Seven new chaenopsid blennies from the western Atlantic.—Copeia 1970(2):280–309.

Tyler, J. C., & D. M. Tyler. 1997. Natural history of the sea fan blenny, *Emblemariopsis pricei* (Pisces, Chaenopsidae), in the western Caribbean.—Smithsonian Contributions to Zoology (in press).

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(1):39–48. 1997.

Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. V. *Periclimenes mclellandi*, a new species, a gorgonian associate from Pine Cay, Turks and Caicos Islands, British West Indies

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Abstract.—Specimens of *Periclimenes mclellandi*, new species, were collected from gorgonians, primarily *Pseudopterogorgia americana* Gmelin, at depths of 14 to 43 m off Pine Cay, Turks and Caicos Islands, British West Indies. The new species belongs to the "*iridescens*" complex and is similar to *P. patae* Heard & Spotte, 1991, also associated with gorgonians at Pine Cay and the Florida Keys, but at shallower depths. *Periclimenes mclellandi* is distinguished from *P. patae* by a bilobate endite on the second maxillae, two rows of combsetae on the propodus of fifth pereopods, shorter and deeper rostrum with fewer rostral teeth, and an overall greenish coloration in life. Both species are distinguished from other described members of the "*iridescens*" complex by the chelae of the second pereopods, which are similar and equal or nearly equal in size, and by the dactyls of pereopods 3-5, which are simple instead of biunguiculate. Some specimens of *P. mclellandi* were parasitized by an unidentified aceolid trematode metacercaria and an undescribed bopyrid isopod.

This report is fifth in a series devoted to the taxonomy, distribution, and ecology of shrimps belonging to the palaemonid subfamily Pontoniinae. Previous contributions to this series are Heard (1986), Heard & Spotte (1991), Heard et al. (1993), and Spotte et al. (1994).

An undescribed species of *Periclimenes* Costa, 1844, was discovered on colonies of gorgonians, primarily *Pseudopterogorgia americana* (Gmelin, 1791), along the forereef slope west of Pine Cay in the Turks and Caicos Islands, British West Indies, near 21°53′N, 72°05′W. The new species resembles *P. patae* Heard & Spotte, 1991, another gorgonian associate from Pine Cay and the Florida Keys. Carapace length (CL) is defined here as the distance from the tip of the rostrum to the posterodorsal margin of the carapace. Type material has been deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and Gulf Coast Research Laboratory Museum (GCRL).

Periclimenes mclellandi, new species
Figs. 1–5

Periclimenes sp. A.—Spotte & Bubucis 1996:229

Material examined.—Holotype, Ovigerous female, CL = 2.40 mm, (USNM 276042), forereef slope west of Pine Cay, Turks and Caicos Islands, British West Indies, on gorgonian *Pseudopterogorgia americana*, 29 m, 14 Nov 1989, colls. S. Spotte and P. M. Bubucis. Paratypes from *P. americana*, same general locality as holotype, colls. S. Spotte and P. M. Bubucis.

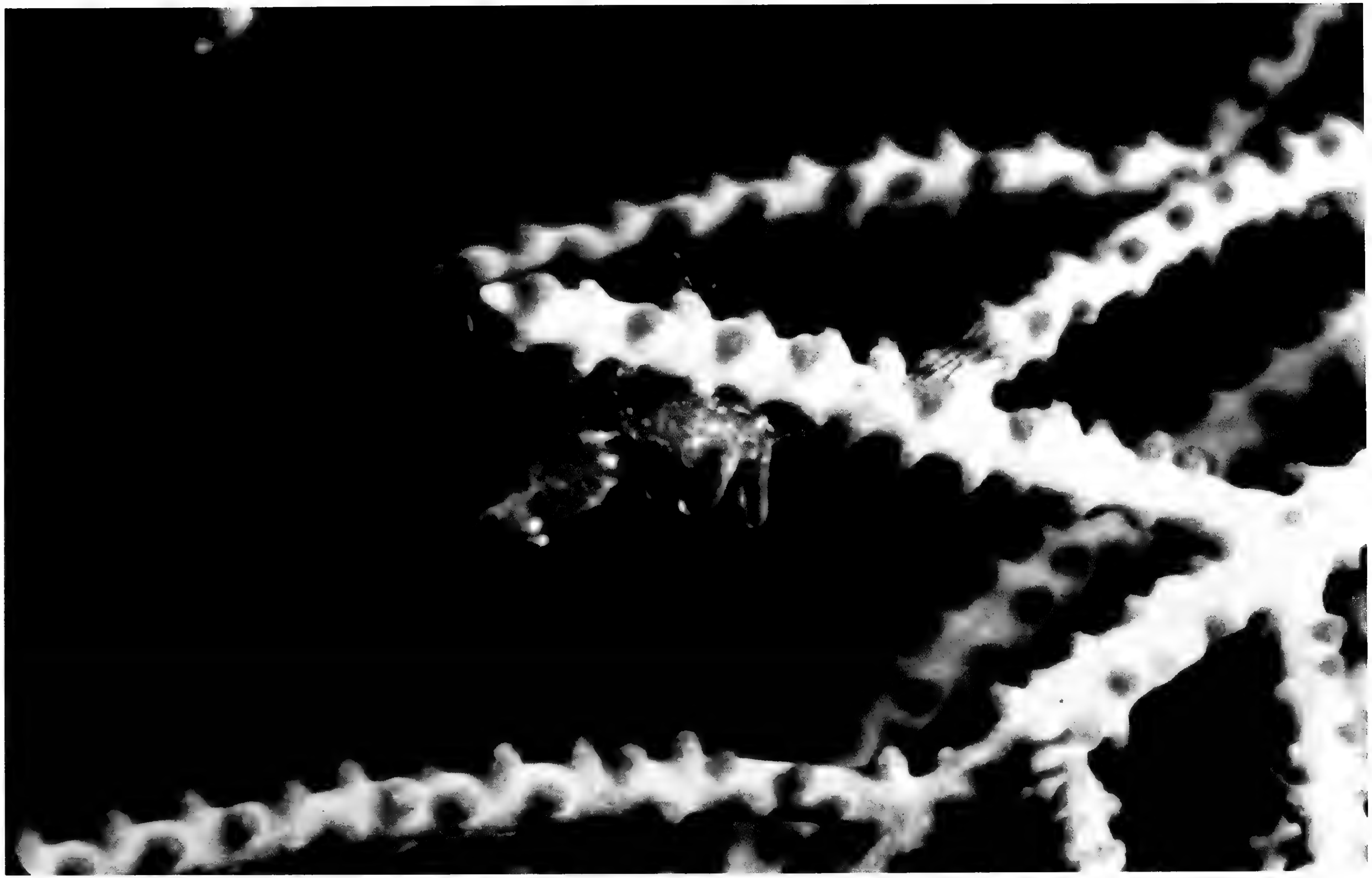

Fig. 1. *Periclimenes mclellandi*, new species, lateral view of an ovigerous female on an unidentified gorgonian. Note the two transverse bands. Photographed in situ at Pine Cay, Turks and Caicos Islands, 5 July 1990, 15 m.

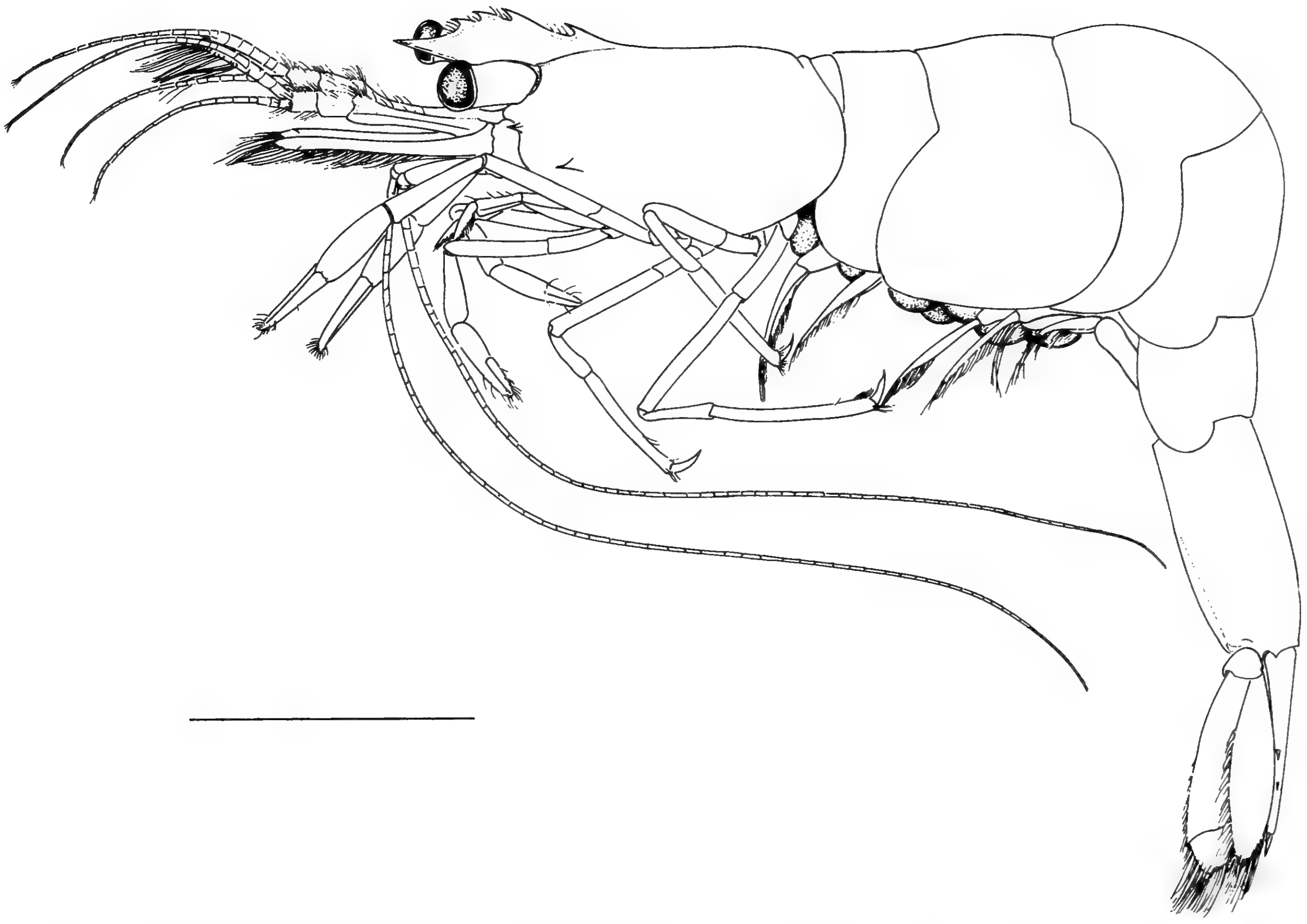

Fig. 2. *Periclimenes mclellandi*, new species, lateral view of ovigerous female. Scale = 2.0 mm.

Male, CL = 1.92 mm, (USNM 276043), 21 m, 8 Nov 1989; male, CL = 1.67 mm, (USNM 276044), 20 m, 9 Nov 1989; 1 ovigerous female, CL = 2.88 mm, 1 male, CL = 2.05 mm, (USNM 276045), 26–29 m, 14 Nov 1989; 2 females, CL = 2.40, 2.43 mm, (USNM 276046), 17–19 m, 10 May 1990; 1 male, CL = 1.92 mm, 1 female, CL = 2.46, (GCRL 1342), 26–32 m, 8 May 1990.

Diagnosis.—Small (CL less than 3 mm), greenish in life. Rostrum deep, unarmed ventrally, nearly straight or curved upward at tip, in females extending anteriorly beyond midsection of first segment of antennular peduncle, in males not extending to midsection of first segment of antennular peduncle; both sexes with as many as 5 dorsal rostral teeth, rarely more than 4 in males. Carapace with well developed antennal and hepatic spines, lacking other spines or ornamentation. Abdominal pleura rounded, abdominal somite 6 twice length of somite 5. Mesial spines on posterior margin of telson ¾ length of intermediate spines. Cornea slightly narrower than eye-stalk, constricted at junction with eye-stalk; accessory pigment spot and associated ommatidia present on dorsoproximal margin of cornea. Maxilla 2, endite bilobate. Pereopods 2 equal or nearly equal, undifferentiated, chelae lacking distinct teeth (vestiges of teeth sometimes present). Pereopods 3–5 with dactyls simple, propodi with 1 spine-seta on distoflexor margin; propodus of pereopods 5 with 2 rows of comb-setae on distal inner margin, (1 or both rows can be absent in small specimens).

Description of adult female (Figs. 1, 2, 4a–f, h, i, 5, 6).—Carapace with rostrum curved slightly upward at tip, not reaching to distal margin of first article of antennular peduncle; 4, or occasionally 5, dorsal teeth interspersed with small setae; first tooth of rostrum usually even with hepatic spine, second tooth usually anterior to posterior margin of orbit; ventral surface without

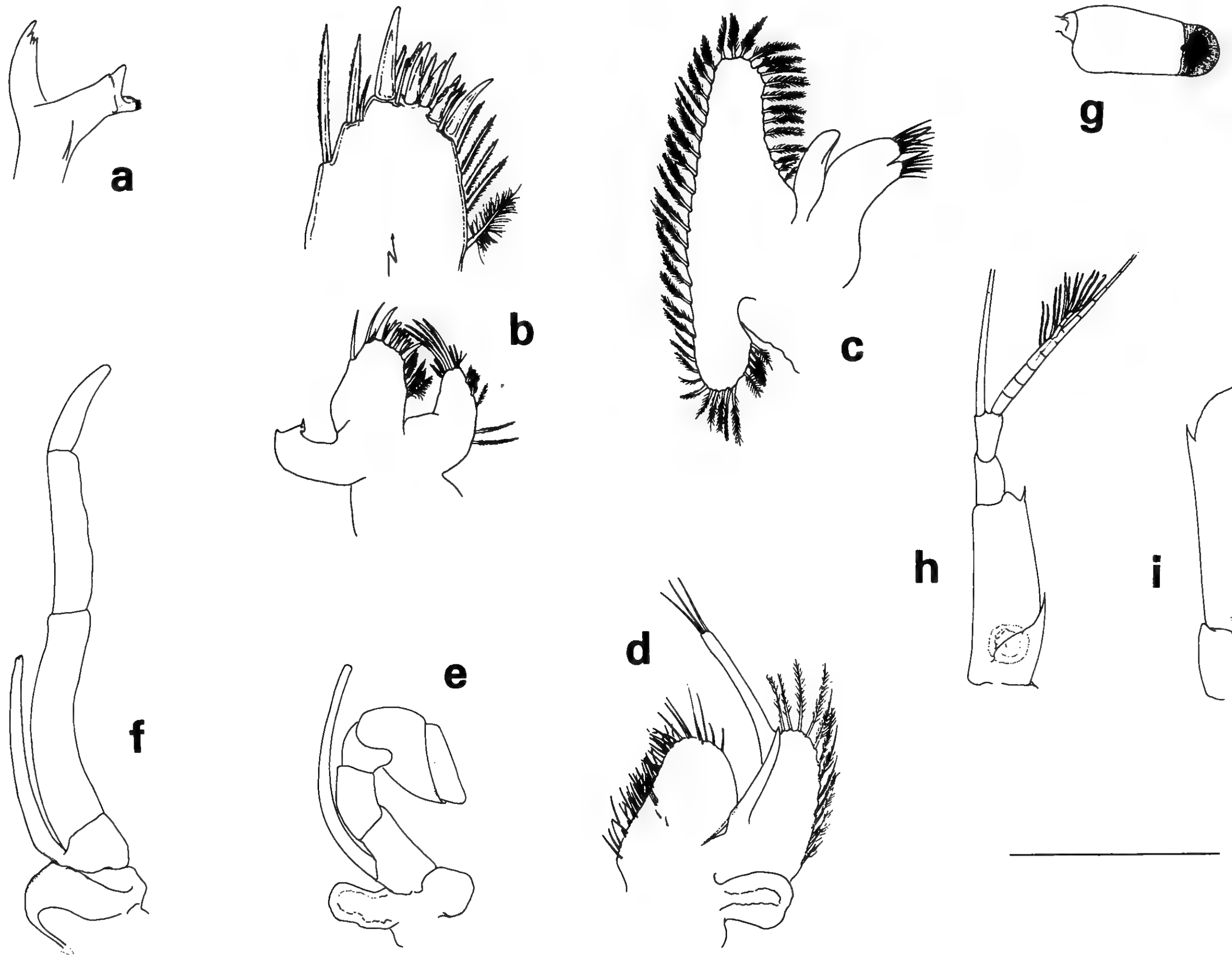

Fig. 3. *Periclimenes mclellandi*, new species: a, mandible; b, maxilla 1; c, maxilla 2; d, maxilliped 1; e, maxilliped 2 (setae omitted); f, maxilliped 3; g, eye; h, left antennule (ventral aspect); i, right antennule (ventral aspect). Scale = 0.4 mm for a–e, 1.0 mm for g–i.

teeth, posterior ½ with setae. Antennal spine well developed. Hepatic spine well developed, slightly larger, more robust, and less attenuated than antennal spine. No other spines or ornamentation on carapace.

Abdominal somites (Fig. 2) with pleura rounded, somite 6 twice length of somite 5 and same length as telson when measured along dorsal margin.

Telson (Fig. 4i) with 2 pairs of dorsolateral spines, anterior pair slightly anterior to mid-length, posterior pair closer to end of telson than to anterior pair. Three pairs of apical spine-setae; lateral pair short; intermediate pair longest, 4 times length of lateral pair; mesial pair plumose, approximately ¾ length of intermediate pair. Minute, acute apical process present between mesial spine-setae.

Antennular peduncle (Fig. 3h) with sharp, slender stylocerite extending nearly to midline of basal article; distolateral margin of basal article with 1 spine; combined length of second and third articles ½ that of basal article. Lateral antennular flagellum with 2 branches fused for approximately 5 articles; shortest unfused part of branch consisting of 3 articles, each bearing aesthetascs (3 on terminal article, 2 on proximal unfused articles), shorter than fused portion, distal articles of which bear 2–4 aesthetascs.

Antennal scale (Fig. 3i) with just overreaching antennular peduncle, length 3 times width, lateral margin nearly straight, distolateral spine well short of anteromesial angle of blade. Antennal peduncle extending to mid-length of blade.

Eye: (Fig. 3g) with cornea diameter distinctly less than proximile diameter of eye-

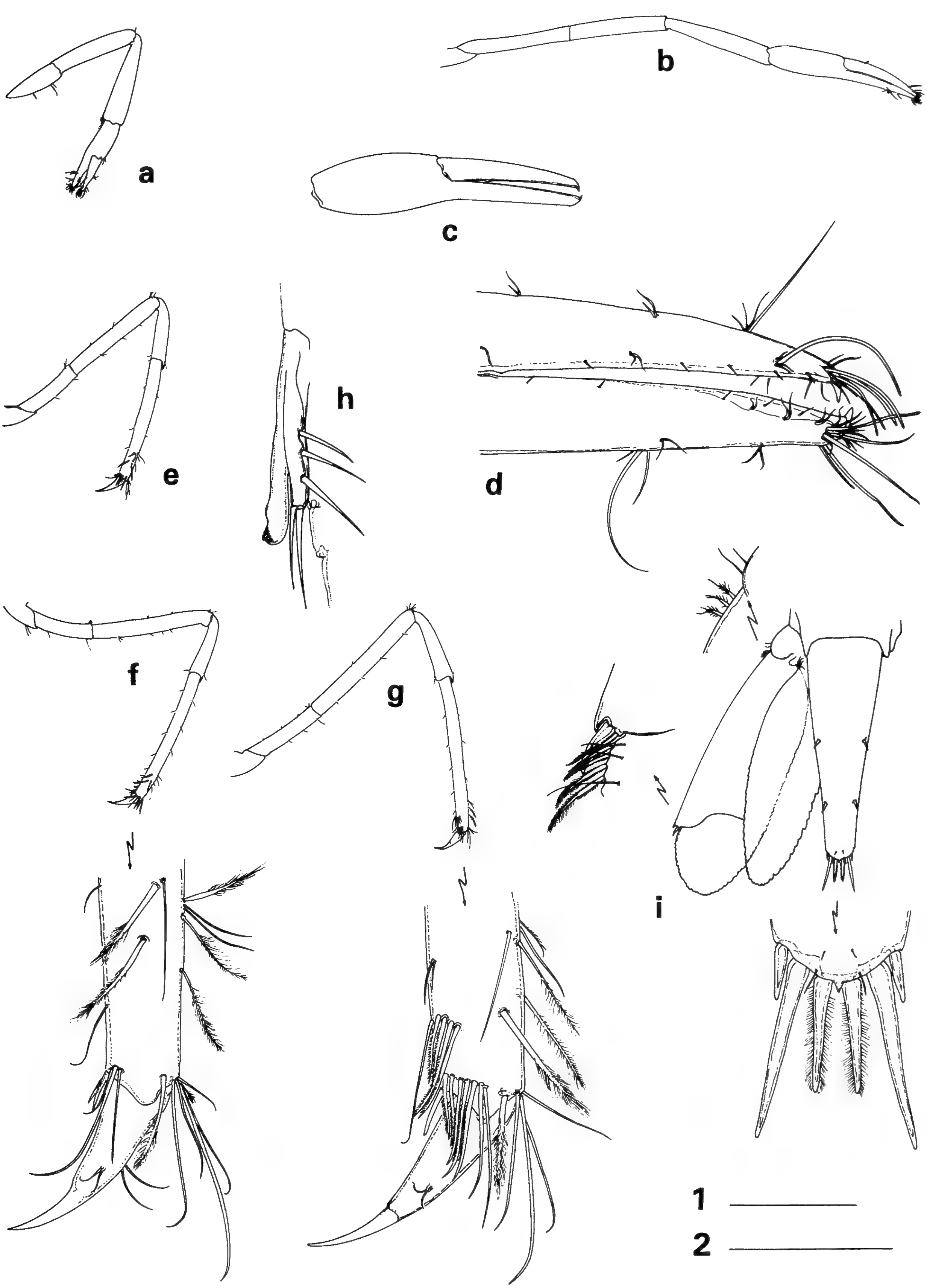

Fig. 4. *Periclimenes mclellandi*, new species (ovigerous female except for g): a, pereopod 1; b, pereopod 2 (dorsolateral aspect); c, same (lateral aspect of propodus and dactyl, setae omitted); d, same (distal aspect of fingers); e–g, pereopods 3–5; h, appendix interna and appendix masculina of adult male (CL 2.1 mm); i, telson and left uropod (fringing plumose setae omitted). Scale 1: a, d–g = 1.0 mm, b = 0.4 mm. Scale 2: c, h = 0.2 mm, i = 1.0 mm.

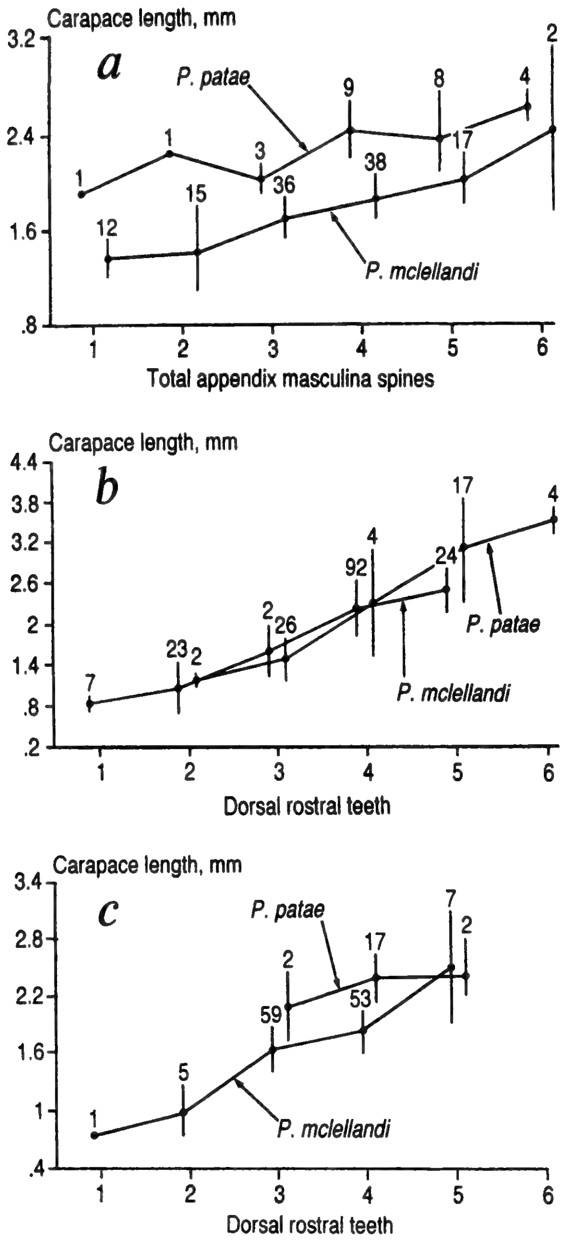

Fig. 5. **a,** Males of *Periclimenes mclellandi*, new species, compared with males of *P. patae*. Standard deviation plot of carapace length against total number of spines on the *appendix masculina* (both apical and lateral). Bars are 1 *SD* with *n* shrimp shown above. Correlation between variables is significant for both species: *P. mclellandi* (Spearman's $r = 0.74$, $t_{n-2} = 11.99$, $P < 0.001$); *P. patae* (Spearman's $r = 0.55$, $t_{n-2} = 3.24$, $P < 0.01$). **b,** Females of *Periclimenes mclellandi*, new species, compared with females of *P. patae*. Standard deviation plot of carapace length against the number of dorsal rostral teeth. Bars are 1 *SD* with *n* shrimp shown above. Correlation between the variables is significant for both species: *P. mclellandi* (Spearman's $r = 0.51$, $t_{n-2} = 6.36$, $P < 0.001$); *P. patae* (Spearman's $r = 0.69$, $t_{n-2} = 5.00$, $P < 0.001$). **c,** Males of *Periclimenes mclellandi*, new species, compared with males of *P. patae*. Standard deviation plot of carapace length against the number of dorsal rostral teeth. Bars are 1 *SD* with *n* shrimp shown above. Correlation between the variables is significant for *P. mclellandi*

stalk, barely constricted at junction with eye-stalk; accessory pigment spot and associated ommatidia present on dorsoproximal margin of cornea.

Mandible (Fig. 3a) with lacking palp; incisor process terminating in 4 distinct teeth, distal tooth of incisor distinctly larger than others; molar process dentate with numerous small spine setae. Maxilla 1 as illustrated (Fig. 3b). Maxilla 2 (Fig. 3c) with bilobate endite; palp slender, lacking setae. Maxilliped 1 (Fig. 3d) having well-developed exopodal flagellum (lash) bearing 3 or 4 terminal plumose setae; epipod present. Maxilliped 2 (Fig. 3e) with well developed exopod bearing 2 terminal setae; epipod present. Maxilliped 3 (Fig. 3f) with well developed exopod bearing 4 terminal plumose setae; exopod (excluding setae), not extending to distal end of antepenultimate article of endopod.

Pereopods 1 (Fig. 4a) of equal size, not extending to distal end of antennal scale; dactyls of chelae weakly bifid, same length as palm; carpus ¼ longer than propodus; merus and carpus of equal length; ischium ½ length of merus. Pereopods 2 (Fig. 4b–d) equal or subequal in size, undifferentiated, weakly developed, both extending past antennal scale by less than length of dactyls; fingers same length as palm, lacking distinct teeth (vestiges of teeth sometimes present; Fig. 4c, d); carpus less than ¾ length of propodus; merus ⅘ length of carpus, slightly shorter than ischium. Pereopods 3–5 (Fig. 4e–g) of nearly equal size and shape, dactyls simple, propodi each with 1 pair of spine-setae on distal flexor margin. Pereopods 3 and 4 nearly equal in size and shape, not extending past antennular peduncle; pereopods 5 longer than 3 or 4, morphologically distinct. Pereopods 3 (Fig. 4e) with propodus 4 times length of

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(Spearman's $r = 0.51$, $t_{n-2} = 6.36$, $P < 0.001$) but not for *P. patae* (Spearman's $r = 0.19$, $t_{n-2} = 0.97$, $P > 0.05$).

Table 1.—*Periclimenes mclellandi* vs. *P. patae*, size comparison based on carapace length (CL).

Species	Mean CL (±*SD*), mm	CL range, mm
P. mclellandi (males)	1.73 (0.33), *n* = 119	0.73–2.91
P. mclellandi (females)	1.95 (0.63), *n* = 172	0.72-3.17
P. patae (males)	2.40 (0.30), *n* = 26	1.82–3.04
P. patae (females)	2.80 (0.97), *n* = 29	1.11–5.02

dactyl, carpus ½ length of propodus, merus slightly less than twice length of carpus, ischium slightly more than ½ length of merus. Pereopods 4 (Fig. 4f) with propodus nearly 5 times length of dactyl, carpus ⅖ length of propodus, merus slightly more than twice length of carpus, ischium slightly less than ½ length of merus. Pereopods 5 (Fig. 4g) longer than pereopods 3 or 4, extending to or beyond proximal end of second article of antennular peduncle; propodus nearly 5 times longer than dactyl, 2 rows of comb-setae on inner distal surface (Fig. 4g) (not always present on small specimens); carpus slightly more than ⅖ length of propodus; merus slightly less than twice length of carpus; ischium slightly more than ½ length of merus.

Uropods (Fig. 4i) with exopods extending well beyond telson; strong, moveable spine-seta between distolateral spine and blade; moveable spine distinctly longer than distolateral spine-seta. Endopods extending beyond telson, shorter than exopod.

Description of male.—Adult usually smaller than adult female (Table 1), less robust. Rostrum deep, relatively short, not extending to cornea or beyond mid-region of basal peduncular article of antennule; shorter branch (fused and unfused parts) of antennule of lateral flagellum bearing 6 to 8 groups of aesthetascs; appendix masculina of second pleopod (Fig. 4h) armed with 1 to 3 weakly serrate apical spine-setae and 0 to 4 simple lateral spine-setae along inner margin. Similar to female in other respects.

Color pattern.—The overall appearance in life is iridescent green shading toward aquamarine; two transverse greenish-gold bands are often evident on large specimens (Fig. 1). Subtle markings vary and probably are not diagnostic. Carapace clear (transparent), speckled faintly with tiny gold and russet spots. Cornea gold, sometimes with an aquamarine ring around base. Eye-stalks with aquamarine spots and smaller spots of russet and ringed distally in deep aquamarine. Antennules and antennular peduncle clear with russet and aquamarine spots; alternatively, antennules clear and tinged with aquamarine, containing spots of gold and russet; antennal peduncle clear with red, russet, and gold spots. Antennal scale, flagella, and rostrum clear; alternatively, antennal scale rimmed with gold. Antennae clear with tiny russet spots. Maxillipeds clear. Abdominal somites edged with faint gold spots, dorsal surfaces marked strongly by two transverse bands of greenish gold. The first band crosses the posterior section of abdominal somite 2; a second band traverses somite 3 directly across the hump. Both bands widen ventrolaterally, becoming narrowest on dorsal surface, sometimes with an underlying band of aquamarine; gold band sometimes contains russet spots; there is occasionally a fainter third band of gold and russet on posterior dorsal surface of abdominal somite 5; somites 4 and 5 often are rimmed at dorsoposterior surface with aquamarine. Pereopods clear. Uropods clear with small gold spots distributed evenly; alternatively, telson and uropods iridescent aquamarine, pigmented most strongly near edges; base of telson sometimes aquamarine tinged with greenish-gold and having a greenish-gold band across base. Pleopods with gold and russet spots. Protopodites with irregular longitudinal markings of aquamarine speckled with gold and russet but mainly clear; exopods and endopods clear. Early ova gold, later (eyed) ova pale aquamarine often tinged with gold.

Habitat.—Associated with the slimy sea plume (*Pseudopterogorgia americana*) and other species of gorgonians along the fringing reefs of Pine Cay in depths from 14 to at least 43 m.

Distribution.—Presently known only from the type locality off Pine Cay, Turks and Caicos Islands, British West Indies.

Etymology.—Named for Jerry A. McLelland, in recognition of his contributions to the investigations of the marine invertebrate fauna of the West Indies.

Remarks.—Lebour (1949) described *Periclimenes iridescens* from an adult female netted off Bermuda. The "*iridescens*" complex comprises several species of close morphological affinity with *P. iridescens* (Heard & Spotte 1991, Heard et al. 1993, Spotte et al. 1994), and we include *P. mclellandi* in this complex. *Periclimenes mclellandi* is similar to *P. patae*, a species also collected on gorgonians at Pine Cay and the Florida Keys (Heard & Spotte 1991) and tentatively reported from the British Virgin Islands as *Periclimenes* cf. *patae* (see Spotte et al. 1995).

Several characters of *Periclimenes mclellandi* appear to be transitional between larger, less highly derived members of the "*iridescens*" complex (e.g., *P. iridescens* Lebour, 1949; *P. iridescens* sensu Holthuis 1951; *P. infraspinis* (Rathbun, 1902); *P. antipathophilus* Spotte, Heard, & Bubucis, 1994), none of which are known to associate with gorgonians, and the apparently more highly derived *P. patae*. The affinity of *P. mclellandi* to the larger members of the "*iridenscens*" complex is indicated by the presence of a bilobate endite on the second maxillae and more than one row of comb-setae on the propodi of pereopods 5.

Periclimenes mclellandi and *P. patae* are distinguished from other described members of the "*iridescens*" complex by: their smaller size, the chelae of pereopod 2 being equal or nearly equal; and having simple dactyls on pereopods 3–5. In these characteristics they resemble juveniles of the larger members of the complex, raising the possibility that a neotenic condition has evolved in *P. mclellandi* and *P. patae* during their close association with gorgonians.

Based on adult specimens, *Periclimenes mclellandi* differs from *P. patae* by its maxilla 2 having a bilobate endite; propodus of pereopods 5 with two rows of comb-setae, rostrum shorter, deeper, and generally with fewer rostral teeth; smaller adult body size (Table 1); smaller corneal diameter relative to eye-stalk; overall greenish coloration in life accentuated by two transverse, greenish-gold bands on the first and second abdominal somites (Fig. 1); and occurrence at a greater mean depth.

To highlight some of the size and meristic differences between *Periclimenes mclellandi* and *P. patae*, we plotted the standard deviation of carapace length against total number of spines on the *appendix masculina* (both apical and lateral) for males of the species (Fig. 5a) and graphed the standard deviation of carapace length against the number of dorsal rostral teeth in the sexes of both species (Fig. 5 b, c). Correlations for the variables were significant for *P. mclellandi* in all comparisons (see Fig. 5). Mean carapace lengths for adults of both sexes are displayed in Table 1, indicating that adults of *P. patae* are larger than those of *P. mclellandi*.

At Pine Cay, *Periclimenes patae* is found at a mean depth of 9.6 m (range 2.7–22.2 m); in contrast, *P. mclellandi* was never collected at depths shallower than 14 m, and its range extended to 43 m (Spotte & Bubucis 1996). We emphasize that 43 m marked our deepest descents. *Pseudopterogorgia americana* occurs even deeper off Pine Cay, and *P. mclellandi* might also.

Associates and symbionts.—Other caridean shrimps, most commonly *Hippolyte nicholsoni* Chace, 1972 and *Pseudocoutierea antillensis* Chace, 1972, co-occurred with *P. mclellandi* on *Pseudopterogorgia americana* and other gorgonians at Pine Cay. Co-inhabiting less frequently the same gorgonian with *P. mclellandi* were three other species, *P. patae*, *Periclimenes* sp. B, and *Tozeuma* sp. (Spotte & Bubucis 1996).

Periclimenes mclellandi serves as the second intermediate host of an opaceolid digenean parasite. When microscopically examining living specimens of *P. mclellandi* that are infected with opaceolid larvae, the oval metacercarial cysts can be easily observed in the shrimp host's transparent abdominal muscles. An unknown gastropod mollusk serves as the first intermediate host. The adult stages of all known members of family Opecoelidae are intestinal parasites of fishes (Yamaguti 1971). At some collection sites, ordinarily between 18 and 26 m, up to 20% of the adult *P. mclellandi* studied were infected with the metacercarial cysts of this larval digenean.

A bopyrid isopod occasionally occurred underneath the abdomen of *P. mclellandi.* This parasite was found most often on shrimp collected in depths between 25 and 30 m. It appears to be an undescribed species of *Hyperphrixus* Niertrasz & Brender á Brandis, 1931, a genus known to parasitize other shrimps of the subfamily Pontoniinae (see Markham 1985).

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Literature Cited

Costa, O. G. 1844. Su due nuovi generi di Crostacei Decapodi Macrouri nota.—Annali della Accademia degli Aspiranti Naturalista, Napoli 2: 285–(?).

Chace, F. A., Jr. 1972. The shrimps of the Smithsonian-Bredin Caribbean Expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia).—Smithsonian Contributions to Zoology 98:1–179.

Gmelin, J. F. 1791. Caroli a Linné Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synomymis, locis. Editio decima tertia, aucta, reformata. Cura Jo. Frid. Gmelin, Lipsiae, Geog, Emanuel, Beer.—1(6):3021–4120, 3 pls.

Heard, R. W. 1986. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. I. The genus *Neopontonides* Holthuis, 1951, with the description of *N. chacei,* new species, and the erection of *Pseudopontonides,* new genus, to receive *N. principis* Criales, 1980.—Journal of Crustacean Biology 6:471–484.

———, & S. Spotte. 1991. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. II. *Periclimenes patae,* new species, a gorgonian associate from shallow reef areas off the Turks and Caicos Islands and Florida Keys.—Proceedings of the Biological Society of Washington 104:40–48.

———, S. Spotte, & P. M. Bubucis. 1993. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. III. *Neopericlimenes thornei,* new genus, new species, from Pine Cay, Turks and Caicos Islands, British West Indies.—Journal of Crustacean Biology 13:793–800.

Holthuis, L. B. 1951. A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. I. The subfamilies Euryrhynchinae and Pontoniinae.—Occasional Papers, Allan Hancock Foundation Publications No. 11, 332 pp.

Lebour, M. V. 1949. Some new decapod Crustacea from Bermuda.—Proceedings of the Zoological Society of London 11(Part IV):1107–1117.

Markham, J. C. 1985. A review of the bopyrid isopods infesting caridean shrimps in the northwestern Atlantic Ocean, with special reference to those collected during the Hourglass Cruises in the Gulf of Mexico.—Memoirs of the Hourglass Cruises 7(3):1–156.

Niertrasz, H. F., & G. A. Brender á Brandis. 1931. Papers from Dr. Th. Morstensen's Pacific Expedition 1914–16. LVII. Epicaridea II. Vidensk Med Dansk naturhist Foren Khobenhavn 91: 147–226.

Rathbun, M. J. 1902. Brachyura and Macrura. Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. VIII.—Proceedings of the Washington Academy of Sciences 4:275–291.

Spotte, S., & P. M. Bubucis. 1996. Diversity and abundance of caridean shrimps associated with the slimy sea plume (*Pseudopterogorgia americana*) at Pine Cay, Turks and Caicos Islands, British West Indies.—Marine Ecology Progress Series 133:229–232.

———, P. M. Bubucis, & R. M. Overstreet. 1995. Caridean shrimps associated with the slimy sea plume (*Pseudopterogorgia americana*) in midsummer at Guana Island, British Virgin Islands, West Indies.—Journal of Crustacean Biology 15:291–300.

———, R. W. Heard, & P. M. Bubucis. 1994. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. IV. *Periclimenes antipathophilus* new species, a black coral associate from the Turks and Caicos Islands and Eastern Honduras.—Bulletin of Marine Science 55:212–227.

Yamaguti, S. 1971. Synopsis of the digenetic trematodes of vertebrates.—Tokyo, Keigaku Publishing Company. Volume 1: 1074 pp; Volume 2: 349 plates.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(1):49–57. 1997.

New records and distribution ranges of shrimps (Crustacea: Decapoda: Penaeoidea and Caridea) in Chilean waters

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Abstract.—Extensions of the geographical distribution are provided for eight species of shrimps. Ranges were mostly extended toward the south (*Haliporoides diomedeae*, *Pasiphaea magna*, *Betaeus emarginatus*, *Alpheus inca*, *Hippolyte williamsi* and *Lysmata intermedia*), while the boundary of the distribution of *Eualus dozei* was shifted to the north. Two species (*Pasiphaea magna* and *Lysmata intermedia*) are reported for the first time from Chilean waters. An additional species, *Ogyrides* sp., was collected from a stomach content of the fish *Eleginops maclovinus* in central-southern Chile, representing the first record of a representative of the family Ogyrididae from Chilean waters. This record is remarkable since species of *Ogyrides* are considered to inhabit warm-temperate and tropical waters.

Chile has an extraordinary long, diversified coastline that lies in two distinct zoogeographic regions (cold-/and warm-temperate region) connected by a transitional zone (Brattström & Johanssen 1983). Several national and international expeditions (see Retamal 1981, Brattström & Johanssen 1983, Arntz et al. 1996, Wehrtmann & Lardies 1996) have carried out intensive collections along the Chilean coast, such as The Lund University Chile Expedition 1948–49 (LUCE), of special importance to the knowledge of the Chilean decapod fauna. Holthuis (1952), in his account of the "macruran" decapods collected during LUCE, noted the relative small number of Decapoda Macrura known from Chile, which included a total of 37 species, 5 of which inhabit freshwater, 13 live in the deep sea or are pelagic, and 19 littoral. Subsequently, Retamal (1981) reported a total of 44 penaeoid and caridean shrimp species from Chilean waters, but excluded *Hippolyte williamsi* Schmitt, 1924, previously reported by Zuñiga et al. (1978). Recently, Retamal (1993), and Retamal & Soto (1995), examined samples collected from deep waters off northern Chile, and reported four additional species from Chile: *Benthesicymus tanneri* (Faxon, 1893), *Sergia phorca* (Faxon, 1893), *Psathyrocaris fragilis* Wood-Mason, 1893 and *Plesionika santaecatalinae* Wicksten, 1983a.

This study updates and summarizes available information concerning species composition and distribution of the penaeoid and caridean shrimp fauna of Chile. We include results from our samplings carried out during the last years as well as from examination of collections of Museo Nacional de Historia Natural (MNHNC), Santiago, Pontifícia Universidad Católica de Chile ("Sala de Sistemática": SS-UC), Santiago, and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The specimens that we collected are deposited in the collections of "Sinergos" (SIN), and the Institute of Zoology (IZUA), Universidad Austral de Chile, Valdivia. Carapace length (CL) was measured from the posterior edge of the orbital arch to the mid-dorsal margin of the carapace. Total length (TL) refers to the distance between the posterior margin of the orbital arch and the distal margin of the telson, excluding setae.

Infraorder Penaeidea Rafinesque, 1815
Family Solenoceridae Wood-Mason, 1891
Haliporoides diomedeae (Faxon, 1893)

Previous known distribution.—Panama (06°30′N) to central Chile (37°40′S); from 240 to 1886 m (Faxon 1895, Del Solar & Mistakidis 1971, Del Solar & Flores 1972, Noziglia & Arana 1976, Pérez-Farfante 1977, Holthuis 1980, Méndez 1981, Retamal R 1993).

Material examined.—1 female (CL 41.0 mm), Gulf of Corcovado, off Morro Yeli (43°32′S), bottom trawl, 50–95 m, May 1996, MNHNC 660025.

Remarks.—The specimen collected extends considerably (approximately 660 km) to the south the known geographical distribution of this species. The depth at which the specimen was collected is the shallowest recorded for this species.

Infraorder Caridea Dana, 1852
Family Pasiphaeidae Dana, 1852
Pasiphaea magna Faxon, 1893

Previous known distribution.—California, U.S.A. (off Point Arena to off Ponit Loma) to Perú (17°05′S); from 509 to 1019 m (Faxon 1893, Schmitt 1921, Méndez 1981).

Material examined.—1 ovig. female (CL 47.9 mm, TL 113.0 mm), off northern Chile (22°13′S, 70°23′W), 815 m, Feb 1981, MNHNC 81085.

Remarks.—This is the first record of this species from Chile, and extends its distribution to the south by approximately 560 km.

Family Oplophoridae Dana, 1852
Acanthephyra pelagica (Risso, 1816)

Previous known distribution.—Mediterranean, North and South Atlantic, Indo Pacific, and, perhaps Panantarctic (Zariquiey 1968, Chace 1986, Tiefenbacher 1994), Argentina between 38°S and 54°S (Boschi et al. 1992), South Africa (without indication of latitude) (Kensley 1981), New Zealand (without indication of latitude) (Richardson & Yaldwyn 1958).

Material examined.—1 male (CL 15 mm), Valle de La Mocha (38°04′S, 73°52′W), 400–548 m, Jun 1965, MNHNC 660011.

Remarks.—The systematic position of the species seems to be unclear (Chace 1986). The specimen studied by us coincides perfectly with Boschi et al.'s (1992: 25) description and illustration of *A. pelagica* from southern Argentina. To our knowledge, this is the first report of this species from central-southern Chile and, therefore, the most northern record for the Pacific Ocean. Vinuesa (1977:14, table 1) reported *A. pelagica* occurring between Magellan Strait and Chiloé Island (approximately 42°S), but he did not indicate where he obtained information on the distribution of this species.

Superfamily Alpheoidea Rafinesque, 1815
Family Alpheidae Rafinesque, 1815
Betaeus emarginatus (H. Milne Edwards, 1837)

Previous known distribution.—Perú (between 06°55′40″S and 14°14′S) and Chile (between 20°16′S and 41°51′S) (Holthuis 1952, Wicksten & Méndez 1983).

Material examined.—2 males (CL 9.84, 15.96 mm; TL 29.26, 47.61 mm) and 1 female (CL 10.10 mm; TL 30.05 mm), west coast of Chiloé Island, Quiutil (42°30′S), Apr 1993, SIN CR(97)023.

Remarks.—This record extends the range of this species slightly to the south by approximately 90 km, and now includes Chiloé Island.

Alpheus inca Wicksten & Méndez, 1981

Previous known distribution.—Galápagos Islands (Wicksten 1991), Perú (between 06°55′S and 13°50′S) and Chile (22°08′S) (Wicksten & Méndez 1981).

Material examined.—1 female (CL 4.66 mm; TL 14.35 mm), Tocopilla (22°S), Jan 1965, SS-UC 2822; 1 male (CL 5.89 mm; TL 17.48 mm) and 1 female (CL 5.32 mm; TL 18.34 mm), Peninsula of Mejillones (23°S), Jan 1965, SS-UC 2759; 2 females (CL 4.73, 6.46 mm; TL 15.66, 21.00 mm), Mejillones Bay (23°S), Jan 1965, SS-UC 2823 and 2802; 4 males (CL 8.97–17.02 mm; TL 25.84–42.28 mm) and 3 females (CL 6.23–8.97 mm; TL 19.61–24.93 mm), Totoralillo-Panul (30°05′S), Jan 1963, SS-UC 764; 1 male (CL 10.64 mm; TL 34.35 mm) and 2 ovig. females (CL 14.29 and 16.26 mm; TL 44.23 and 49.25 mm), Los Molles (32°14′S), Jan 1963, SS-UC 451; 1 ovig. female (CL 16.72 mm; TL 50.77 mm), Los Molles (32°14′S), Jan 1963, SS-UC 452; 1 male (CL 9.42 mm; TL 34.05 mm), El Tabo (33°28′S), Feb 1960, SS-UC 33; 1 female (CL 5.99 mm; TL 17.67 mm), Las Cruces (33°35′S), Oct 1966, SS-UC 3769; 1 male (CL 4.94 mm; TL 17.58 mm), Duao (35°S), Jan 1963, SS-UC 615.

Remarks.—The present report extends the southern limit of this species from Mejillones (22°08′S) to Duao (35°S), a distance of approximately 1430 km.

Family Hippolytidae Dana, 1852

Hippolyte williamsi Schmitt, 1924

Previous known distribution.—México, Gulf of California to Chile (between 20°14′30″S, 70°10′50″W to Isla Santa María (23°24′30″S, 70°36′10″W) (Zuñiga et al. 1978, Wicksten & Hendrickx 1992).

Material examined.—7 females (CL 3.7, 3.4, 2.5, 3.2, 3.7, 3.6 and 2.7 mm; TL 22.2, 17.2, 12.3, 16.3, 20.0, 19.3 and 13.9 mm, respectively) and 9 males (CL 2.0, 2.1, 2.1, 2.4, 2.9, 3.5, 3.2, 3.0 and 3.1 mm; TL 10.2, 10.9, 10.6, 13.3, 14.7, 17.1, 15.9, 14.9 and 14.4 mm, respectively) associated with *Ulva* sp., Bahía de Coquimbo (29°50′S, 71°15′W), 2 m, 15 Mar 1995, IZUA 540; 1 female (CL 4.3 mm; TL 24.0 mm) and 3 males (CL 2.8, 2.4 and 2.8 mm; TL 16.3, 13.7 and 15.6 mm, respectively) associated with *Ulva* sp., Calbuco (51°50′S, 73°05′W), 2 m, 5 Nov 1994, IZUA 541; 3 females (CL 6.23, 6.00 and 5.62 mm; TL 36.01, 35.11 and 32.83 mm, respectively) and 2 males (CL 4.56 and 4.03 mm; TL 25.80 and 21.81 mm, respectively), Lechagua, near Ancud, Chiloé Island (41°52′S, 73°52′W), 6 Feb 1958, MNHNC 940002; 3 females (CL 6.23, 4.15 and 6.08 mm; TL 34.50, 35.12 and 34.35 mm, respectively), Lechagua, near Ancud, Chiloé Island (41°52′S, 73°52′W), 6 Feb 1958, MNHNC 940005; 4 males (CL 4.26, 4.56 and 4.86 mm; TL 25.84, 24.48 and 26.76 mm, respectively; 1 individual incomplete), Lechagua, near Ancud, Chiloé Island (41°52′S, 73°52′W), 6 Feb 1958, MNHNC 940008; 1 ovig. female (CL 7.3 mm; TL 38.0 mm) associated with mussel raft culture, Putemún, Chiloé Island (42°25′S, 73°43′W), approximately 5 m, 12 May 1994, IZUA 542.

Remarks.—The present material extends considerably the southern limit of this species from northern (Isla Santa María, 23°S) to southern Chile (Isla Chiloé, 42°S), a distance of approximately 2030 km. Thus, the range of this species now covers the area between the Gulf of California and southern Chile (see Wicksten 1990). *Hippolyte williamsi* has been confused with *H. californiensis* in the Gulf of California, but the two can be separated by the number of spines on the distal end of the first antennular segment (Wicksten 1983b). *H. californiensis* has one or rarely two spines, whereas *H. williamsi* has three. Zuñiga et al. (1978) pointed out some differences between the original description (Schmitt 1924) and the specimens collected in northern Chile. Additionally, we have observed the following variations: (1) The first segment of antennular peduncle bears 3–4 and (2) the merus of the fourth pereiopod has 2 or 3 spines. Our measurements indicate a latitudinal cline in adult size (TL, CL), with considerably larger individuals in Chiloé Island (largest female from Putemún: 38.0 mm) compared to specimens from northern Chile (Coquimbo: mean female TL of 17.3 mm). A similar tendency has been reported by Boschi et al. (1969) for the brachyuran crab *Halicarcinus planatus* (Fabricius) from the Argentinean coast.

Eualus dozei (A. Milne-Edwards, 1891)

Previous known distribution.—Southern Chile (between 55°36′S, 67°40′W and 42°20′S, 72°22′W), from 8 to 300 m (A. Milne-Edwards 1891, Holthuis 1952, Aracena & López 1973).

Material examined.—1 ovig. female collected from sand and shell, Galápagos Islands (Tagus Cove, Isla Isabela), 15 Jan 1934, 18–33 m, *Velero III* station 157-34; collection of the USNM 276061; 4 females (CL 2.2, 2.2, 2.4 and 2.0 mm; TL 12.3, 12.1, 12.1 and 12.9 mm, respectively) associated with suspended scallop culture, Bahía de Guanaqueros (30°08′S, 71°25′W), approximately 5 m, 13 Nov 1993, IZUA 538; 2 females (CL 2.8 and 2.6 mm; TL 12.9 and 12.4 mm, respectively) associated with suspended scallop culture, Bahía de Tongoy (30°13′S, 71°32′W), approximately 5 m, 27 Jul 1992, IZUA 539.

Remarks.—Our material represents the northernmost record of this species, and the first from Galápagos Islands. So far, the species has not been reported from Perú (see Méndez 1981) or Argentina (Boschi et al. 1992). Zarenkov (1970) reported a single specimen from 53°S 52′S-64°10′E, but was unable to determine it with certainty due to the poor condition. It is of interest to note that our material as well as those of *E. dozei* collected during the LUCE (see Holthuis 1952) and the Soviet Antarctic Expedition (see Zarenkov 1970), are all females. As indicated by our material, this species occurs in relatively deep and shallow waters (approximately 5 to 300 m).

Lysmata intermedia (Kingsley, 1878)

Previous known distribution.—Florida Keys to Tobago and Curaçao; Azores; Galápagos Islands (Wicksten 1990); eastern Pacific: from México to Perú (03°30′S–03°44′S) (Méndez 1981, Wicksten & Méndez 1983, Hendrickx & Wicksten 1987); up to 36 m (Méndez 1981).

Material examined.—1 male collected from suspended scallop cultures (CL 8.2 mm, TL 33.8 mm), Bahía de Guanaqueros (30°08′S; 71°25′W), approximately 8 m, 31 Jul 1993, IZUA 537.

Remarks.—This is the first report of a species of *Lysmata* from Chile. The specimen collected extends the known geographical distribution of the species by almost 27° of latitude (approximately 2960 km) to the south. Monthly sampling in the Bahía de Guanaqueros did not produce additional specimens of this species.

Genus *Ogyrides* Stebbing, 1914
Ogyrides sp.

Material examined.—1 female (CL 5.8 mm, TL 21.1 mm) obtained from a stomach content of *Eleginops maclovinus* (Pisces, Nototheniidae), Mehuín, estuary of river Lingue (39°25′S, 73°13′W), Feb 1991, IZUA 543.

Remarks.—Species of *Ogyrides* are known from warm-temperate and tropical waters (Wicksten & Méndez 1988); however, our sampling site (Mehuín) lies in the cold-temperature region (see Brattström & Johanssen 1983). The specimen collected is a noteworthy record, representing the first account of a representative of the family Ogyrididae from Chile. Two species of *Ogyrides* have been reported from the eastern Pacific Ocean (Carvacho & Olson 1984, Wicksten & Méndez 1988): *O. alphaerostris* (Kingsley 1880) and *O. tarazonai* Wicksten & Méndez, 1988. Due to the incomplete condition of our specimen, we were unable to identify it to the species level. Our specimen clearly has more than one spine on the dorsal midline of the carapace

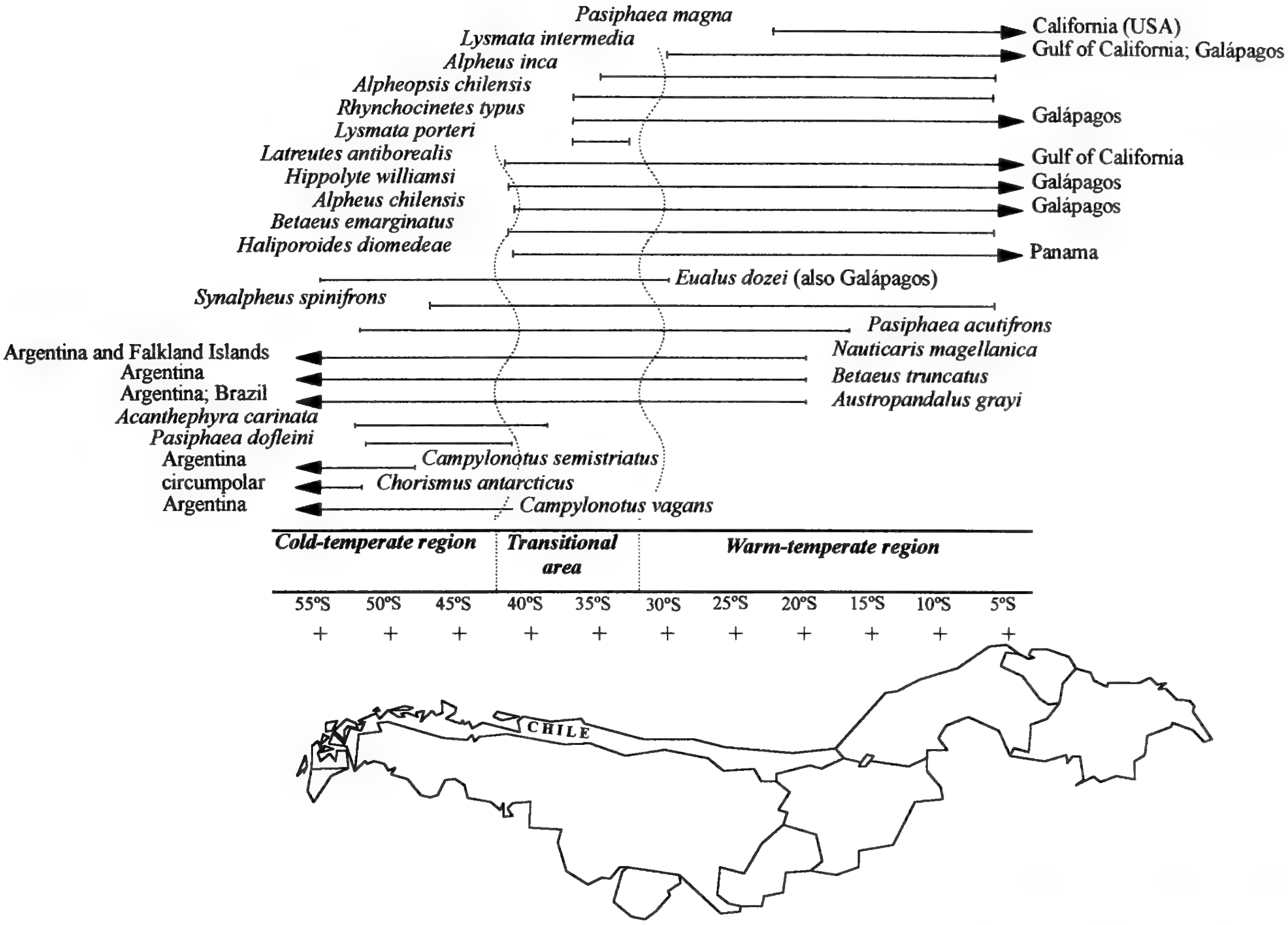

Fig. 1. Eastern Pacific distribution of 22 shrimps inhabiting the continental shelf along the Chilean coast. Ranges extending to the Atlantic coast of South America are also indicated.

(at least 4–5 spines). Our individual is not *O. tarazonai*, known from Nicaragua and Perú, or *O. hayi*, from Puerto Rico and eastern United States (North Carolina to Florida and Mississippi), both of which have a single dorsal spine on the carapace (see Williams 1981).

Zoogeographic Affinities

According to Brattström & Johanssen (1983), who reviewed the ecological and regional zoogeography of the marine benthic fauna of Chile, three zoogeographic zones can be distinguished on this coast: cold-temperate and warm-temperate region zones, separated by a transitional zone (see also Dahl 1960). The following remarks are based on shrimp species known from the continental shelf (0–200 m) of Chile. Deep-water (>200 m) species are excluded. The distributions of the species considered are summarized in Fig. 1.

Of the species reported from Chile, a relatively small group occur in the subantarctic or cold-temperate regions; these are *Acanthephyra carinata* Bate 1888, *Pasiphaea dofleini* Schmitt 1932, *Campylonotus semistriatus* Bate 1888, *C. vagans* Bate 1888 and *Chorismus antarcticus* (Pfeffer 1887). Members of this group generally inhabit waters around 50°S and 55°S of latitude, although the range of one species (*A. carinata*) extends its northernmost distribution up to Chiloé Island (42°S).

Another group of species, *Pasiphaea acutifrons* Bate 1888, *Nauticaris magellanica* (A. Milne Edwards 1891), *Betaeus truncatus* Dana 1852 and *Austropandalus grayi* (Cunningham 1871), seems to be fairly eurythermic with distributions that include warm-temperate as well as cold-temperate regions. The most distinctive feature of this group is the capacity of its members to cross the Chiloé boundary (see Brattström & Johanssen 1983).

The majority of the species considered show clear boreal affinities, with their northern distribution limit [except *Lysmata porteri* (Rathbun 1907)] extending to the Peruvian Province. Chiloé Island is the southern limit of the distribution of five species, which confirms that the area around 42°S serves as a separation zone between the cold-/and warm-temperate regions described by Brattström & Johanssen (1983) for the Chilean coast. The southern distribution limit of the remaining species of this group is between 30° (Coquimbo) and 42°S (Chiloé Island), which according to Brattström & Johanssen (1983) corresponds to a transitional area between the Magellanic and Peruvian Provinces. As is typical for transitional zones, this area does not contain an endemic fauna, although one species (*Lysmata porteri*) is found exclusively in this area. The boundary between this transitional area and the Peruvian Province is not clear, but probably is located around Coquimbo (30°S). Additional information on the shrimp fauna of northern Chile is needed to properly evaluate the various zoogeographic boundaries.

The influence of the Peruvian Province on the caridean fauna of Chile becomes apparent from Coquimbo (30°S) on northward. A distributional boundary apparently is located around Iquique (20°S), where the northern limit of four eurythermic species (*Pasiphaea acutifrons*, *Nauticaris magellanica*, *Betaeus truncatus* and *Austropandalus grayi*) is located. However, this observation could be attributed to the much more intense sampling programs in this area (Holthuis 1952, Retamal & Soto 1993). The northern limit of carideans from the Peruvian Province seems to be located around the equator.

The several distribution patterns of carideans from Chile are influenced by the prevailing current system (see Brattström & Johanssen 1983, and references cited therein). The Chiloé boundary corresponds to the area where the Westwind Drift reaches the continent and splits into the Perú Coastal Current (northward) and the Cape Horn Current (southward). The Perú Coastal Current gradually joins the South Equatorial Current, which may explain, in part, the presence of some species [*Alpheus chilensis* Coutière (in Lenz 1902), *Hippolyte williamsi*, *Eualus dozei*, *Lysmata intermedia* and *Glyphocrangon loricata* Faxon 1895] that occur both in Chile and the Galápagos Islands (see Chávez & Brusca 1991, Wicksten 1991).

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Literature Cited

Aracena P., O., & M. T. López. 1973. Observaciones biológicas en organismos encontrados en substratos artificiales. Caleta Leandro, Talcahuano, Chile. I. Crustacea Decapoda Macrura.—Trabajo de V Congreso Latinoamericano de Zoología 1:40–48.

Arntz, W. E., M. Gorny, I. S. Wehrtmann, M. Lardies, & R. Soto. 1996. Crustacea Decapoda: summary report. Pp. 57–59 *in* W. Arntz & M. Gorny, eds., Cruise Report of the Joint Chilean-German-Italian Magellan "Victor Hensen" Campaign 1994. Berichte zur Polarforschung 190.

Bate, C. S. 1888. Report on the Crustacea Macrura collected by H. M. S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H. M. S. "Challenger" during the Years 1873–76, 24:1–942.

Boschi, E. E., C. E. Fischbach, & M. I. Iorio. 1992. Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina.—Frente Marítimo, Montevideo 10:7–94.

———, M. A. Scelzo, & B. Goldstein. 1969. Desarrollo larval del cangrejo, *Halicarcinus planatus* (Fabricius) (Crustacea, Decapoda, Hymenosomidae), en el laboratorio, con observaciones sobre la distribución de la especies.—Bulletin of Marine Science 19:225–242.

Brattström, H., & A. Johanssen. 1983. Ecological and regional zoogeography of the marine benthic fauna of Chile.—Sarsia 68:289–339.

Carvacho, A., & R. Olson. 1984. Nuevos registros para la fauna carcinológica del noreste de México y descripción de una nueva especia: *Eualus subtilis* n.sp. (Crustacea: Decapoda: Natantia).—The Southwestern Naturalist 29:59–71.

Chace, F. A. 1986. The Caridean Shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907–1910, Part 4: Families Oplophoridae and Nematocarcinidae.—Smithsonian Contribution to Zoology 432:1–182.

Chávez, F. P., & R. C. Brusca. 1991. The Galápagos Islands and their relation to oceanographic processes in the Tropical Pacific. Pp. 9–33 *in* M. J. James, ed., Galápagos marine invertebrates. Plenum Publishing Cooperation, New York, 474 pp.

Cunningham, R. O. 1871. Notes on the Reptiles, Amphibia, Fishes, Mollusca, and Crustacea obtained during the voyage of H. M. S. "Nassau" in the years 1866–69.—Transactions of the Linnean Society of London 27:465–502.

Dahl, E., 1960. The cold temperate zone in Chilean seas.—Proceedings of the Royal Society, B 152:631–633.

Dana, J. D. 1852. Conspectus Crustaceorum quae in Orbis Terrarum Circumnavigatione, Carolo Wilkes e Classe Reipublicae Foederatae Duce, lexit et descripsit.—Proceedings of the Academy of Natural Sciences of Philadelphia 1852: 10–28.

Del Solar, E., & M. Mistakidis. 1971. Informe del crucero SNP-1 7105. Exploración de Crustáceos.—Instituto del Mar del Perú, Serie de Informes Especiales IM-89:1–10.

———, & L. A. Flores. 1972. Exploraciones de Crustáceos (Zona Sur), Crucero SNP-1 7201.—Instituto del Mar del Perú, Serie de Informes Especiales IM-107:1–8.

Fabricius, J. C. 1798. Supplementum Entomologiae Systematicae. Hafniae, Copenhagen, 572 pp.

Faxon, W. 1893. Reports on the dredging operations off the west coast of Central America to the Galápagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross" during 1891, Lieut. Commander Z. L. Tanner, U.S.N., Commanding, VI: Preliminary descriptions of new species of Crustacea.—Bulletin of the Museum of Comparative Zoology Harvard 24(7):149–220.

———. 1895. The stalk-eyed Crustacea. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galápagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut. commander Z.L. Tanner, U.S.N., commanding.—Memoirs of the Museum of Comparative Zoology Harvard 18: 1–292.

Hendrickx, M. E., & M. K. Wicksten. 1987. Studies of the coastal marine fauna of southern Sinaloa, Mexico. VIII. Additional report on the caridean crustaceans.—Anales del Instituto de Ciencias del Mar y Limnología de la Universidad Nacional Autónoma de México 14(1):13–20.

Holthuis, L. B. 1952. Reports of the Lund University Chile Expedition 1948–49. 5. The Crustacea Decapoda Macrura of Chile.—Lunds Universitets Årsskrift N.F. Avd. 2, Band 47(10):109 pp.

———. 1955. The recent genera of the Caridean and Stenopodidean shrimps (class Crustacea, order Decapoda, supersection Natantia) with keys for their determination.—Zoologische Verhandelingen, Leiden 26:1–157.

———. 1980. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries.—FAO Fisheries Synopsis 125:1–261.

Kensley, B. 1981. On the zoogeography of southern African decapod Crustacea, with a distributional checklist of the species.—Smithsonian Contribution to Zoology 338:1–64.

Kingsley, J. S. 1878. Notes on the North American Caridea in the Museum of the Peabody Academy of Science at Salem, Massachusetts.—Proceedings of the Academy of Natural Science of Philadelphia 1878:89–98.

———. 1880. On a collection of Crustacea from Virginia, North Carolina and Florida with a revision of the genera of Crangonidae and Palaemonidae.—Proceedings of the Academy of Natural Science of Philadelphia 31:383–427.

Leach, W. E. 1814. Crustaceology. Pp. 383–437 *in* D. Brewster, ed., Edinburgh Encyclopedia, Volume 7.

Lenz, H. 1902. Die Crustaceen der Sammlung Plate (Decapoda und Stomatopoda).—Fauna chilensis 2(3). Zoologische Jahrbücher, supplement 5: 731–772.

Méndez, G. M. 1981. Claves de identificación y distribución de los langostinos y camarones (Crustacea: Decapoda) del Mar y ríos de la costa del Perú.—Boletín del Instituto del Mar de Perú-Callao 5:1–170.

Milne-Edwards, A. 1881. Description de quelques Crustacés Macroures provenant des grandes profondeurs de la mer des Antilles.—Annales Sciences Naturelles, Paris, Zool., ser. 6, vol. 11: 1–16.

———. 1891. Crustacés.—Mission scientifique du Cap Horn. 1882–1883, 6, Zool., 1–54.

Milne Edwards, H. 1837. Histoire Naturelle des Crustacés, comprenant l' anatomie, la physiologie et la classification de ces animaux. Volume 2, Roret, Paris, 532 pp.

Noziglia, L., & P. Arana. 1976. Observaciones biológico-pesqueras de la gamba, *Hymenopenaeus diomedeae* Faxon, 1893, en el Pacífico sur oriental.—Revista de la Comisión Permanente del Pacífico Sur 5:187–195.

Pérez Farfante, I. 1977. American solenocerid shrimps of the genera *Hymenopenaeus, Haliporoides, Pleoticus, Hadropenaeus* new species and *Mesopenaeus* new genus.—Fishery Bulletin 75:261–346.

Pfeffer, G. 1887. Die Krebse von Süd-Georgien nach der Ausbeute der Deutschen Station 1882–83.—1. Teil. Jahrbuch der Hamburger wissenschaftlichen Anstalt 4:41–150.

Rafinesque, C. S. 1815. Precis des decouvertes et travaux somiologiques. Rouale Typographie Militarie, Palerme, 55 pp.

Rathbun, M. J. 1907. South American Crustacea.—Revista Chilena de Historia Natural 11:45–50.

Retamal, M. A. 1981. Catálogo ilustrado de los crustáceos decápodos de Chile.—Gayana Zoología 44:7–110.

———, M. A. 1993. Crustáceos decápodos abisales de la zona Iquique-Arica.—Estudios Oceanológicos 12:1–8.

Richardson, L. R., & J. C. Yaldwyn. 1958. A guide to the natant decapod Crustacea (shrimps and prawns) of New Zealand.—Tuatara 7:17–41.

Risso, A. 1816. Histoire naturelle des Crustáces des environs de Nice. Librairie Grecque-Latine-Allemand, Paris, 175 pp.

Savigny, J.-C. 1816. Mémoires sur les animaux sans vertèbres, pt. 1, pp. 1–117.

Schmitt, W. L. 1921. The marine decapod Crustacea of California.—University of California Publications in Zoology 23:1–470.

———. 1924. Report of the Macrura, Anomura and Stomatopoda collected by the Barbados-Antigua Expedition from the University of Iowa in 1918.—University of Iowa Studies in Natural History 10:65–99.

———. 1932. A new species of *Pasiphaea* from the Strait of Magellan.—Journal of the Washington Academy of Sciences 22:333–335.

Stebbing, T. R. R. 1914. South African Crustacea (Part VII of South African Crustacea, for the marine investigations in South Africa).—Annals of the South African Museum 15:1–55.

Thallwitz, J. 1892. Decapoden-Studien, insbesondere basirt auf A. B. Meyer's Sammlungen im Ostindischen Archipel, nebst einer Aufzählung der Decapoden und Stomatopoden des Dresdener Museums.—Abhandlungen und Berichte des zoologisch-anthropologischen Museums Dresden, 1890–91:1–55.

Tiefenbacher, L. 1994. Decapode Crustaceen aus westantarktischen Gewässern gesammelt von der R. V. "John Biscoe," Reise 11.—Spixiana 17(1): 13–19.

Vinuesa, J. H. 1977. Aportes al conocimiento de los crustáceos decápodos de Tierra del Fuego con algunas observaciones zoogeográficas.—Physis, Sección A, 36(92):9–19.

Wehrtmann, I. S., & M. Lardies. 1996. Species composition and geographical distribution of caridean shrimps (Decapoda: Caridea). Pp. 63–66 *in* W. Arntz & M. Gorny, eds, Cruise Report of the Joint Chilean-German-Italian Magellan "Victor Hensen" Campaign 1994. Berichte zur Polarforschung 190.

Wicksten, M. K. 1983a. *Plesionika santaecatalinae*: a new species of deep sea shrimp from the Eastern Pacific (Caridea, Pandalidae).—Bulletin Southern California Academy of Sciences 3: 138–143.

———. 1983b. Shallow water caridean shrimps of the Gulf of California, Mexico.—Allan Hancock Monographs in Marine Biology 13:59 pp.

———. 1990. Key to the hippolytid shrimp of the eastern Pacific Ocean.—Fishery Bulletin, U.S. 88:587–598.

———. 1991. Caridean and stenopodid shrimp of the Galápagos Islands. Pp. 147–156 *in* M. J. James, ed., Galápagos marine invertebrates. Plenum Publishing Cooperation, New York, 474 pp.

———, & M. E. Hendrickx. 1992. Checklist of penaeoid and caridean shrimps (Decapoda: Penaeoidea, Caridea) from the eastern tropical Pacific.—Proceedings of the San Diego Society of Natural History 9:1–11.

———, & M. Méndez G. 1981. *Alpheus inca*: a new snapping shrimp (Caridea: Alpheidae) from western South America.—Journal of Crustacean Biology 1:137–142.

———, & ———. 1983. Nuevos registros de camarones carídeos en el Perú.—Boletín de Lima 25:1–15.

———., & ———. 1988. New records for *Ogyrides alphaerostris* and a new species, *Ogyrides tarazonai* (Crustacea: Ogyrididae), from the eastern Pacific Ocean.—Proceedings of the Biological Society of Washington 101:622–625.

Williams, A. B. 1981. Western Atlantic species of the caridean shrimp genus *Ogyrides*.—Journal of Crustacean Biology 1:143–147.

Wood-Mason, J. 1891. Class Crustacea. Pp. 268-286 *in* J. Wood-Mason & A. Alcock, eds., Natural history notes from H.M. Indian Marine Survey Steamer "Investigator," Commander R.F. Hoskyn, R. N., commanding. Series II., No. 1. On the results of deep-sea dredging during the season 1890–1891.—Annals and Magazine of Natural History 6(8).

———. 1893. Natural history notes from H.M. Indian Marine Survey Steamer "Investigator," Commander R.F. Hoskyn, R. N., commanding. Series II. N° 1. Notes on the results of the last season's deep sea dredging during the season 1890–1891.—Annals and Magazine of Natural History 6(11):161–172.

Zarenkov, N. A. 1970. Crustacean Decapoda collected by the Soviet Antarctic expeditions in the antarctic and antiboreal regions.—Biological Reports of the Soviet Antarctic Expedition (1955–1958) 4:153–201.

Zariquiey, R. 1968. Crustáceos Decápodos Ibéricos.—Investigaciones Pesqueras 32:510 pp.

Zuñiga R., O., H. Baeza K., & R. Castro R. 1978. Nuevos registros de Hippolytidae para Chile (Crustacea, Decapoda, Natantia).—Noticiario Mensual del Museo Nacional de Historia Natural, Santiago, Chile 23(264):3–7.

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A new species of the genus *Petrolisthes* Stimpson, 1858 (Crustacea: Decapoda: Anomura: Porcellanidae) from Yonaguni Island, the Ryukyu Islands

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Abstract.—A new species of the genus *Petrolisthes* Stimpson, 1858, *P. donanensis*, is described and illustrated on the basis of two specimens collected from Yonaguni Island, the Ryukyu Islands. This species closely resembles *P. decacanthus* Ortmann, 1897, but is distinguishable from the latter species by the following characters: sinuously triangular rostrum; absence of hepatic spines; antennular peduncles with basal segment unarmed on anterior margin except for a strong spine on lateral corner; chelipeds with palm bearing a small spine at subdistal corner of dorsoflexor margin; and ambulatory legs with slenderer propodi, and dactyli bearing four flexor spines.

The porcellanid crab genus *Petrolisthes* Stimpson, 1858, includes numerous intertidal or subtidal species. Eighteen species have been reported from the Ryukyu Islands, southwestern Japan (Miyake 1982, Kropp 1986, Osawa 1996), some of which are conspicuous on the intertidal boulder beaches of the islands (Asakura 1991).

Through the courtesy of Mr. K. Nomura of the Kushimoto Marine Park and Dr. T. Komai of the Natural History Museum and Institute, Chiba, I had the opportunity to examine two porcellanid crabs collected from the intertidal zone of Yonaguni Island (24°27′N, 122°56′E), the westernmost of the Ryukyus chain. The examination revealed that the two specimens belong to an undescribed species of the genus *Petrolisthes*. This new species is herein described and illustrated.

The carapace length (CL) and width (CW), as indications of specimen size, were measured, CL from the anterior tip of the rostrum to the median posterior end of the carapace, and CW at the broadest part. Measurements of ambulatory legs were made as follows: lengths of carpus and propodus along extensor margin, and height of propodus at midline. The type specimens are deposited in the Natural History Museum and Institute, Chiba (CBM).

Petrolisthes donanensis, new species
Figs. 1, 2

Type material.—Holotype: ovig. female (CL 8.6 mm, CW 8.9 mm), Yonaguni Island, Ryukyu Islands, intertidal, 15 Apr 1995; CBM-ZC 2147. Paratype: 1 female (CL 5.9 mm, CW 5.9 mm), same data as holotype; CBM-ZC 2148.

Description.—Carapace (Fig. 1A, B) weakly convex dorsally, slightly broader than long or as long as broad, broadest on posterior branchial regions. Branchial margins strongly convex, with longitudinal tuberculated edges, posterior branchial margins with strong transverse rugae. Rostrum (Fig. 1C) moderately broad, slightly bent ventrally, sinuously triangular; median lobe strongly produced; dorsal surface with numerous small, flattened tubercles. Protogastric ridges distinct, divided into 2 lobes by median groove extending to tip of rostrum. Orbits (Fig. 1G) deep; orbital margin armed

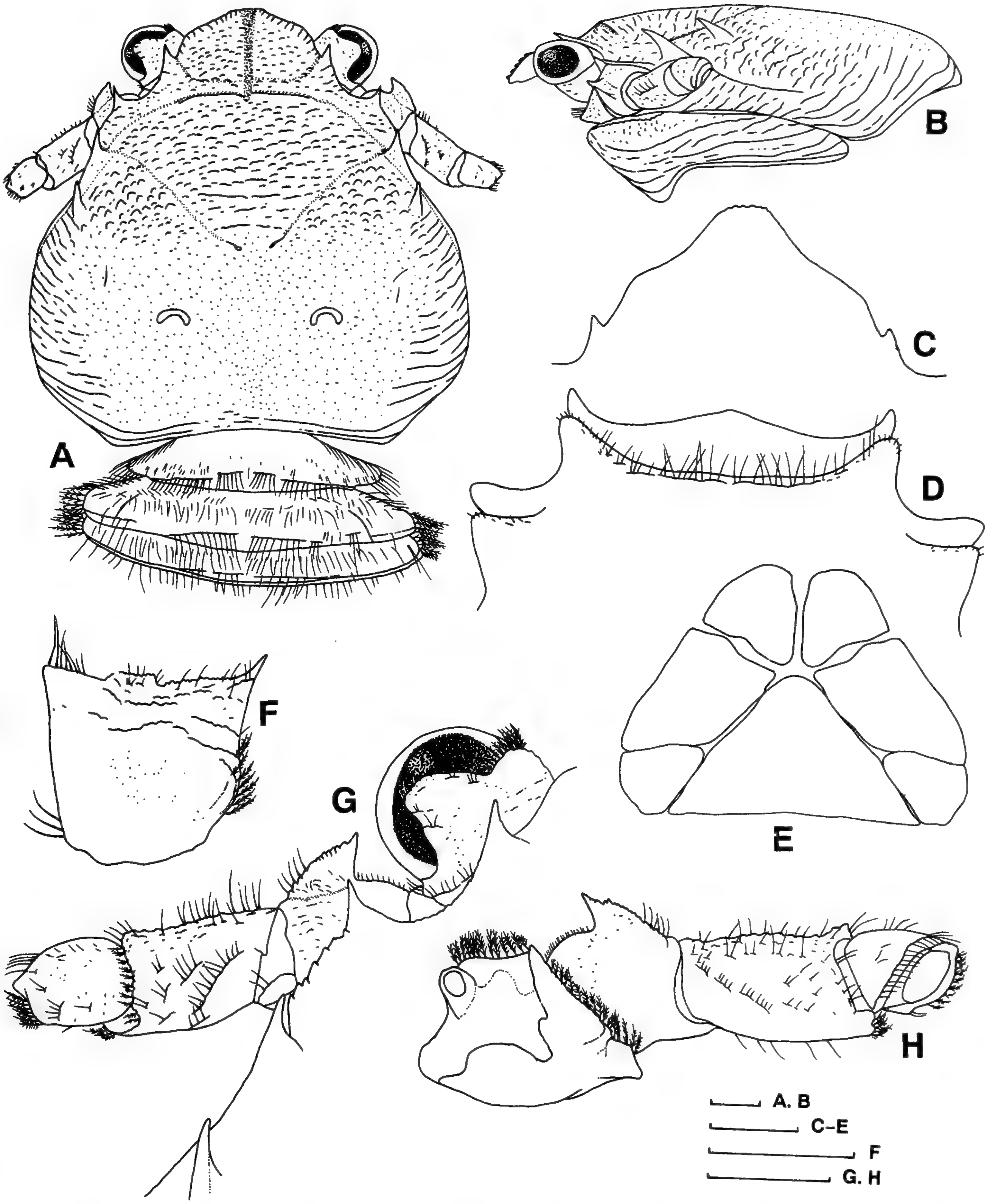

Fig. 1. *Petrolisthes donanensis*, new species. Holotype, ovigerous female (CL 8.6 mm, CW 8.9 mm; CBM-ZC 2147). A, carapace and proximal somites of abdomen, dorsal; B, carapace and pterygostomian flap, lateral; C, rostrum, frontal; D, thoracic sternites, ventral; E, telson, exposed; F, left basal segment of antennular peduncle, ventral; G, left eye and antennal peduncle, dorsal; H, left antennal peduncle, ventral. Scales equal 1.0 mm.

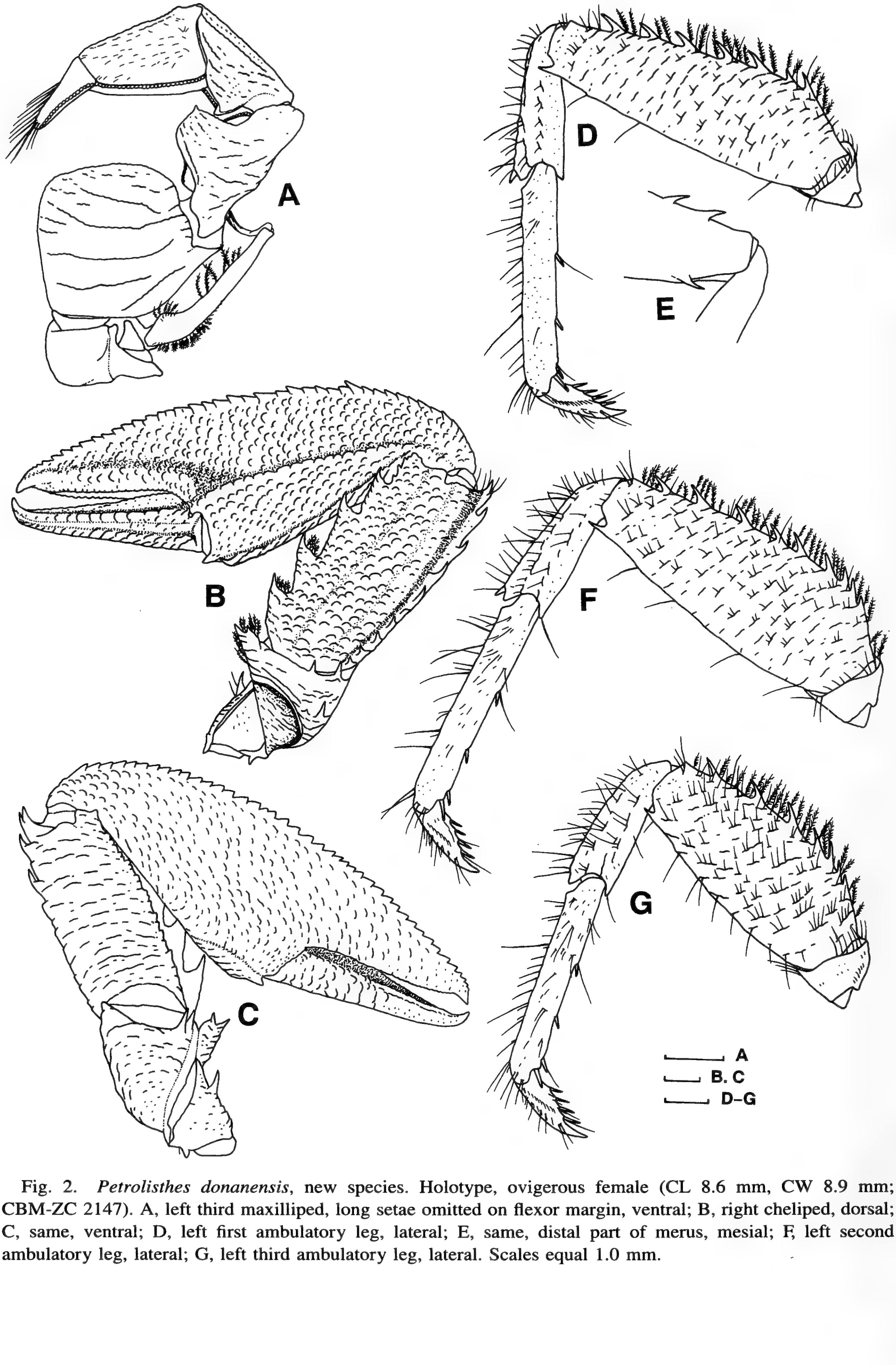

Fig. 2. *Petrolisthes donanensis*, new species. Holotype, ovigerous female (CL 8.6 mm, CW 8.9 mm; CBM-ZC 2147). A, left third maxilliped, long setae omitted on flexor margin, ventral; B, right cheliped, dorsal; C, same, ventral; D, left first ambulatory leg, lateral; E, same, distal part of merus, mesial; F, left second ambulatory leg, lateral; G, left third ambulatory leg, lateral. Scales equal 1.0 mm.

with well developed supraocular spine; outer orbital angle produced into strong, acute spine. Gastric region with numerous flattened tubercles and short, transverse rugae; metagastric region with rugae longer and more distinct. Hepatic margins tuberculate, lacking spines. Cervical grooves moderately marked. Two epibranchial spines well developed on each side. Anterior branchial regions with weakly developed tubercles. Posterior branchial and cardiac regions covered with short plumose or simple setae. Rugae and flattened tubercles on carapace fringed with short plumose or simple setae anteriorly.

Pterygostomian flaps (Fig. 1B) provided with longitudinal ridges, anterodorsal margin fringed with small tubercules.

Third thoracic sternite (Fig. 1D) strongly depressed, trilobate anteriorly; median lobe not exceeding laterals, with broadly rounded apex. Fourth sternite provided with series of short rugae along concave, anterior margin.

Telson (Fig. 1E) as illustrated.

Ocular peduncles (Fig. 1G) moderately large, short, with several short striae on dorsal surface; dorsal extension onto cornea rounded; anterodistal margin fringed with short plumose setae.

Basal segment of antennular peduncles (Fig. 1F) transversely rugose on anterior region of ventral surface; anterior margin weakly produced, tuberculate, with strong, acute spine laterally.

Antennal peduncles (Fig. 1G, H) 4-segmented; first segment immovable, following segments movable. First segment not strongly produced forward in lateral view, with small projection anterodistally. Second segment armed anteriorly with triangular crest bearing small tuberculate spine at proximal end, dorsal and ventral surfaces relatively smooth. Third segment rectangular, anterior margin minutely crenulate, dorsal and ventral surfaces with oblique rugae. Fourth segment smooth.

Third maxillipeds (Fig. 2A) robust. Ischium broad, ovate, transversely rugose on ventral surface. Merus provided with laminate and subrectangular lobe with small tuberculate spine on ventroflexor margin, transversely rugose on ventral surface. Carpus with distinct projection on subproximal region of flexor margin, and longitudinal rugae on ventral surface, one of those rugae along ventroextensor margin forming ridge. Propodus with scattered short setae on ventral surface, and longitudinal striae along extensor margin. Dactyl subtriangular, ventral surface smooth. Exopod laminate, slender, inflated proximally, with distal flagellum. Rugae on ventral surface of ischium to carpus fringed with short plumose setae on anterior sides.

Chelipeds (Fig. 2B, C) subequal (left cheliped missing in holotype). Ischium armed with strong, acute spine near distal end of ventroflexor margin. Merus short; dorsal surface transversely rugose, with distinct transverse ridge submedially, and 1 median spine near extensor margin; dorsoflexor margin provided with crenulate lobe with 1 or 2 small spines at distal end; dorsodistal margin armed with 2 spines; ventral surface rugose, distoflexor margin with 2 spines. Carpus (excluding flexor marginal teeth) 2.3 times as long as broad; dorsal surface with numerous small, flattened or weakly developed tubercles, median, longitudinal, weak ridge (composed of series of squamae in paratype) and shallow sulcus along extensor margin; dorsoflexor margin armed with 4 strong acute teeth serrated or crenulate along edges; dorsoextensor margin provided with 8–10 spines along entire length, distal spine with double-pointed apices; ventral surface transversely rugose, flexor margin crenulate. Palm with extensor margin thin, weakly arched and serrated; dorsal surface with distinct, median, longitudinal ridge extending from proximal end of palm to base of dactyl, and composed of series of flattened, squamose tubercles; surface between flexor margin and longitudinal ridge with numerous small, flattened tubercles; surface between extensor margin and longitudinal ridge with numerous small, flattened or weakly to moderately developed tubercles; dorsoflexor margin with longitudinal rugose ridge and 1 small but distinct spine at subdistal corner; ventral surface with numerous short, oblique rugae. Fixed finger with numerous small, weakly developed tubercles on dorsal surface; ventral surface rugose as in palm. Dactyl with dorsal surface armed with longitudinal ridge of flattened and imbricated tubercles along midline, and rugose ridge along flexor margin; ventral surface with small, flattened tubercles. Rugae and tubercles on dorsal surface of merus to dactyl fringed with short plumose setae arising from distal sides.

Ambulatory legs (Fig. 2D–G) relatively slender. Merus elongate, narrowing distally; extensor margin serrate, number of spines 5–7 in first, 7–9 in second, and 5–7 in third legs, and furnished with short, plumose or simple setae; lateral surface with numerous short, transverse rugae; distoflexor margin armed with 1 acute spine (lacking on third leg of paratype); flexor margin on mesial surface provided with 1 strong spine subdistally. Carpus relatively long, with short, longitudinal rugae furnished with simple, short and long setae on lateral surface; subdistoextensor angles of first and second legs armed with 1 spine (lacking on second leg of paratype), unarmed on third leg. Propodus slender, long, approximately 1.4 times as long as carpus and 6.6–7.1 times as long as high; lateral surface and extensor margin with scattering, simple, short and long setae; flexor margin armed with 2 or 3 movable spines in addition to distal pair. Dactyl terminating in slightly curved claw, flexor margin with 4 movable spines.

Color (preserved in ethanol).—Carapace, chelipeds, and ambulatory legs dark or light reddish except for following parts of ambulatory legs: distal part of merus, proximal and distal parts of carpus and propodus (whitish), and dactyl (whitish but dark brown in distal claw).

Distribution.—So far known only from the type locality, Yonaguni Island, the westernmost of the Ryukyus; intertidal.

Etymology.—This specific name is derived from "Donan," which means Yonaguni Island in the Ryukyu dialect.

Remarks.—Haig & Kropp (1988) described *Petrolisthes eldredgei*, and redescribed two poorly known species, *P. decacanthus* Ortmann, 1897 and *P. bispinosus* Borradaile, 1900, all from the Indo-West Pacific. They mentioned that the three species stand out as a group quite distinct from other Indo-West Pacific congeners by the sharing of the following characters: transversely rugose carapace; presence of two pairs of the epibranchial spines; unarmed mesobranchial margins; and merus of the first ambulatory leg with a strong subdistal spine on the mesial flexor margin. These four characteristics are also found in the present new species, therefore, *P. donanensis* can be considered the fourth member of this group.

Petrolisthes donanensis most closely resembles *P. decacanthus*. These two species share the following characters: orbital angles produced into a strong spine; presence of a pair of supraocular spines; and chelipeds with carpus and palm covered with numerous imbricated tubercles and granules on the dorsal surface. The second feature also distinguishes the two species from *P. bispinosus* and *P. eldredgei*. In addition to these characters, the spine on the ventroflexor margin of the ischium of the chelipeds found in *P. donanensis*, which has not been described previously for any species of *Petrolisthes*, was also confirmed in specimens of *P. decacanthus* from Guam (R. K. Kropp, pers. comm.), and in the figure of this species by Haig & Kropp (1988: fig. 3e), although the spine was rather weak. *Petrolisthes donanensis*, however, differs from *P. decacanthus* in: the sinuously triangular rostrum (trilobate in *P. decacanthus*); absence of hepatic spines; antennular peduncles with basal segment unarmed on the anterior margin except for a strong spine at the lateral corner (with several strong spines and denticles in *P. decacanthus*); chelipeds with palm bearing a small spine at the subdistal corner of the dorsoflexor margin; and ambulatory legs with slenderer propodi and dactyli bearing four flexor spines (three spines in *P. decacanthus*).

The presence of a pair of supraocular spines and two pairs of epibranchial spines in *P. donanensis* and *P. decacanthus*, also links these to several Indo-West Pacific species such as *P. scabriculus* (Dana, 1852), *P. militaris* (Heller, 1862), *P. perdecorus* Haig, 1981, and *P. heterochrous* Kropp, 1986. Based on the examination of material of *P. militaris* from the Ryukyus and Indonesia, the species has been found to possess a strong subdistal spine on the mesial flexor margin of the merus of the first ambulatory leg, as well as *P. bispinosus*, *P. eldredgei*, *P. decacanthus*, and *P. donanensis*.

A key to the Indo-west Pacific species with a pair of supraocular spines and two pairs of epibranchial spines is provided below.

1. Branchial margins of carapace armed with spines 2
– Branchial margins of carapace unarmed 5
2. Orbits deep. Dorsal surface of carapace with dense, short pubescence and scattered, long setae . . . . *P. perdecorus*
– Orbits rather shallow 3
3. Inner orbital angles produced into small spine . . . . *P. scabriculus*
– Inner orbital angles unarmed 4
4. Rostrum trilobate . . . . *P. heterochrous*
– Rostrum sinuously triangular . . . . *P. militaris*
5. Rostrum trilobate . . . . *P. decacanthus*
– Rostrum sinuously triangular . . . . *P. donanensis*, new species

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Literature Cited

Asakura, A. 1991. Differences in the patterns of distribution of the porcelain crab, *Petrolisthes japonicus* on an oceanic island (Chichijima, Ogasawara) and on a continental island (Zamami, Okinawa).—Researches on Crustacea 20:23–28.

Borradaile, L. A. 1900. On the Stomatopoda and Macrura brought by Dr. Willey from the South Seas. Pp. 395–428 *in* A. Willey, ed., Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897. Part IV, University Press, Cambridge.

Dana, J. D. 1852. Crustacea, Part 1.—United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wikes, U. S. N. 13:1–685. (Sherman, Philadelphia.)

Haig, J. 1981. Three new species of *Petrolisthes* (Decapoda, Anomura, Porcellanidae) from the Indo-West Pacific.—Journal of Crustacean Biology 1:265–271.

———, & R. K. Kropp. 1988. *Petrolisthes eldredgei*, a new porcellanid crab from the Indo-West Pacific, with redescription of two related species.—Micronesia 20:171–186. [Issue dated December 1987.]

Heller, C. 1862. Neue Crustaceen gesammelt während der Weltumseglung der K. K. Fregatte "Novara." Zweiter vorläufiger Bericht.—Verhandlungen der kaiserlich-königlichen Zoologisch-Botanischen Gesellschaft in Wien 28:519–528.

Kropp, R. K. 1986. A neotype designation for *Petrolisthes tomentosus* (Dana), and description of *Petrolisthes heterochrous*, new species, from the Mariana Islands (Anomura: Porcellanidae).—Proceedings of the Biological Society of Washington 99:452–463.

Miyake, S. 1982. Japanese crustacean decapods and stomatopods in color. I. Macrura, Anomura and Stomatopoda. Hoikusha Publishing Co., Osaka, 261 pp.

Ortmann, A. E. 1897. Carcinologische Studien.—Zoologische Jahrbücher. Abtheilung für Systematik, Geographie und Biologie der Thiere 10: 258–372.

Osawa, M. 1996. Two new species of the genus *Petrolisthes* (Decapoda: Anomura: Porcellanidae) from the Indo-West Pacific.—Journal of Crustacean Biology 16:602–612.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in expeditione ad oceanum pacificum septentrionalem, a republica federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit. Pars VII. Crustacea Anomoura.—Proceedings of the Academy of Natural Sciences of Philadelphia 10:225–252.

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A new species of *Pachycheles* from the Hawaiian Islands (Crustacea: Decapoda: Porcellanidae)

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Abstract.—*Pachycheles attaragos*, new species, is described from two males from the Hawaiian Islands. The species is characterized by a relatively elongated, tufted carapace; carapace sidewalls with a large anterior piece but only a single vestigial posterior fragment; subequal chelae with a distinctive carpus margin; and third maxillipeds with an acutely triangular meral lobe.

Although porcelain crabs are well represented in tropical waters of both Indo-Pacific and eastern Pacific waters, only two species, *Pachycheles pisoides* (Heller, 1865) and *Petrolisthes coccineus* (Owen, 1839), are known from the Hawaiian Islands. Here we describe a distinctive new species, which we discovered during examination of the porcellanid collections of the Museum of Comparative Zoology (MCZ). These specimens are part of a large collection of Hawaiian marine invertebrates and fishes made in the mid-1800's by the conchologist Andrew Garrett for the MCZ through the patronage of a wealthy Boston merchant named James M. Barnard (Thomas 1954).

Carapace length (CL) is provided as an indicator of specimen size. Illustrations were created with the approach used by Harvey & De Santo (1996): specimen images were first captured on a Macintosh™ computer with a digital camera connected to a Wild M8 dissecting microscope, then prepared for publication using the programs Adobe Photoshop™ and Adobe Illustrator™.

Pachycheles attaragos, new species
Fig. 1

Holotype.—Male (CL 3.85 mm), Sandwich Islands (= Hawaiian Islands), coll. A. Garrett, donated to MCZ by J. M. Barnard, MCZ 11851a.

Paratype.—Male (CL 2.90 mm), Sandwich Islands (= Hawaiian Islands), coll. A. Garrett, donated to MCZ by J. M. Barnard, MCZ 11851b.

Diagnosis.—Carapace longer than broad, with lateral margins convex, regions poorly defined. Front triangular in dorsal view, with tuft of setae. Sidewall of carapace consisting of 1 large anterior plate and 1 very small posterior fragment. Basal segment of antennule armed with 2 blunt spines on anteromesial margin and smaller lateral spine on anterior surface. Merus of third maxilliped with pronounced medial lobe, acutely triangular in shape. Chelipeds subequal. Carpus of cheliped with strongly projecting, angular lobe occupying proximal half of anterior margin, and joining distal portion of margin in broad, smooth curve. Manus of cheliped covered with small flattened granules. Walking legs with scattered marginal setae. Telson 5-plated. Second pleopods present in males. Females unknown.

Description.—Carapace (Fig. 1A) longer than broad; regions faintly defined; dorsal surface with posterolateral regions plicate, otherwise punctate; anterolateral regions with scattered short setae, front with tuft of short plumose setae; dorsolateral ridges pronounced; posterolateral margins convex; posterior margin straight. Front triangular

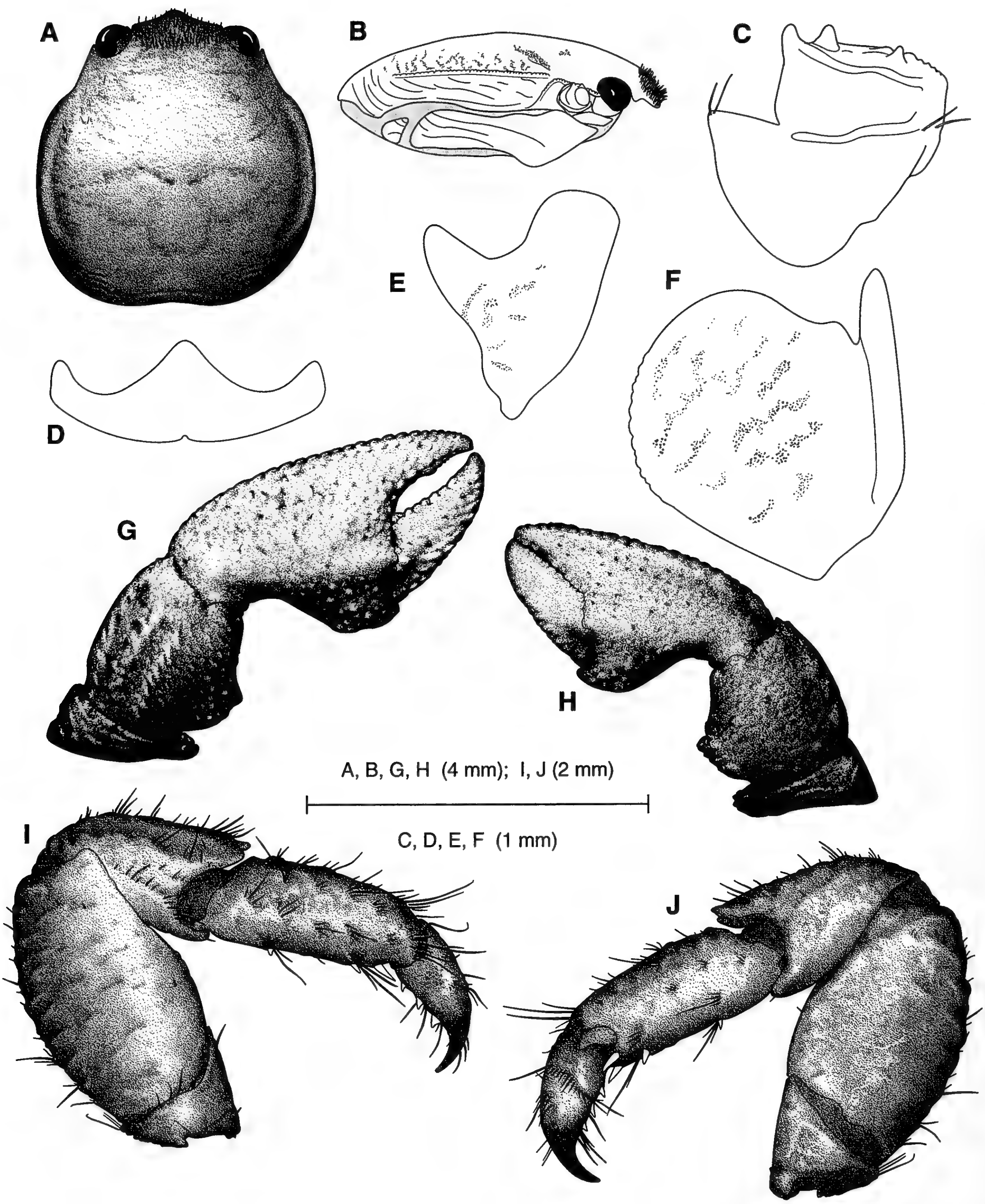

Fig. 1. *Pachycheles attaragos*, new species; holotype male, MCZ 11851a. A, carapace; B, sidewall of carapace; C, basal segment of left antennule, ventral view; D, sternite of outer maxillipeds, ventral view; E, merus of left outer maxilliped, ventral view; F, ischium of left outer maxilliped, ventral view; G, major cheliped; H, minor cheliped; I, third right pereopod, lateral view; J, third right pereopod, mesial view.

in dorsal view, trilobate in frontal view, median lobe projecting farther than lateral lobes. Outer orbital angle produced into acute tooth, inner orbital angle approximately right-angled. Orbits deep and broad, eyes large. Sidewall of carapace (Fig. 1B) consisting of 1 large anterior plate and 1 very small posterior fragment.

Basal segment of antennule (Fig. 1C) armed with 2 large, blunt spines on anteromesial margin (visible from dorsal view); with 1 somewhat smaller lateral spine on anterior surface; ventral surface with 2 transverse granular lines. Second segment of antenna with low crest on anterior margin; third segment with proximal tubercle, low medial crest and distal tubercle along anterior margin. Flagella with short setae.

Outer maxillipeds with trilobate sternite (Fig. 1D), median lobe exceeding lateral lobes; merus (Fig. 1E) with pronounced medial lobe, acutely triangular in shape, with anterior margin entire; ischium (Fig. 1F) with medioproximal angle obtuse.

Chelipeds (Fig. 1G, H) subequal in length, major manus somewhat wider than minor manus. Merus with granular tooth on anterior margin, not projecting as far as carpus tooth; ventral margin of merus distinct, ventrodistal angle granular. Carpus and manus with very short, often vestigial, plumose setae arising in scattered groups from distal side of larger granules; less apparent on major chela. Carpus about as broad as long, with strongly projecting angular lobe occupying proximal half of anterior margin, and joining distal portion of margin in broad, smooth curve; dorsal surface rugose; carpus of major chela with medial and mediolateral longitudinal ridges, each topped with row of enlarged granules. Manus covered with small granules, more pronounced near base of dactyl; posterior margin of fixed finger with 2 parallel rows of granules; dorsal surface of fingers with smaller, flattened granules. Major manus with single medial tubercle on cutting edge of pollex; dactyl with basal tubercle on cutting edge; fingers gaping, crossing at tips, with trace of setae in gape. Minor cheliped with fingers meeting entire length of cutting edge, crossing at tips.

Walking legs (Fig. 1I, J) with scattered setae on anterior margins of merus, carpus and propodus. Carpus with medial longitudinal ridge on lateral surface; with 1 or 2 granules at anterodistal angle. Propodus with 2 distal, 1 subdistal and 1 medial movable spines ventrally. Dactyl with 3 corneous spines on ventral margin.

Abdomen smooth; telson with 5 plates in males (females unknown). Second pleopods present in males.

Distribution.—At present, known only from the type locality; bathymetric and habitat distributions unknown.

Etymology.—From the Greek *attaragos*, meaning small piece or bit, and referring to the unusually small posterior fragment of the sidewall of the carapace. Used as a noun in apposition.

Remarks.—*Pachycheles attaragos* possesses several features unusual within the genus. The shape of the anterior lobe of the carpus of the cheliped is unlike any other species of *Pachycheles*, and strongly resembles that of porcelain crabs in the genus *Allopetrolisthes* (Haig, 1960). The elongate, acutely triangular meral lobe of the outer maxilliped is more similar to certain species of *Petrolisthes* than to other species of *Pachycheles*. Perhaps the most distinctive feature of the genus *Pachycheles*, the fragmentation of the sidewall of the carapace, is barely evident in *P. attaragos,* which has only a single very small fragment posterior to the large anterior plate. Likewise, the difference in size between the major and minor chelipeds of *P. attaragos* is among the smallest in the genus (A. Harvey and E. M. De Santo, pers. obs.).

Pachycheles attaragos is easily distinguished from *P. pisoides*, the only other species in the genus reported from Hawaii. In *P. pisoides*, the carapace is broader than long; the front lacks a tuft of setae and is nearly straight; the posterior plate of the sidewall is quite large (approximately half the size of the anterior plate); and the anterior margin of the carpus of the chelipeds possesses three or four acute, forwardly-pointing teeth.

Pachycheles attaragos appears to be most closely related to three species, *P. pectinicarpus* Stimpson, 1858, currently known only from Hong Kong; the eastern Pacific *P. grossimanus* (Guérin-Méneville, 1835); and the western Atlantic *P. laevidactylus* Ortmann, 1892. Characters shared by these species include the tuft of setae on the carapace front; relatively elongated carapace; lack of teeth on the anterior margin of the carpus of the chelipeds; anterior spines on the basal antennular segment; granules along the ventrodistal margin of the merus of the cheliped; and the pattern and degree of setation of the major and minor chelae (Harvey & De Santo 1996).

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Literature Cited

Guérin-Méneville, F. E. 1835. Observations sur les Porcellanes.—Bulletin de la Societé Naturelle de France:115–116.

Haig, J. 1960. The Porcellanidae (Crustacea Anomura) of the eastern Pacific.—Allan Hancock Pacific Expedition 24:1–440.

Harvey, A. W., & E. M. De Santo. 1996. On the status of *Pachycheles laevidactylus* Ortmann, 1892 (Crustacea: Decapoda: Porcellanidae).—Proceedings of the Biological Society of Washington 109:707–714.

Heller, C. 1865. Crustaceen.—Reise der oesterreichischen Fregatte "Novarra" um die Erde, in den Jahren 1857, 1858, 1859, unter den Befehlen des Commodore B. von Wüllerstorf-Urbair.—Zoologischer Theil 2(3)(1):1–280.

Ortmann, A. E. 1892. Die Decapoden-Krebse des Strassburger Museums IV. Thiel. Die Abtheilungen Galatheidea und Paguridea.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 6:241–326.

Owen, R. 1839. Crustacea. Pp. 77-88 *in* The Zoology of Captain Beechey's Voyage; Compiled from the Collections and Notes Made by Captain Beechey, the Officers and Naturalist of the Expedition, during a Voyage to the Pacific and Behring's Straits Performed in His Majesty's Ship Blossom, under the Command of F.W. Beechey, R.N., F.R.S., &c. &c. in the Years 1825, 26, 27, and 28. London, Henry G. Bohn.

Stimpson, W. 1858. Prodromus descriptions animalium evertebratorum. Pars VII. Crustacea Anomura.—Proceedings of the Academy of Natural Sciences, Philadelphia 10:225–252.

Thomas, W. S. 1954. King of shell collectors—Pacific Ocean style. Hawaiian Shell News 2:69–71.

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A new genus for the Central American crab *Pinnixa costaricana* Wicksten, 1982 (Crustacea: Brachyura: Pinnotheridae)

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Abstract.—A new monotypic genus, *Glassella*, is recognized from the tropical East Pacific for *Pinnixa costaricana* Wicksten, 1982. This genus shares with *Alarconia* Glassell, 1938, *Indopinnixa* Manning & Morton, 1987, *Scleroplax* Rathbun, 1893 and *Pinnixa* White, 1846, a carapace wider than long, and third pair of walking legs the longest. *Glassella* is distinguished from other genera by: MXP3 with ischium-merus pyriform, carpus larger than the conical propodus, and small digitiform dactylus inserted sub-distally on the inner face of propodus. The type species is redescribed and illustrated.

Pinnixa costaricana was originally described by Wicksten (1982) and placed in the genus *Pinnixa* White, 1846, because of its carapace shape and relative length and shape of the walking legs. During a recent revision of the *Pinnixa*-complex from the eastern Pacific, *P. costaricana* was compared to other *Pinnixa* species and to species of other genera in the Pinnotheridae with a *Pinnixa*-like morphology: *Alarconia* Glassell, 1938, *Indopinnixa* Manning & Morton, 1987, and *Scleroplax* Rathbun, 1893. We concluded that *P. costaricana* should be removed from the genus *Pinnixa* and placed in a new genus herein diagnosed. The morphological analysis of *P. costaricana* was based upon the study of the female holotype (AHF 806) deposited in Los Angeles County Museum of Natural History. Other species studied were: the type species of *Alarconia*, *A. seaholmi*, the type species of *Scleroplax*, *S. granulata*, and the species of *Pinnixa* reported by Bonfil et al. (1992), Zmarzly (1992), Martin & Zmarzly (1994), and Hendrickx (1995), all deposited in the San Diego Natural History Museum and at the Invertebrates Laboratory, Facultad de Ciencias, Universidad Autónoma de Baja California. The information used on the type species of *Indopinnixa*, *I. sipunculana*, was obtained from published description and figures, although critical features were confirmed by Dr. Raymond B. Manning from types deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Comparison of these genera is provided in a dichotomous key based on adult characters.

The third maxilliped is abbreviated to MXP3 and the walking legs are indicated as WL1-WL4. AHF is an acronym for Allan Hancock Foundation.

Family Pinnotheridae

Glassella, new genus

(Figs. 1, 2)

Diagnosis.—Carapace suboblong, dorsal surface pockmarked, wider than long, integument firm, regions not defined; cardiac ridge lacking; front truncated, with shallow median sulcus. MXP3 with ischium-merus pyriform, fused, separated by faint line and distal margin truncated; palp as long as ischium-merus, 3-segmented, dactylus small,

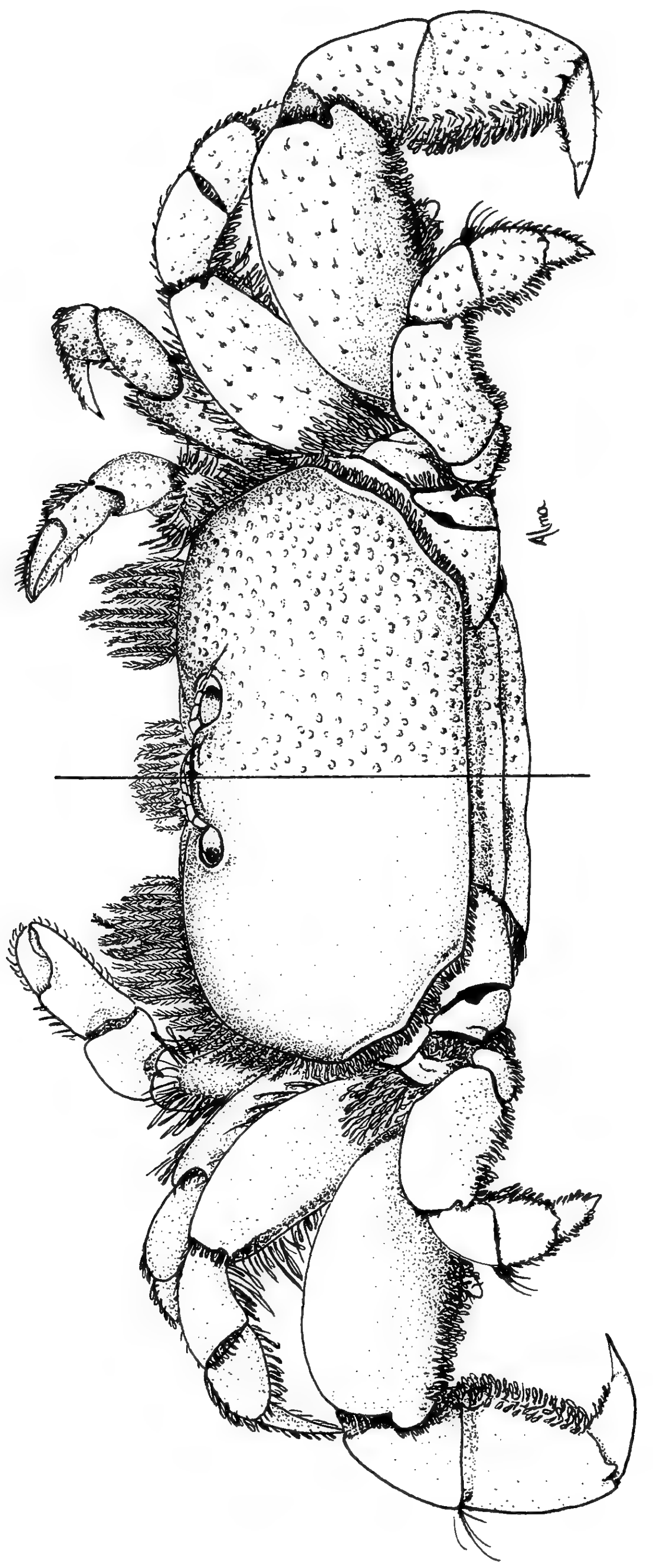

Fig. 1. *Glassella costaricana* (Wicksten, 1982), holotype AHF 806. Dorsal view. Carapace length 1.8 mm, width 4.2 mm.

digitiform, inserted sub-distally on inner face of conical propodus; carpus stout, longer than combined length of propodus and dactylus; exopod with median lobe on outer margin, flagellum 2-segmented. WL1-4 pockmarked, relative length 3 > 2 > 1 > 4, WL3 considerably the longest. Abdomen of female with 6 somites and telson free, widest at third somite; tapering from fourth somite to triangular telson.

Male unknown.

Etymology.—Named in honor of Steve A. Glassell, who studied the pinnotherid crabs of the eastern Pacific and made invaluable contributions on this group. Gender feminine.

Type species.—*Pinnixa costaricana* Wicksten, 1982, by present designation and monotypy.

Glassella costaricana (Wicksten, 1982), new combination
(Figs. 1, 2)

Pinnixa costaricana Wicksten, 1982:579–582. fig. 1, 2A–D; Hendrickx, 1995:148.

Material examined.—Female (holotype AHF 806).

Redescription.—(Modified from Wicksten 1982). Carapace suboblong, cylindrical, dorsal surface pockmarked, regions not defined; anterolateral margins diverging posteriorly, forming shoulders from which side walls drop vertically; lacking anterolateral crest or cardiac ridge. Posterior margin straight. Front not advanced, truncate; with shallow median sulcus. Carapace margin with setae, especially on ventral surface. Orbits small, slightly inclined downward, filled by eyes when retracted. Antennule plicate in small fossettes. Antenna large, multi-articulated.

Cheliped slender, setose. Margins of chela subparallel; ventral margin of propodus with small tubercles. Manus with group and lines of tiny tubercules. Fingers slender; tips pointed, curved, and leaving no gape when closed; dorsal margin of dactylus with blunt and acute tubercles.

WL1-2 slender; meri trigonal; dactyli sharp, nearly straight. WL1 twisted, somewhat smaller than second, nearly reaching end of propodus of WL2. WL2 reaching carpus of WL3. WL3 very wide; merus

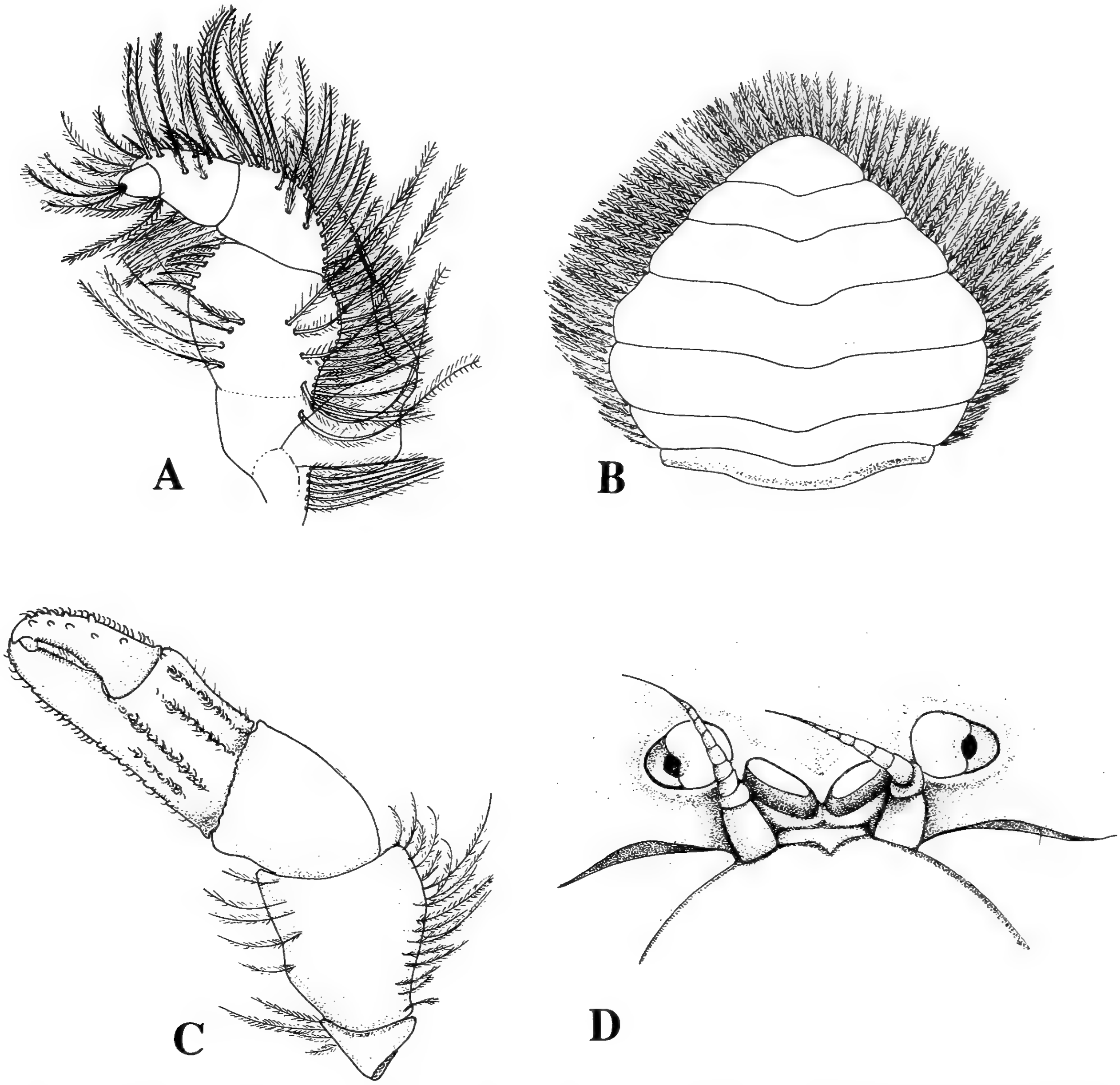

Fig. 2. *Glassella costaricana* (Wicksten, 1982), holotype AHF 806. A, third maxilliped (inner view); B, female abdomen; C, left chela (outer view); D, front, anterior view.

1.25× as long as wide, with stout tooth and small teeth and tubercles on ventral margin; carpus without teeth; propodus 1.5× as long as wide, with granules along flexor margin; dactyl sharp, slightly curved. WL4 short, reaching almost to end of WL3; dactyl stout, and triangular. All legs pilose and pockmarked.

Distribution and habitat.—Known only from the type locality, Playa de Coco, Provincia de Guanacaste, Costa Rica (about 10°5′N, 85°45′W); low intertidal zone, sand and rock.

Remarks.—As noted in the key given below, the genus *Glassella* most resembles *Pinnixa*, *Alarconia*, *Indopinnixa* and *Scleroplax*, all of which have a firm carapace that is wider than long and a third pair of WL considerably longer than the rest. Differences among these genera include: shape, degree of development of regions and hardness of the carapace; shape, degree of fusion, articulation point and relative length of the MXP3 articles; relative length of WL; and, width and degree of fusion of the abdominal somites.

Glassella costaricana can be distinguished from all other pinnotherids by the following presumed autapomorphies: MXP3 with pyriform ischium-merus;

shape, relative length and insertion point of the articles of the palp; and shape of the abdomen.

Key to *Pinnixa*-like genera of the world (Carapace wider than long, firm or hard; third pair of walking legs longest.)

1. Palp of MXP3 with dactylus shorter than and inserted sub-distally on inner face of propodus; carpus larger than propodus .... *Glassella*, new genus (Pacific coast of Costa Rica; type species *Pinnixa costaricana* Wicksten, 1982; host unknown).
– Palp of MXP3 with dactylus as long as or longer than and inserted proximally on ventral margin of propodus; carpus shorter than propodus 2
2. Ischium and merus of MXP3 not fused, subequal in length; carapace regions well defined; gonopods protruding from sternal trench and reaching to buccal cavity .... *Alarconia* Glassell, 1938 (Mexican Pacific; type species *Alarconia seaholmi* Glassell, 1938; host unknown).
– Ischium shorter than merus or both articles fused; carapace regions not well defined, gonopods not protruding from sternal trench and not reaching the buccal cavity 3
3. Carapace subpentagonal, hard, dorsally very convex; WL1-4 of similar shape, third pair slightly longer, fourth not noticeably reduced .... *Scleroplax* Rathbun, 1893 (Eastern Pacific, British Columbia, Canada to Baja California, Mexico; type species *Scleroplax granulata* Rathbun, 1893; hosts: in burrows of Crustacea-Decapoda (Callianassidae) and Echiurida.
– Carapace oblong, firm but not hard, flat or slightly convex; WL1-4 very dissimilar in shape, third pair stout and longer, and fourth noticeably shorter 4
4. Propodus of MXP3 elongated, distal end expanded far beyond mid-length of dactylus, both articles of similar shape; male abdomen of 6 free somites and telson .... *Pinnixa* White, 1846 (Western Atlantic [Massachusetts, U.S.A. to Argentina]; Eastern Pacific [Alaska, U.S.A. to Chile]; Indo West Pacific [Japan, East Africa]; type species *Pinnotheres cylindricum* Say, 1818; host: Polychaeta, Enteropneusta, Echiurida, Sipunculida, Holothuroidea, Mollusca-Bivalvia, Crustacea-Decapoda [Callianassidae], Tunicata).
– Propodus of MXP3 short and stout, distal end not reaching far beyond middle length of dactylus, both articles very dissimilar in shape; male abdomen with fifth and sixth somites fused .... *Indopinnixa* Manning & Morton, 1987 (Indo West Pacific [Hong Kong]; type species *Indopinnixa sipunculana* Manning & Morton, 1987; in burrows of Sipunculida).

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Literature Cited

Bonfil, R., A. Carvacho, & E. Campos. 1992. Los cangrejos de la Bahía de Todos Santos, Baja California. Parte II. Grapsidae, Pinnotheridae y Ocypodidae (Crustacea; Decapoda: Brachyura).—Ciencias Marinas (México) 18(3):37–56.

Glassell, S. A. 1938. New and obscure decapod Crustacea from the west American coasts.—Transactions of the San Diego Society of Natural History 8(33):411–454.

Hendrickx, M. E. 1995. Checklist of brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific.—Bulletin de L'Institut Royal des Sciences Naturelles de Belgique (Biologie) 65: 125–150.

Manning, R. B., & B. Morton. 1987. Pinnotherids (Crustacea: Decapoda) and Leptonaceans (Mollusca: Bivalvia) associated with sipunculan worms in Hong Kong.—Proceedings of the Biological Society of Washington 100:543–551.

Martin, J., & D. L. Zmarzly. 1994. *Pinnixa scamit*, a new species of Pinnotherid crab (Decapoda: Brachyura) from the continental slope off California.—Proceedings of the Biological Society of Washington 107:354–359.

Rathbun, M. J. 1893. Scientific results of explorations by the U.S. Fish commission steamer Albatross, XXIV. Description of new genera and species of crabs from the west coast of North America and the Sandwich Islands.—Proceedings of the United States National Museum 16:233–260.

Say, T. 1817–1818. An account of the Crustacea of the United States.—Journal of the Academy of Natural Sciences of Philadelphia 1(1–2):57–63, 65–80, 97–101, 155–160, 161–169 [all 1817], 235–253, 313–316, 317–319, 374–380, 381–401, 423–441 [all 1818].

Wicksten, M. K. 1982. *Pinnixa costaricana*, a new species of crab from Central America (Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 95:579–582.

White, A. 1846. Notes on four new genera of Crustacea.—Annals and Magazine of Natural History 18(118):176–178.

Zmarzly, D. L. 1992. Taxonomic review of pea crabs in the genus *Pinnixa* (Decapoda: Brachyura: Pinnotheridae) occurring on the California shelf, with description of two new species.—Journal of Crustacean Biology 12:677–713.

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New records of marine Isopoda from Cuba (Crustacea: Peracarida)

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Abstract.—Seven new species are described from localities on both the north and south coasts of Cuba: *Cyathura (Cyathura) esquivel, Mesanthura frances, Joeropsis juvenilis, Joeropsis unidentata, Dynamenella nuevitas, Paraimene ibarzabalae, Paraimene tumulus*. Several new records, including *Carpias harrietae, Caecijaera horvathi*, and *Sphaeromopsis mourei* are noted. The material was collected from a range of habitats, including shallow coral reefs, mangroves, seagrass beds, coastal lagoons, river mouths, rocky and sandy shore inter-/and shallow infratidal areas.

Knowledge of the marine, freshwater, and cave isopod fauna of Cuba has grown slowly, from the earliest records of two species of *Aega* by Schioedte & Meinert in 1879. Numerous short papers, often describing a single species, have accumulated over the years. The first cave isopod was described by Hay in 1903; since then several additional species especially in the genus *Cyathura* have been added to the list. Coineau & Botosaneanu (1973) produced the only report on interstitial isopods from Cuba. Ortiz et al. (1987) provided an updated list of Cuban isopods along with a bibliography. From the relatively small number of species in this list, it is obvious that many more await discovery, as many regions of the island's shallow and deep waters have not been collected. In an attempt to fill some marine distributional gaps, and to document the diversity of several groups of shallow water marine organisms, two collecting trips, in April 1994, and May/June 1995, were carried out jointly by Cuban and Smithsonian Institution scientists. This work was sponsored chiefly by the Center for Marine Conservation, Washington, D.C. The 1994 trip was based aboard the *R/V Ulises*, which travelled along the north coast through the Archipielago de Camagüey as far as Bahia de Nuevitas, stopping at several localities to carry out intensive sampling. The 1995 trip was to the south-western part of the island, mainly in the region around the Isla de la Juventud.

The material reported in this paper was collected primarily by the authors, although several other individuals assisted. K-CUBA station numbers refer to field notes for the two trips. Holotypes have been deposited in the Centro Colecciones Naturales Marinas, Instituto de Oceanologia (IO), Havana, Cuba; paratypes and additional materials are deposited in both the CCNM and the National Museum of Natural History (USNM), Smithsonian Institution. An annotated checklist of the marine isopod fauna of Cuba is being compiled, based on a variety of sources of material.

Dimensions in millimeters are always total length measured along the dorsal midline.

Systematic Section

Suborder ANTHURIDEA Leach, 1814

Family Anthuridae Leach, 1814

Cyathura (Cyathura) esquivel, new species

Figs. 1, 2

Material.—Holotype, IO-12.055, ♂ 2.5 mm, Allotype, IO-12.057, ovigerous ♀ 4.0

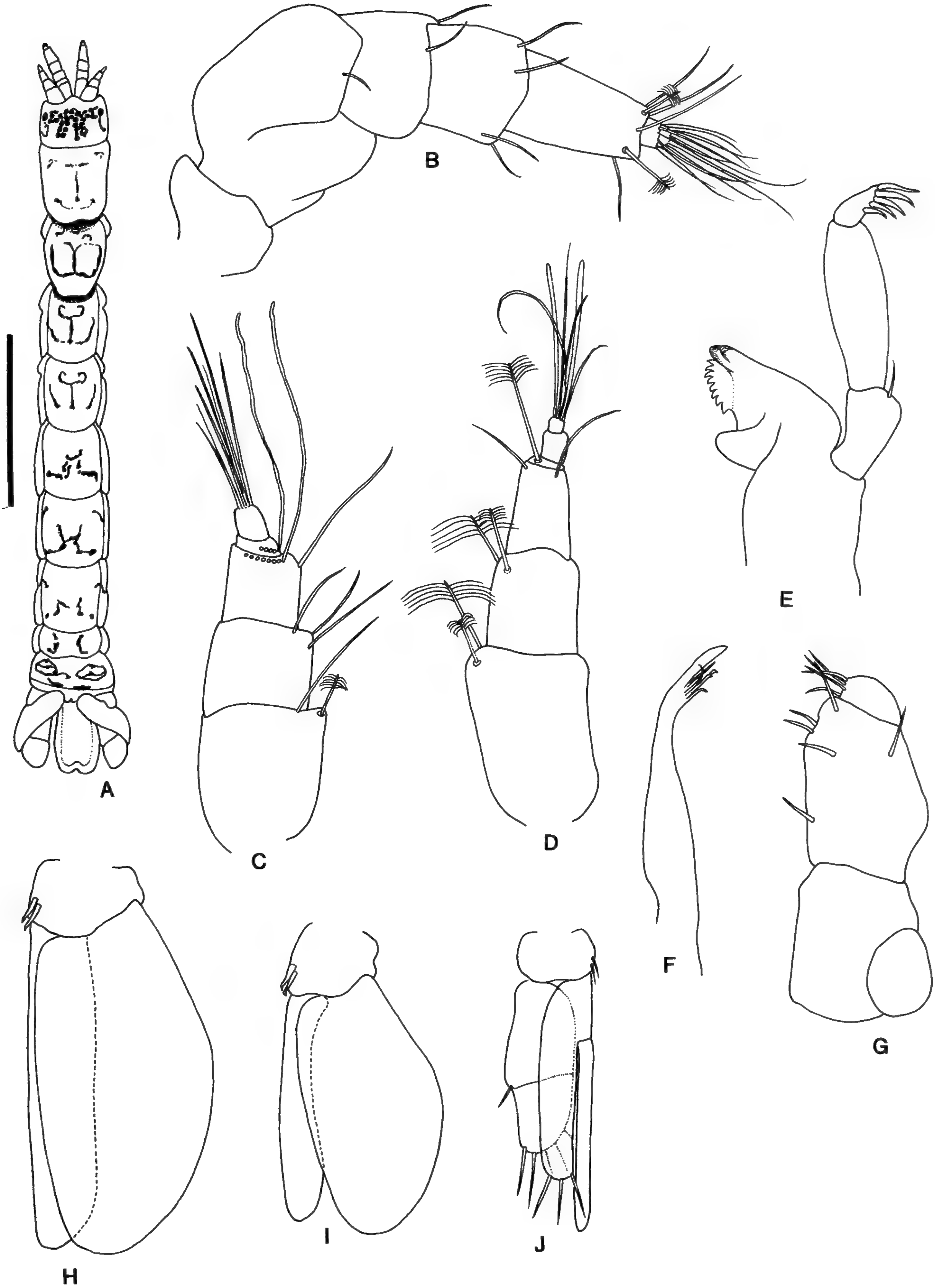

Fig. 1. *Cyathura esquivel*, new species. A, Ovigerous female in dorsal view, scale = 1 mm; B, Antenna; C, ♂ Antennule; D, ♀ Antennule; E, Mandible; F, Maxilla; G, Maxilliped; H, ♀ Pleopod 1; I, ♂ Pleopod 1; J, ♂ Pleopod 2.

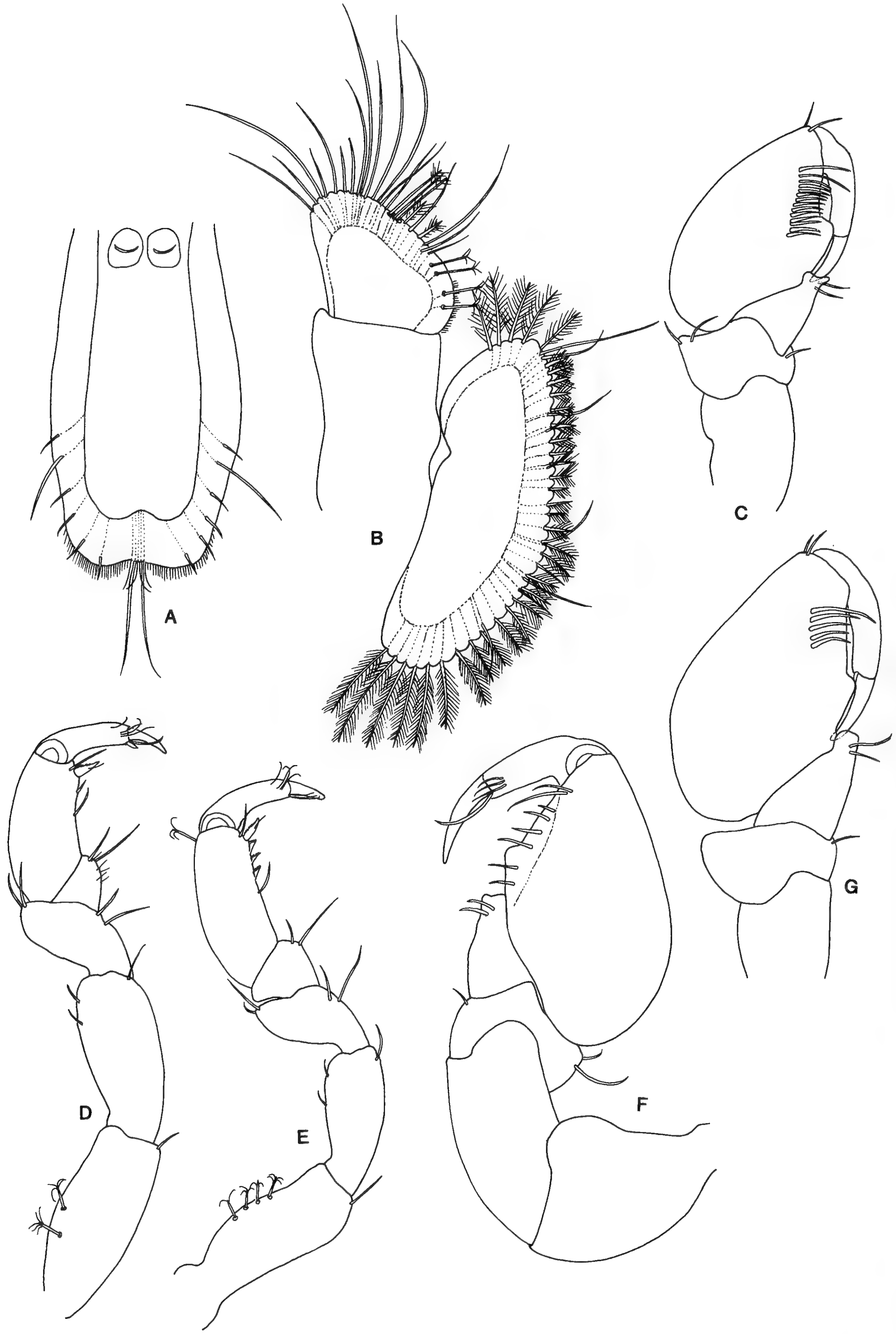

Fig. 2. *Cyathura esquivel*, new species. A, Pleotelson; B, Uropodal endopod and exopod; C, ♂ Pereopod 1, mesial surface; D, Pereopod 2; E, Pereopod 7; F, ♀ Pereopod 1, lateral surface; G, ♀ Pereopod 1, mesial surface.

mm, Paratypes, IO-12.056, 4 ♂, 4 ovigerous ♀, 5 non-ovigerous ♀; Paratypes, USNM 253270, 5 ♂, 4 ovigerous ♀, 9 non-ovigerous ♀, 4 manca, sta K-CUBA-22, Cayo Esquivel, north coast of Cuba, coral rubble from exposed side of cay, 2–2.5 m, 12 Apr 1994.—4 ♂ 2.5 mm, 2 non-ovigerous ♀, 12 manca 1.8–2.2-mm, sta K-CUBA-35, Cayo Coco, north coast of Cuba, coral rubble from shallow reef area, 1.5–2 m, 14 Apr 1994.

Description.—Male: Antennule with peduncle article 3 shorter than in female, carrying distal band of fine aesthetascs; flagellum of 2 articles, basal article also carrying band of fine aesthetascs. Pereopod 1, mesial surface of propodus having row of about 14 setae. Pleopod 1, endopod shorter than, and about ⅓ width of exopod. Pleopod 2, endopod having slender, parallel-sided copulatory stylet articulating in proximal half of mesial margin, with 3 distal plumose marginal setae; exopod with transverse suture in distal half, 5 plumose marginal setae distally.

Pigment pattern similar in male and female, with large red-brown chromatophores in band between eyes and forming 2 posterior lobes on dorsal cephalon. Pereonites each with fine dorsal squiggles, those on pereonite 2 forming 2 contiguous rings being most characteristic. Pleon with pair of irregular lateral rings often with intersecting line.

Ovigerous female: Body proportions: C<1>2>3=4=5=6>7>P. Cephalon wider than middorsal length, with low rounded rostrum. Eyes well pigmented. Body bent between pereonites 1 and 2. Anterior fused segments of pleon short. Pleotelson with broad transparent marginal band, having 6 pairs of submarginal setae in posterior half, slightly bilobed posterior margin with elongate pair of setae submesially.

Antennule having 3 relatively large articles; flagellum of 3 short articles, together shorter than peduncle article 3; terminal article bearing 2 aesthetascs. Antennal peduncle with article 2 stout, grooved to accommodate antennule; articles 3 and 4 subequal; article 5 longer than 4; flagellum of 2 very short setose articles. Mandibular incisor of 3 sclerotized cusps; lacinia dentata having 8 teeth; molar thin-walled, distally rounded; palp with article 2 twice length of article 1; article 3 short, bearing 5 stout setae. Maxilla having single strong spine and several slender subsidiary spines. Maxilliped of 3 articles, article 2 slightly longer than 1, with few setae submesially; article 3 semicircular, with 5 mesial setae; endite lacking. Pereopod 1, carpus short, lacking free anterior margin, with 2 setae distally; propodus expanded, with transparent palmar flange bearing 6 setae on lateral surface, with low rounded proximal protuberance, with row of 5 setae on mesial surface; unguis ⅔ length of rest of dactylus. Pereopods 2 and 3 with short triangular carpus lacking free anterior margin; propodus roughly rectangular, with stout serrate posterodistal spine; unguis ½ length of rest of dactylus, with small accessory spine at its base. Pereopods 4–7 similar, carpus triangular, with short free anterior margin; propodus with several posterodistal scales and stout serrate posterodistal spine. Pleopod 1 protopod with 2 coupling hooks; exopod opercular; endopod subequal to exopod in length, between ½ and ⅓ width of exopod. Uropodal endopod roughly ovate, with broad transparent border and numerous marginal setae; exopod with broad transparent border, almost 3 times longer than wide, lateral margin crenulate with plumose setae set in each gap.

Remarks.—The only species of the subgenus *Cyathura* previously recorded from Cuba (and from the general Caribbean region), is *C. cubana* Negoescu, 1979, an estuarine species also known from the mainland of Belize (Kensley & Schotte 1989). *Cyathura cubana* differs from *C. esquivel*, which occupies fully marine habitats, in having a more heavily pigmented and setose body, in having an evenly rounded posterior margin of the pleotelson, a much shorter uropodal exopod, a much shorter endopod of pleopod 1, and a more elongate mandibular palp. *Cyathura tridentata* Wagner, 1990, from the interstitial intertidal of the Dominican Republic, is a blind and unpigmented species, differing in many appendage characters from the present species.

Etymology.—The specific name derives from the type locality, Cayo Esquivel.

Mesanthura frances, new species
Fig. 3

Material.—Holotype, IO-12.058, non-ovigerous ♀ 8.2 mm, Paratypes, IO-12.059, 2 non-ovigerous ♀, Paratypes, USNM 253271, 3 non-ovigerous ♀, sta K-CUBA-27, Cayo Francés, from clumps of Halimeda in Thalassia flat, shallow infratidal, 13 Apr 1994.—Non-ovigerous ♀ 4.1 mm, sta K-CUBA-35, Cayo Coco, coral rubble from shallow reef area, 1.5–2 m, 14 Apr 1994.

Description.—Non-ovigerous female: Body proportions: C<1=2<3<4=5>6>7<P. Cephalon having low rostral point; with well pigmented eyes. Pleonite 6 short, dorsally demarked by pair of posteromedial points. Pleotelson ovate, widest at midlength, posteriorly evenly rounded, bearing 4 pairs of setae.

Antennule with basal article subequal to 2 following articles; flagellum of 3 articles, terminal article bearing 3 aesthetascs. Antennal flagellum of 4 articles. Mandible with 4 serrations in lacinia dentata; molar low, rounded; palp article 3 bearing 6 fringed setae. Maxilla having 6 distal spines. Maxilliped with terminal article set lateral to mesial line of rest of articles, bearing 2 circumplumose setae; short endite with short terminal seta present. Pereopod 1, carpus triangular, with 3 rounded scales forming posterodistal apex; propodus expanded, palm having low lobe formed by 3 or 4 scales, 6 simple setae along palmar margin; unguis about half length of rest of dactylus. Pereopod 2, carpus triangular, lacking free anterior margin; propodus, rectangular, with serrate posterodistal spine. Pereopods 4–7, carpus having short free anterior margin, short sensory posterodistal spine present; propodus rectangular, bearing serrate posterodistal spine. Pleopod 1, exopod operculiform, with 15 plumose marginal setae; endopod slightly shorter than, and about one-third width of exopod, bearing 5 plumose marginal setae distally. Uropodal endopod distally ovate, basal width about ¾ greatest length, bearing numerous simple marginal setae; protopod bearing 7 plumose marginal setae; exopod about twice longer than greatest width, with slight subdistal notch in lateral margin, bearing numerous plumose marginal setae.

Color pattern: Strong red-brown patches on cephalon, pereonites, pleon and telson, patches continuous across articulations, each having open unpigmented central area and one or two lateral lobes extending ventrolaterally on pereonites.

Male: unknown.

Remarks.—The color pattern of *M. frances* bears some resemblance to *M. bivittata* Kensley, 1987, from Belize, and *M. looensis* Kensley & Schotte, 1987, from the Florida Keys, but the shape of the individual patches which run together middorsally is distinctive. Of the nine species of *Mesanthura* known from the broad Caribbean region, only *M. paucidens* Menzies & Glynn, 1968, and *M. reticulata* Kensley, 1982, have six spines on the terminal mandibular palp article. The color patterns of these two species are so distinctive as to prevent any confusion with the present species.

Etymology.—The specific name derives from the type locality, Cayo Francés on the north coast of Cuba.

Suborder Asellota Latreille, 1803
Family Janiridae Sars, 1899
Caecijaera horvathi Menzies, 1951
Fig. 4

Caecijaera horvathi Menzies, 1951:3, Figs. 1–3.—Cooke, 1977:105, Fig. 1.—Mal-

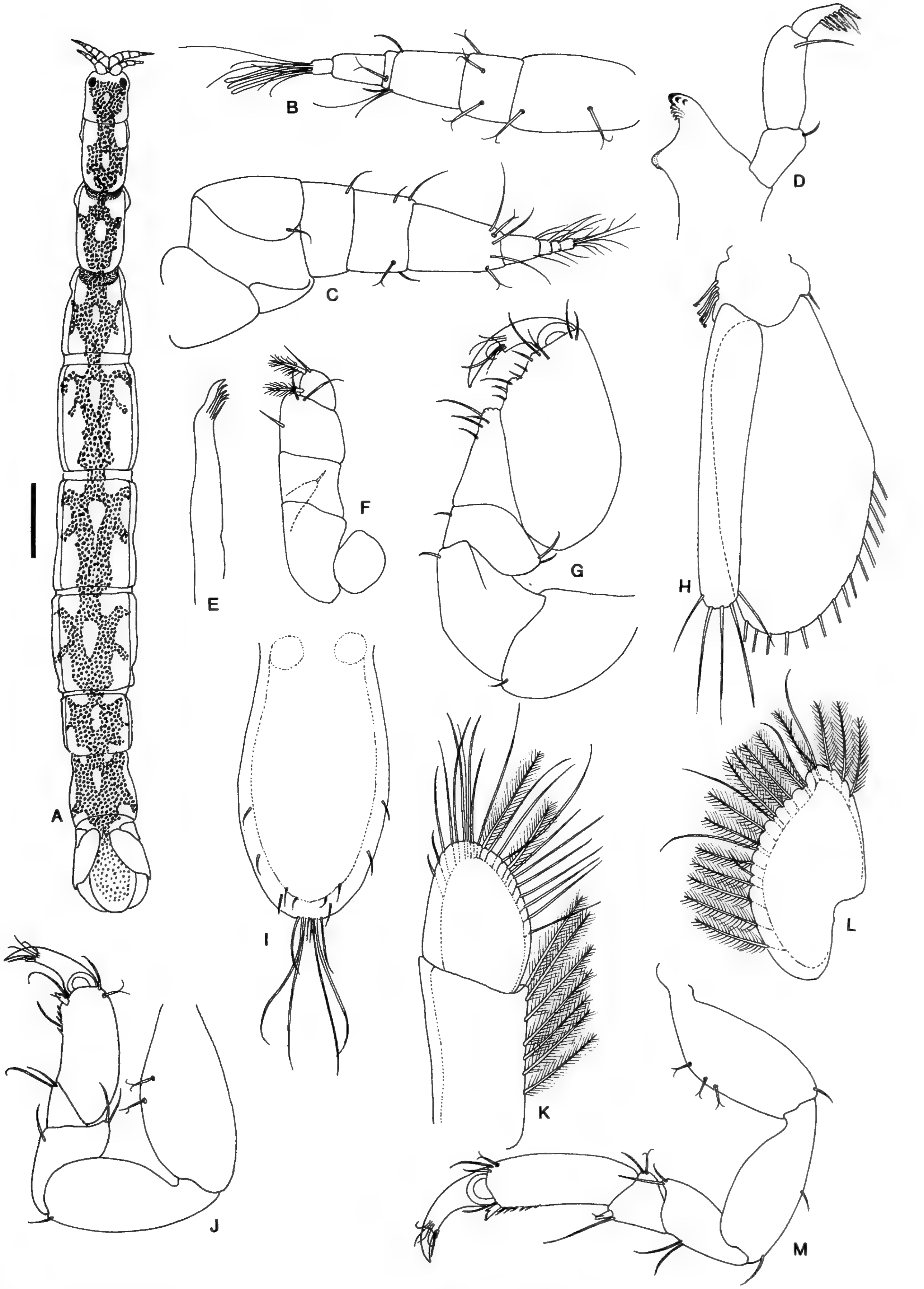

Fig. 3. *Mesanthura frances*, new species. A, Holotype, non-ovigerous ♀, scale = 1 mm; B, Antennule; C, Antenna; D, Mandible; E, Maxilla; F, Maxilliped; G, Pereopod 1; H, Pleopod 1; I, Pleotelson; J, Pereopod 2; K, Uropodal endopod; L, Uropodal exopod; M, Pereopod 7.

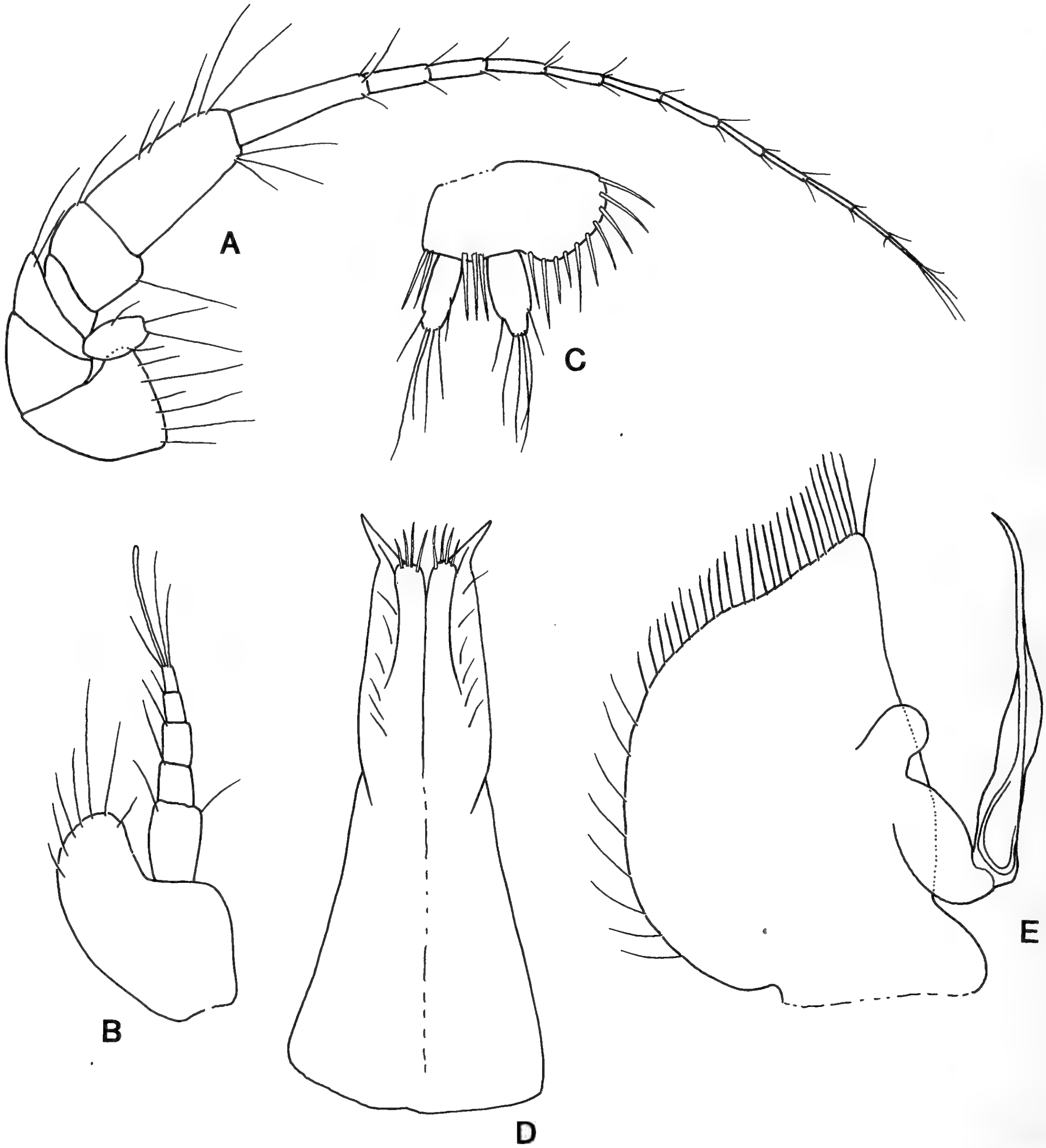

Fig. 4. *Caecijaera horvathi* Menzies, 1951. A, Antenna; B, Antennule; C, Uropod; D, ♂ Pleopod 1; E, ♂ Pleopod 2.

yutina, 1994:33.—Wilson & Wägele, 1994:694.

Material.—USNM 253273, 5 ♂ 1.0–1.5 mm, sta K-CUBA-6, Cayo Mendoza, north coast of Cuba, with *Limnoria* sp. in wood of rotten and decaying barges lying in mud, 0.5 m, 10 Apr 1994.

Remarks.—Ortiz & Lalana (1993) described *Caecijaera cojimarensis* from limnoriids in wood pilings from Cojimar Bay, close to Havana. The present material differs from *C. cojimarensis* in having four (as opposed to three) apical setae on each ramus of ♂ pleopod 1, a more slender ♂ pleopod 2, and more slender rami of the uropod.

Menzies (1951) described *Caecijaera horvathi* as a commensal of *Limnoria* sp. from California. The species was later recorded from Hawaii (Cooke 1977). The present material closely resembles this species, in overall proportions, and in the details of the antennules and antennae, uro-

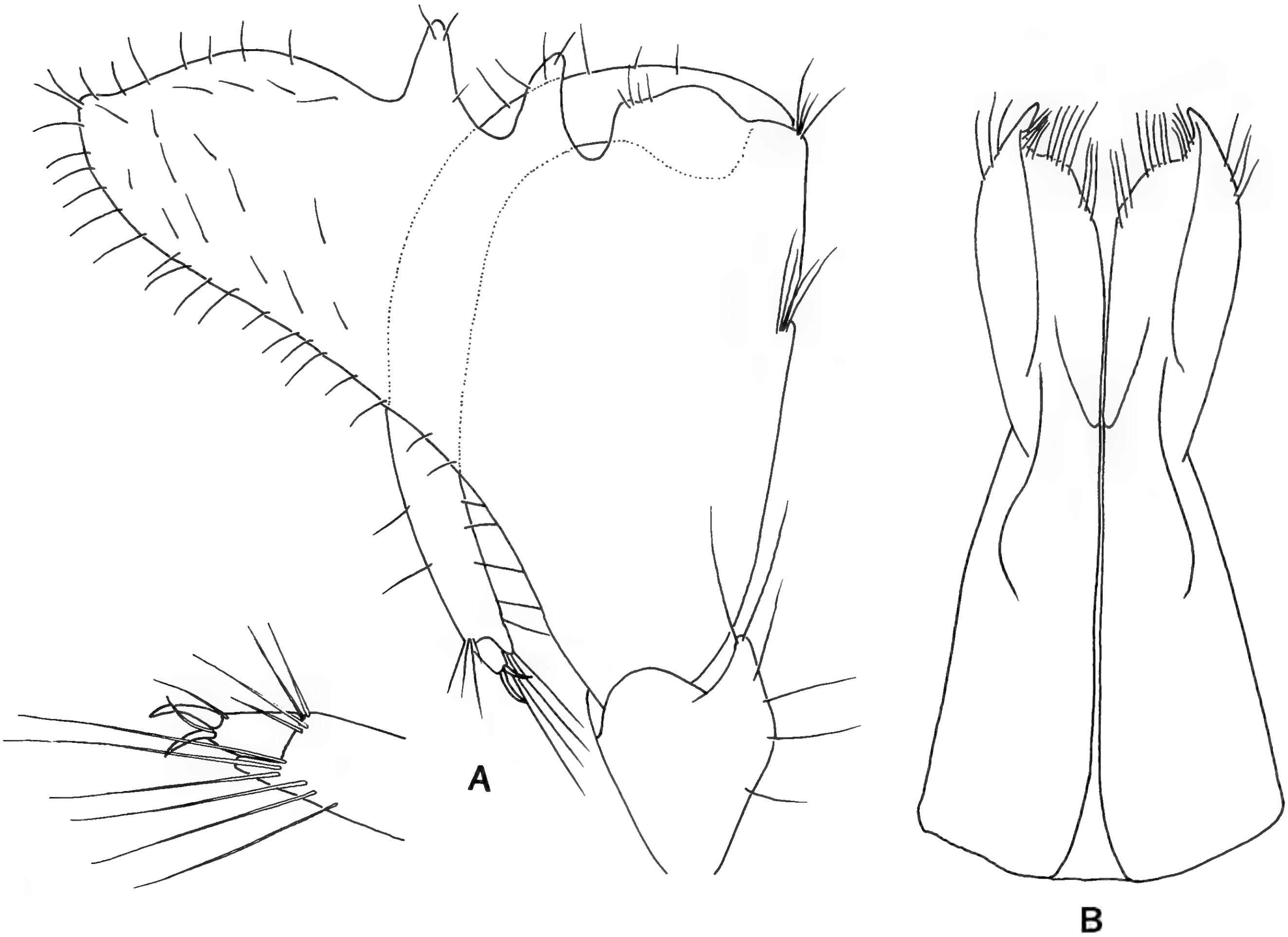

Fig. 5. *Carpias harrietae* Pires, 1981. A, ♂ Pereopod 1, with dactylus enlarged; B, ♂ Pleopod 1.

pods, and especially in the structure of pleopod 1 ♂ as illustrated by Cooke (1977, fig. 1b), (see Fig. 4D). Wilson & Wägele (1994:695), however, suggested that the Hawaiian material might be a separate species, based on the structure of pleopod 1 ♂. Three of the five previously described species of *Caecijaera* (subgenus *Caecijaerella* Kussakin, 1962), all from the Pacific, are characterized by a distally broadly truncate pleopod 1 ♂, and an extremely elongate coiled stylet of pleopod 2 ♂. *C. kussakini* Malyutina, 1994, from Vietnam, however, is very similar to Menzies' species, even agreeing in the number of antennular flagellar articles. Given the commensal habit of *Caecijaera* with the wood-boring *Limnoria*, a broad, perhaps disjunct distribution would not be surprising. A degree of uncertainty must remain regarding the identity of both the earlier Cuban species as well as the present material. More specimens would give some idea of variation, and careful dissections may resolve the issue.

Carpias harrietae Pires, 1981
Fig. 5

Carpias harrietae Pires, 1981:206, figs. 1-20.—Kensley & Schotte, 1989:84, fig. 38F, G.

Material.—USNM 253272, 7 ♂, 3 ovigerous ♀, 6 ♀, sta K-CUBA-35, Cayo Coco, north coast of Cuba, coral rubble from shallow reef area, 1.5–2 m, 14 Apr 1994.

Remarks.—The Cuban material reported here includes males with first pereopods as illustrated by Pires (1981), but also two males having an even larger first pereopod, with a far more expanded posterodistal region of the carpus. It is concluded that the male of Pires' original description is the penultimate stage in the maturation of the

Table 1.—Distinguishing characters of Caribbean species of *Joeropsis.*

	Cephalon margins	Pleotelson margins	Rostrum	Pigment pattern
bifasciata	Entire	6 teeth	Convex	Cephalon and pereonite 4
coralicola	Entire	5 teeth	Indented	Overall reticulation on dorsum
juvenilis	Entire	6 teeth	Straight	Cephalon wider than long
nigricanita	Entire	5 teeth	Indented	Cephalon; pereonites 2–4; light on pereonites 6 and 7, pleotelson
paradubia	Entire	5 teeth	Convex	Cephalon
personata	Serrate	7–8 teeth	Triangular	Cephalon dark, reticulation on rest of dorsum
rathbunae	Entire	5–6 teeth	Convex	Overall reticulation on dorsum
tayronae	Entire	Entire	Indented	Patches on cephalon, pereonites 1, 2, and 4
tobagoensis	Entire	3 teeth	Convex	Cephalon
unidentata	Entire	1 tooth	Convex	Dimorphic; ♂ cephalon; ♀ cephalon and pereonites 2–4

male, the final molt being the one illustrated here.

Family Joeropsidae Nordenstam, 1933

Joeropsis Koehler, 1885

Remarks.—The genus *Joeropsis* is well represented in coral reef habitats, often with three or more species co-occurring. Five primary characters serve to distinguish the species: pigment pattern, body setation, presence or absence of cephalon serrations, presence or absence of pleotelson serrations, and shape of the rostrum. More subtle differences such as the general body proportions, and the shape of the lateral parts of the pereonites are also apparent. Of the 11 species from the broad Caribbean region, eight have a dark pigmented dorsum of the cephalon, while three have additional dark banding on pereonites 2–4 or just on pereonite 4. One of the species described here displays sexually dimorphic color patterns. Dimorphic color patterns are also known for an undescribed species from Dominica, and an undescribed species from the Indian Ocean. In the case of *J. unidentata* from Cuba, the three dark dorsal pereonites in the female correspond with the position of the brood pouch on the ventrum. These pigment patterns presumably have some camouflage function in reef rubble habitats, and can be seen in a range of reef organisms, including the anthurids *Minyanthura corallicola* and *Mesanthura punctillata*, the amphipods *Concarnes concavus* and *Anamixus hanseni*, as well as in tanaidaceans and cumaceans.

Table 1 distinguishes the 11 species of *Joeropsis* recorded from the Caribbean and Bermuda.

Joeropsis juvenilis, new species

Fig. 6

Material.—Holotype, IO-12.053, ♂ 2.2 mm, Paratype, USNM 253274, ♂ 2.0 mm, sta K-CUBA-80, Punta del Este, Isla de la Juventud, coral rubble with mixed algae, 2–3 m, 11 Jun 1995.—2 ♂ 1.3–1.6 mm, sta K-CUBA-78, Punta del Este, Isla de la Juventud, coral rubble and algae between coral heads, 1.5 m, 11 Jun 1995.

Description.—Body length slightly less than 3 times greatest width. Rostrum 2.5 times wider than median length, anterior margin straight. Lateral margins of cephalon entire. Anterolateral angle of pereonite

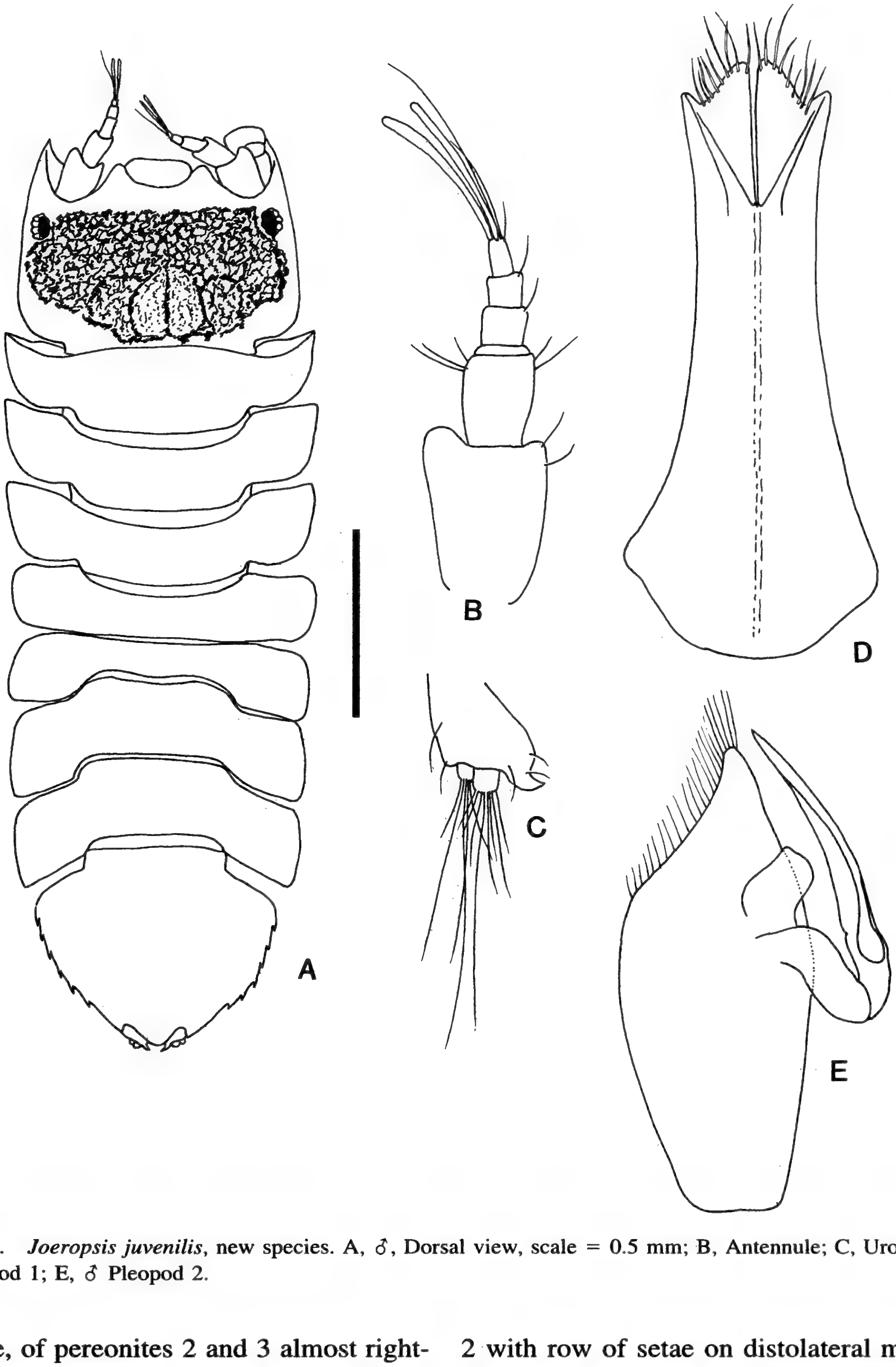

Fig. 6. *Joeropsis juvenilis*, new species. A, ♂, Dorsal view, scale = 0.5 mm; B, Antennule; C, Uropod; D, ♂ Pleopod 1; E, ♂ Pleopod 2.

1 acute, of pereonites 2 and 3 almost right-angled, of pereonite 4 rounded. Lateral margins of pleotelson having 6 teeth.

Antennular flagellum of 3 articles, terminal article bearing 2 aesthetascs. Antenna missing in all specimens. Pleopod 1 of ♂ having 9 setae on distomesial lobe. Pleopod 2 with row of setae on distolateral margin, apex narrowly rounded. Uropod with strong mesially directed tooth.

Female: unknown.

Color pattern: Dense patch of pigment on cephalon, stretching between eyes and covering most of dorsum.

Remarks.—The very broad rostrum of this species is its most distinctive feature.

Etymology.—The specific name, from the Latin 'of youth', refers to the type locality, Isla de la Juventud, the Isle of Youth.

Joeropsis unidentata, new species
Fig. 7

Material.—Holotype, IO-12.050, ♂ 2.0 mm, Allotype, IO-12.052, ovigerous ♀ 1.9 mm, Paratypes, IO-12.051, 2 ♂, 3 ♀, PARATYPES, USNM 253275, 3 ♂, 2 ovigerous ♀, 4 ♀, sta K-CUBA-31, Cayo Francés (north coast), intertidal algal turf on beach rock, scattered coral in shallow infratidal, strong wave action; 13 Apr 1994.

Description.—Body length almost four times greatest width. Rostrum broadly rounded, semicircular, with anteromesial band of short bristles. Lateral margins of cephalon entire. Anterolateral angle of pereonite 1 narrowly rounded, of pereonites 2–4 broadly rounded. Posterolateral angle of pereonites 5–7 broadly rounded. Lateral margin of pleotelson with single tooth.

Antennular flagellum of 3 articles, terminal article bearing 2 aesthetascs. Antennal flagellum of 6 articles. Pleopod 1 of ♂ having 8 or 9 setae on distomesial lobe. Pleopod 2 with dense band of setae on lateral margin. Uropod with strong mesially directed tooth. Operculum of ♀, width slightly less than median length, distally tapered, apically rounded.

Color pattern: Dimorphic; male with most of dorsum of cephalon strongly pigmented; dorsum of pereonite 4 with solid band posteriorly across segment, becoming more diffuse anteriorly. Female with most of dorsum of cephalon strongly pigmented; pereonites 2-4 with most of dorsum strongly pigmented.

Remarks.—The single tooth on the pleotelsonic margin is the most distinctive feature of this species.

Etymology.—The specific name refers to the abovementioned single tooth on the lateral margin of the pleotelson.

Suborder FLABELLIFERA Sars, 1882
Family Sphaeromatidae H. Milne Edwards, 1840
Dynamenella nuevitas, new species
Fig. 8, 9

Material.—Holotype, IO-12.048, ♂ 2.4 mm, Allotype, IO-12.049, non-ovigerous ♀ 2.4 mm, Paratypes, IO-12.047, 6 immature, north coast of Cuba, sta K-CUBA-1, Cayo Mendoza, off La Isabela, algal turf on scattered intertidal rocks, 10 Apr 1994, coll. BK, MS et al.—Paratype, USNM 253276, ♂, sta K-CUBA-17, Cayo Esquivel near La Isabela, 80°03′30″W, 23°02′12″N, algal turf on intertidal mangrove roots, 12 Apr 1994.—Paratype, USNM 253277, 1 non-ovigerous ♀, sta K-CUBA-47, Bahia de Nuevitas, mouth of Saramaguacan River, intertidal rocky beach, hand net, coll. MS, 16 Apr 1994.

Description.—Male: Eubranchiate sphaeromatid with posterolateral margins of pleotelson curved ventrally to form closed, posteriorly-directed tube. Body length approximately twice greatest width; surface of cephalon, pereonites and pleotelson smooth and unornamented. Pereonites 2–6 subequal in length, pereonite 7 shortest. Coxal sutures distinct. Two pleonal sutures extending to posterior margin of pleon only. Pleotelson strongly domed, tapering to relatively short tube, in ventral aspect about 17% length of pleotelson. Pleotelsonic tube entirely closed ventrally in mature specimens, foramen broadly oval to circular in shape.

Antennular peduncle articles colinear, article 1 not extended anteriorly; articles 1 and 3 subequal in length, article 2 considerably longer; article 3 with 2 plumose setae. Antennular flagellum of 7 articles, aesthetascs present on articles 5 and 6. Antennal peduncle with article 5 longest; flagellum of 9 articles.

Epistome somewhat triangular in shape with small lateral bulges; anterior margin truncate, length about 1.7 greatest width, somewhat shorter than labrum. Right mandible with four-cusped incisor, lacinia mob-

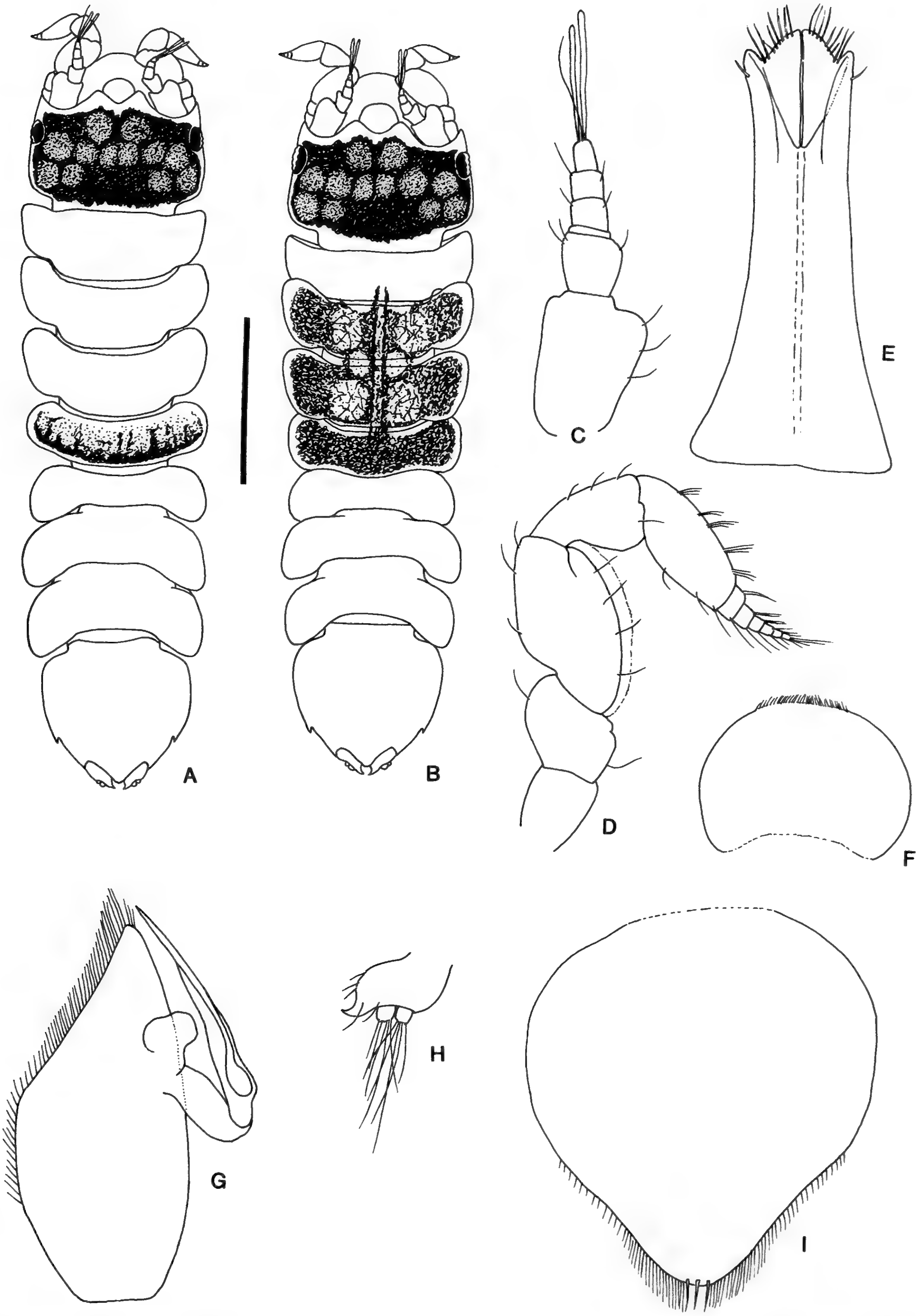

Fig. 7. *Joeropsis unidentata*, new species. A, ♂ Dorsal view, scale = 0.5 mm; B, Ovigerous ♀ dorsal view; C, Antennule; D, Antenna; E, ♂ Pleopod 1; F, Rostrum; G, ♂ Pleopod 2; H, Uropod; I, ♀ Operculum.

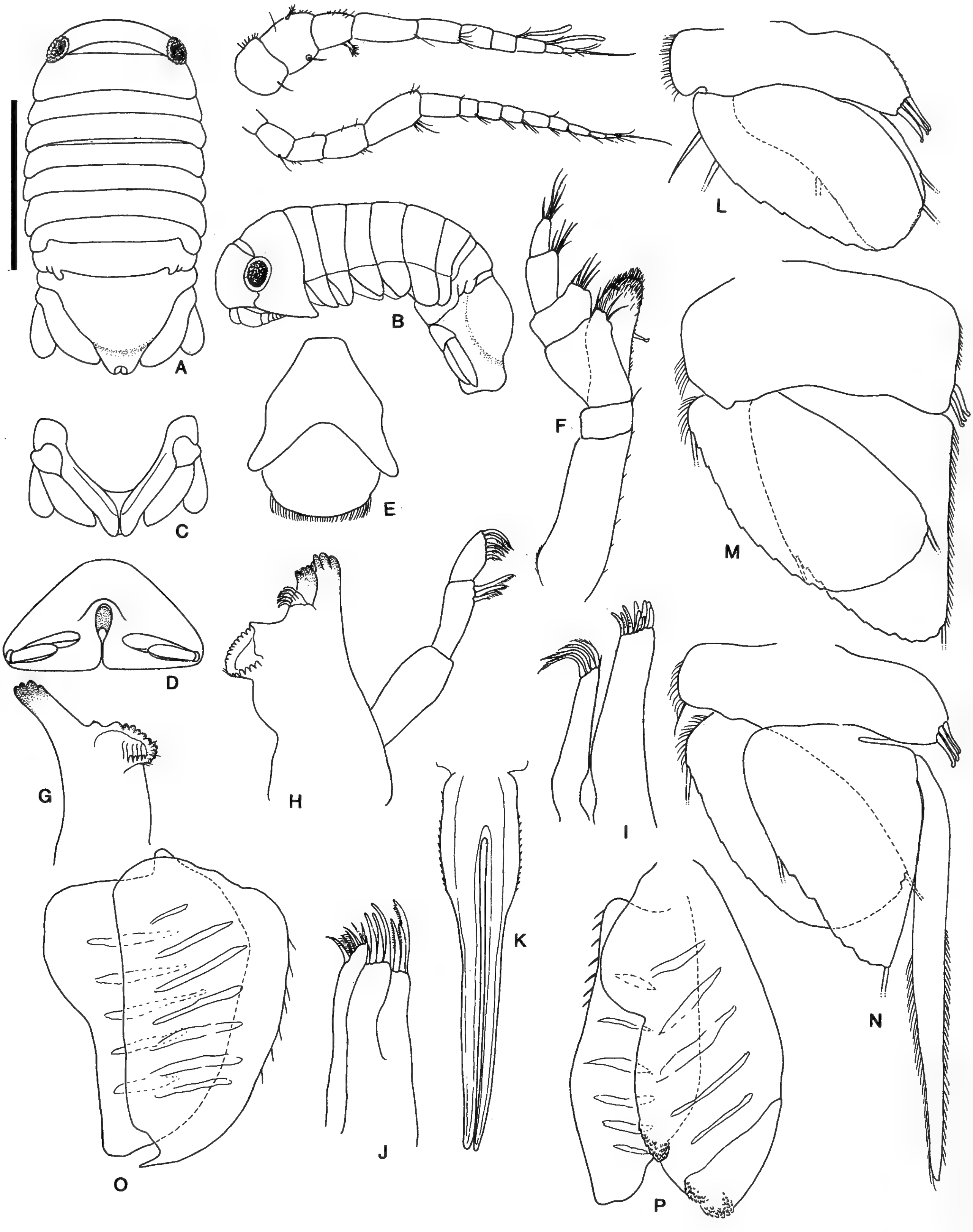

Fig. 8. *Dynamenella nuevitas*, new species. A, ♂ Dorsal view, scale = 1 mm; B, ♂ Lateral view; C, Posterior pleotelson in ventral view; D, Posterior pleotelson viewed end-on; E, Epistome; F, Maxilliped; G, Left Mandible; H, Right mandible; I, Maxilla 1; J, Maxilla 2; K, Penes; L, Pleopod 1; M, Pleopod 3; N, ♂ Pleopod 2; O, Pleopod 4; P, Pleopod 5.

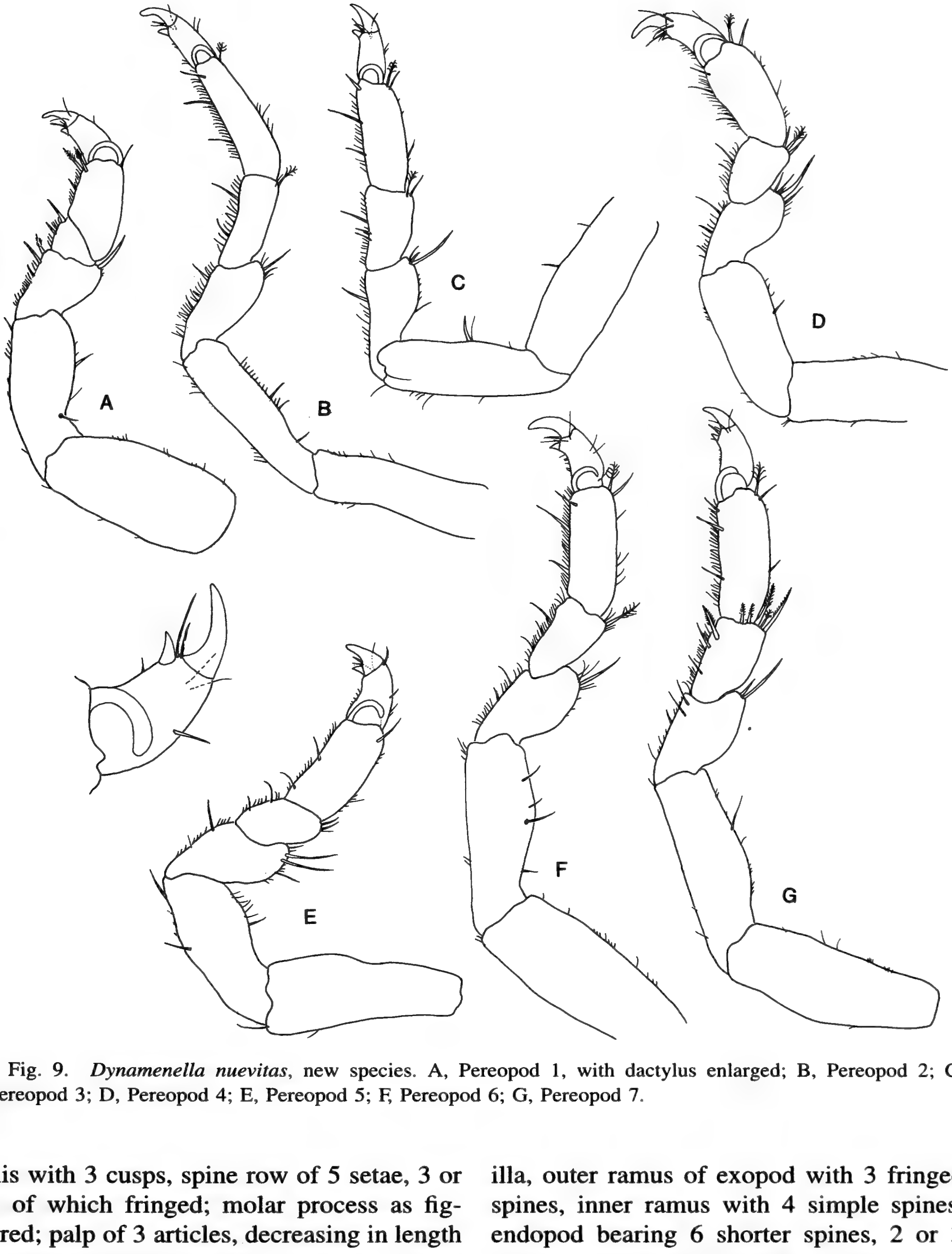

Fig. 9. *Dynamenella nuevitas*, new species. A, Pereopod 1, with dactylus enlarged; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Pereopod 5; F, Pereopod 6; G, Pereopod 7.

ilis with 3 cusps, spine row of 5 setae, 3 or 4 of which fringed; molar process as figured; palp of 3 articles, decreasing in length distally, terminal article bearing 5 setose spines, penultimate article with 3 dentate spines. Left mandible with incisor of 4 cusps, molar as figured. Maxillule, inner ramus with 4 fringed setae and single short spine; outer ramus with 7 rather blunt spines and 3 sharper, dentate spines. Maxilla, outer ramus of exopod with 3 fringed spines, inner ramus with 4 simple spines, endopod bearing 6 shorter spines, 2 or 3 fringed. Maxillipedal endite somewhat narrow, with one coupling hook; several small, blunt spines on distal margin and setose distally; palp with 5 articles, all setose on distomedial margins; lobes 2 and 3 somewhat produced distomedially.

Pereopods 1–7 with simple accessory

spine on dactylus and 2 setae between unguis and accessory spine; all pereopods with fringe of short setae on posterior margin of propodus, carpus, and merus. Pereopod 1, propodus with 2 dentate spines at posterodistal margin; merus having 1 long, simple on anterodistal margin and 1 dentate spine on posterolateral margin. Pereopod 2, longer and more slender than pereopod 1, bearing single plumose seta each at anterodistal corners of propodus and carpus. Pereopod 3, shorter than pereopod 2, having single plumose seta each on anterodistal margin of propodus and carpus. Pereopods 4 and 6, single plumose seta each at anterodistal margin of propodus and carpus. Pereopod 5, 2 long and 1 shorter spine on anterodistal margin of merus. Pereopod 7, single plumose seta at anterodistal margin of propodus; dentate spine at posterodistal corner of carpus; 4 dentate spines, 2 long and 2 short, plus single plumose seta on distal margin of propodus.

Penes long (length five times greatest width) and slender, fused at base, fused area about 1/6 of total length; rami narrowing at about ⅕ of length and tapering to narrowly rounded apices.

Pleopod 1 neither indurate nor triangular, 3 coupling hooks on peduncle; exopod and endopod subequal in length, endopod much narrower, width less than one-half of length. Pleopod 2, peduncle with 3 coupling hooks; appendix masculina slender, more than twice length of endopod and bearing short marginal setae on distal half of length. Exopod of pleopod 3 without articulation. Pleopod 4, both rami with pleats; exopod with several setae on outer margin, apex produced into acute tip. Pereopod 5, exopod with distal suture and 3 spinulose bosses; endopod with setae on proximal half of outer margin; both rami pleated.

Uropodal rami unornamented, setose along external margin and apically, shorter than pleotelson; exopod broadly rounded at apex, ⅔ to ¾ length of endopod; endopod narrowly rounded apically.

Female: Sexual dimorphism not apparent. Ovigerous female unknown.

Remarks.—The new species is clearly related to members of the large subfamily Dynameninae Bowman, 1981, in having a pleotelsonic apex in the male with a notch or foramen, the exopod of pleopod 4 unjointed, and usually with branchial folds on pleopods 4 and 5. Those species having a posteriorly-directed pleotelsonic tube were most often assigned to the genus *Cymodocella*, but Bruce (1995) has shown that the pleotelsonic tube in sphaeromatids may be a homoplasic character that evolved more than once. Because pleotelsonic foramina are variable within genera (e.g., *Ischyromene*), Bruce (1995) and Harrison & Holdich (1982) do not regard that character as useful for generic separation.

With regard to characters for the *Ischyromene* group enumerated by Bruce (1995), *D. nuevitas* seems not to fall within this cluster of genera. Placement of this new species in *Dynamenella* is provisional, since it differs in a number of supposedly significant generic characters. Like those species of *Dynamenella s.s.*, *D. nuevitas* possesses long, tapering fused penial rami, a simple unguis on all pereopods, and lacks dorsal processes. Differences include the lack of sexual dimorphism, a posteriorly-directed pleotelsonic tube instead of a dorsally-directed foramen, and a tapering but elongate appendix masculina. The new species differs from *Paradella* for the same reasons. The lack of information on the morphology of the brood pouch and oostegites in the ovigerous female further obscures its correct placement. Discovery of similar specimens and the description of the female sexual features may justify erecting a new genus in the future.

The samples containing this species were all collected in the intertidal on exposed sides of islands with strong wave action, either among pebbles on a rocky beach, on algal-covered rocks (with *Padina, Caulerpa*, etc.) or on *Rhizophora* mangrove roots.

Etymology.—The specific epithet is part of the name of a paratypic locality, Bahia de Nuevitas, on Cuba's northern coast.

Paraimene ibarzabalae, new species
Fig. 10, 11

Material.—Holotype, IO-12.045, ♂ 2.8 mm, Allotype, IO-12.046, 3.0 mm, sta K-CUBA-74, Punta Francés, Isla de la Juventud, coral rubble with mixed algal turf in spoil bank near reef flat, 2–4 m, 10 Jun 1995. Paratypes, USNM 253279, 1 ♂, 1 ovigerous 9, 25 ♀, 9 immature, sta K-CUBA-22, Cayo Esquivel, large chunks of dead coral rubble from exposed side of cay, 2–2.5 m, 12 Apr 1994.—1 ♀, sta K-CUBA-35, Cayo Coco, rubble from hollows in shallow reef area, 1.5–2 m, 14 Apr 1994.—1 ♂, sta K-CUBA-38, off Cayo Coco, coral rubble encrusted with coralline algae, 12–15 m, 14 Apr 1994. Other material—1 ♂, sta K-CUBA-45, Bahia de Nuevitas, algae on rocks and pebbles, 0.5 m, 16 Apr 1994.

Description.—Male: Body length 2.1 times greatest width; dorsal integumental surface smooth, with scattered setae at lateral margins and on pleotelson. Cephalon with rostral point dorsally visible; epistome broadly rounded, crescent shaped, "arms" barely extending over labrum; labrum very setose distally; eyes large, dorsal. Pereonal tergites 1–4 without ornamentation; pereonites 5 and 6 each with single, low, transverse carina, extending nearly full width of segment; pereonite 7 shorter than, and overlapped by, 6. Suture lines on pleon reaching posterior margin only. Pleotelson markedly domed with 8 small protuberances in 2 rows of 4 each, all bearing a single short seta; posterior half tapering to narrow apex in dorsal view, edges of pleotelson folding ventrally to form vertical slit when viewed posteriorly. Lateral margins of tergites 2–7, pleon and anterior pleotelson upcurved to produce concave submarginal area.

Antennule with 3 basal articles subequal in length; flagellum with 7 articles, 5–7 bearing aesthetascs. Antenna slender, with 9 setose articles in flagellum. Mandible bearing incisor with 3 cusps; lacinia mobilis of 5 cusps, spine row of 2 fringed spines; palp of 3 articles, article 2 with 3 fringed setae on distolateral margin, article 3 bearing 5 fringed setae distolaterally. Maxilla 1, inner ramus with 4 fringed setae; outer ramus bearing 10 blunt spines. Maxilla 2, inner ramus with 7 spines, 3 of which fringed; outer lobes with 3 and 5 spines each. Maxillipedal endite with 4 blunt spines plus 3–4 slender, fringed spines on distal margin; 1 coupling hook; palp with 5 articles, articles 2–5 with distomesial lobe bearing numerous setae. Pereopod 1 shortest, with stout spines on posterodistal margin of propodus, carpus, and merus. Pereopod 2 with plumose seta at anterodistal margin of propodus and several small, slender setae on posterior margins of propodus, carpus, merus and ischium. Pereopod 3, with dense fringe of setules on posterior margins of propodus, carpus, merus and posterodistal margin of ischium; 2 long spines each on anterodistal margins of propodus and merus. Pereopod 4, dense fringe of setules on posterior margins of propodus, carpus, merus, and posterodistal margin of ischium; plumose seta on anterodistal margin of propodus; two strong spines on anterior margin of merus. Pereopod 5, fringe of setules on posterior margin of propodus, carpus, and merus; anterior margin of ischium indented to accomodate merus, having two long spines on anterodistal margin. Pereopod 6, fringe on setules on posterior margin of carpus, merus, and posterodistal margin of ischium. Pereopod 7, fringe of setules on propodus and merus; carpus with 6 fringed spines at distal margin. Penes short, unfused, and distally rounded. Pleopod 1 with 3 coupling hooks on basis; strong spine on anterolateral margin of endopod. Pleopod 2, appendix masculina articulating basally, width ca. 9 times length, tapering to rounded apex, extending beyond endopod by 1/6 of length. Pleopod 3 with 3 coupling hooks on basis; complete transverse suture in dis-

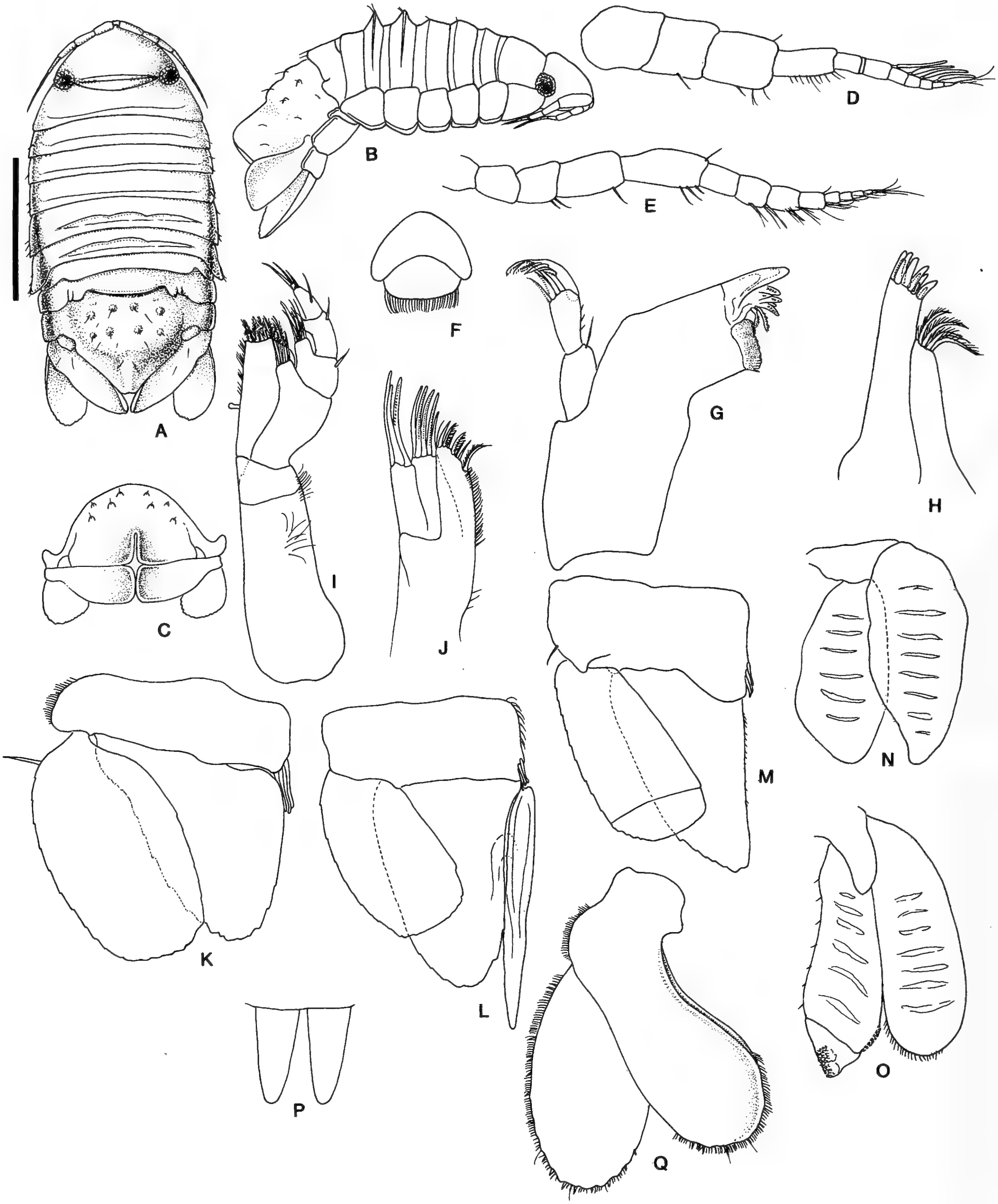

Fig. 10. *Paraimene ibarzabalae*, new species. A, ♂ Dorsal view, scale = 1 mm; B, Lateral view; C, Posterior pleotelson viewed end-on; D, Antennule; E, Antenna; F, Epistome; G, Left mandible; H, Maxilla 1; I, Maxilliped; J, Maxilla 2; K, Pleopod 1; L, ♂ Pleopod 2; M, Pleopod 3; N, Pleopod 4; O, Pleopod 5; P, Penes; Q, Uropod.

tal fifth. Pleopod 4, both rami membranous, pleated, endopod acute distally. Pleopod 5, both rami membranous, pleated; exopod with 3 spinulose bosses, sparse setae on outer margin; endopod with setae distally. Endopods of uropod distally setose, upturned distally to meet at midline; mesial margin deeply grooved to accommodate margin of pleotelson. Exopod densely fringed on lateral and distal margins, ex-

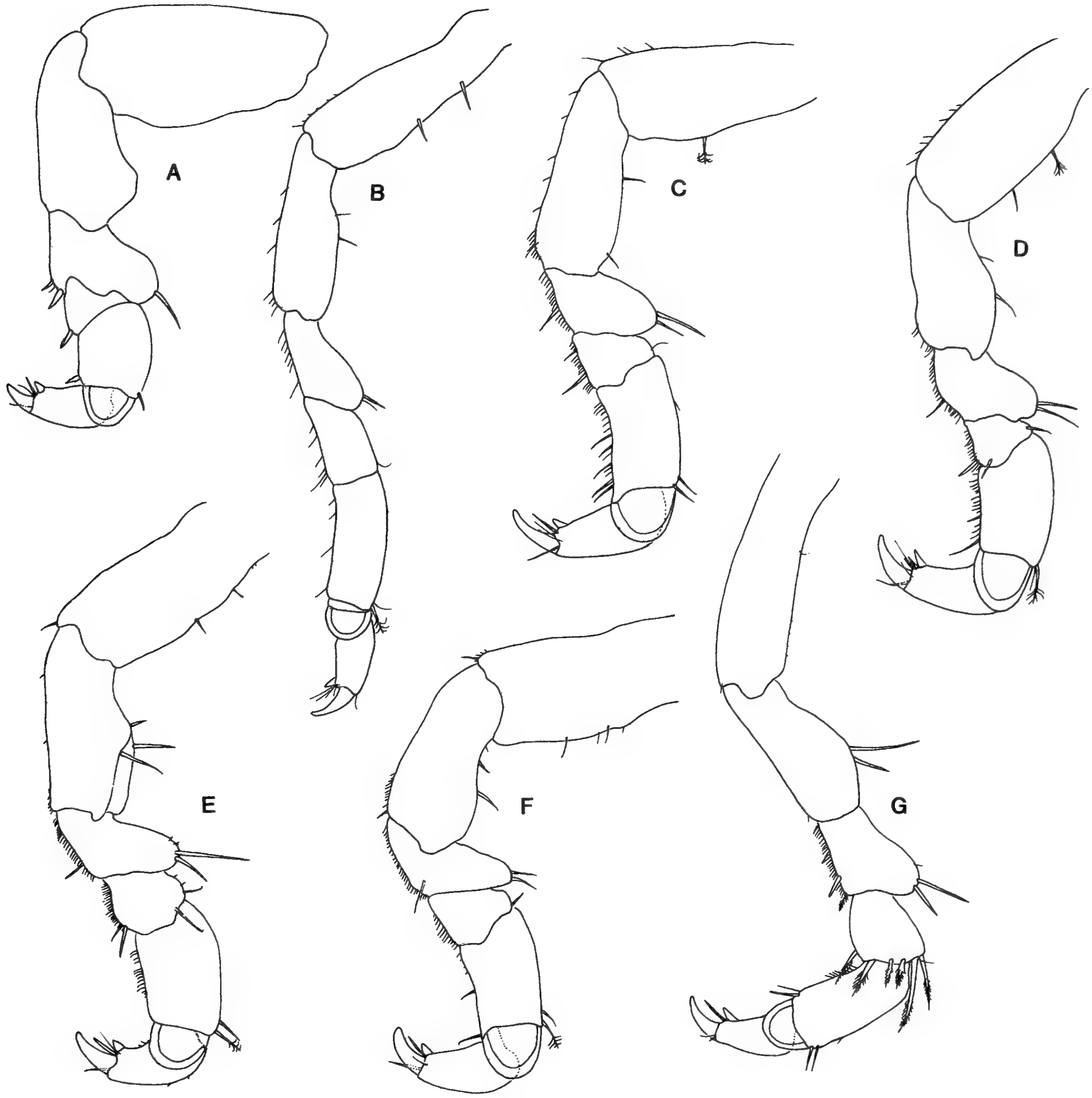

Fig. 11. *Paraimene ibarzabalae*, new species. A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Pereopod 5; F, Pereopod 6; G, Pereopod 7.

tending somewhat beyond endopod; both rami of uropod reaching well beyond apex of pleotelson.

Female: Differs from male in absence of carinae on tergites 5 and 6.

Color pattern: Brown pigmentation somewhat variable, sometimes dense, often on pereonites 1, 6, 7, pleon and pleotelson; scattered chromatophores sometimes on rami of uropods.

Remarks.—The present species is the second to be discovered in the western hemisphere, following *Paraimene charlesae* Kensley & Schotte, 1994, from Dominica. *Paraimene ibarzabalae* is easily separated by the presence of eight protuberances on the pleotelson, upturned lateral margins of the tergites, uropodal endopods with distomesially upturned margins which meet at midline of body, and by the presence of low carinae on pereonites 5 and 6 in the male.

Further differences in the epistome, mandible, maxilla 2 and in the relative length of the appendix masculina are also noted. As in the type species *P. tuberculata* Javed

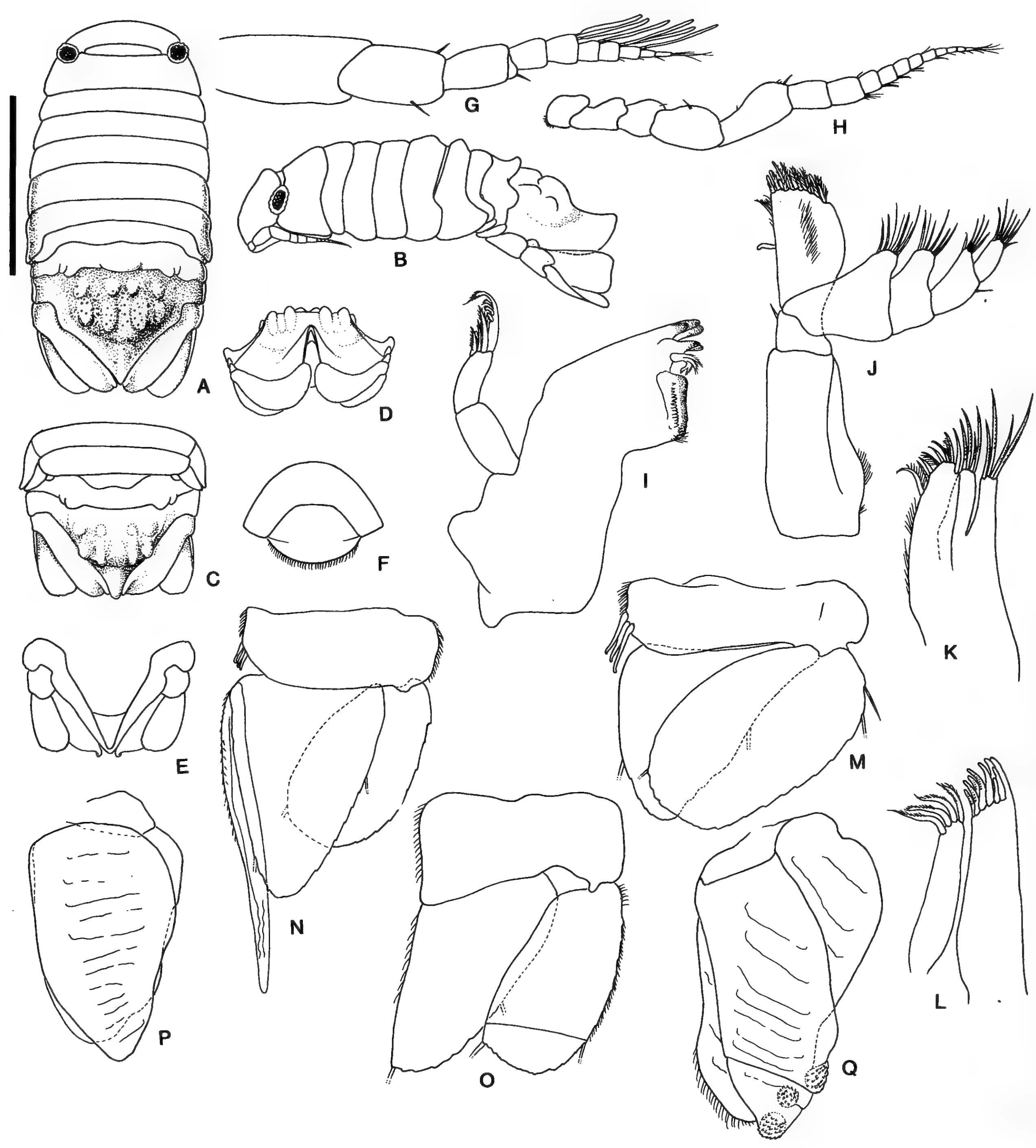

Fig. 12. *Paraimene tumulus*, new species. A, ♂ Dorsal view, scale = 1.5 mm; B, ♂ Lateral view; C, ♀ Pleotelson; D, Posterior pleotelson viewed end-on; E, Posterior pleotelson in ventral view; F, Epistome; G, Antennule; H, Antenna; I, Left Mandible; J, Maxilliped; K, Maxilla 2; L, Maxilla 1; M, Pleopod 1; N, 6 Pleopod 2; O, Pleopod 3; P, Pleopod 4; Q, Pleopod 5.

& Ahmed, 1988, from Pakistan, the second pereopod in both Caribbean species is longer, more slender and less sclerotized than either pereopods 1 or 3. This feature is probably a generic feature. In the generic diagnosis the coxa of pereopod 7 is described as a narrow dorsally curved tubular structure. In both Caribbean species, it is a subtriangular and not overlapped by the coxa of pereopod 6. Differences between the new species and the Pakistani type are most readily seen in the ornamentation of the pleotelson and pereonites.

Etymology.—The species is named for Mrs. Diana Ibarzabal, who kindly aided us in field work and collected the new species.

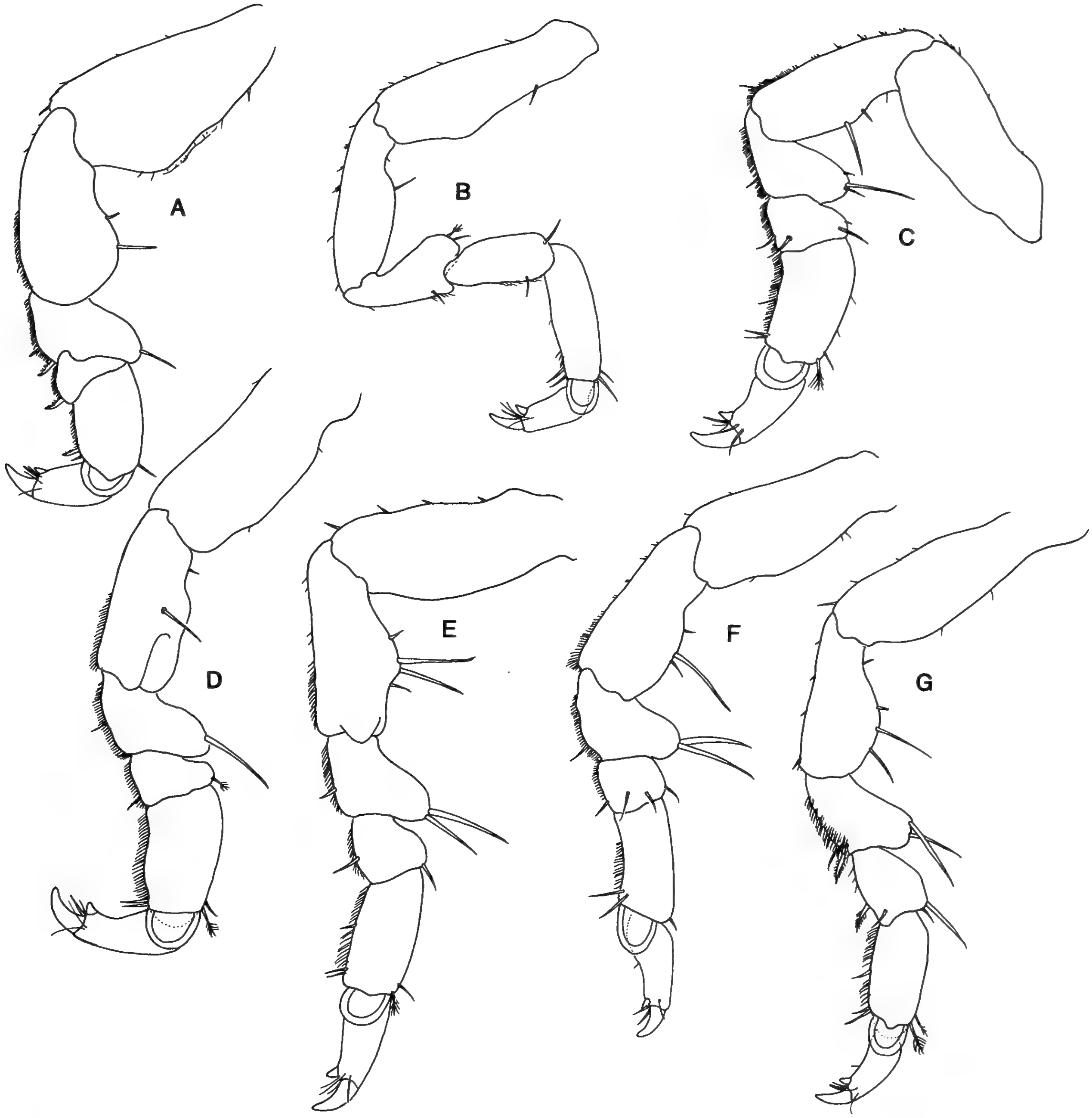

Fig. 13. *Paraimene tumulus*, new species. A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Pereopod 5; F, Pereopod 6; G, Pereopod 7.

Paraimene tumulus, new species
Fig. 12, 13

Material.—Holotype, IO-12.060, ♂ 3.0 mm, Allotype, USNM 253280, ♀ 2.6 mm, Paratype, USNM 253281, ♂, sta K-CUBA-31, Cayo Francés, algal turf on beach rock on exposed side of cay, shallow infratidal, 13 Apr 1994.

Description.—Male: Body length twice greatest width; dorsal integument of pereon smooth, glabrous. Cephalon domed, tiny rostral point barely visible in dorsal view; epistome nearly semi-circular anteriorly, diverging extensions squared distally; eyes large, dorsolateral. Pereonites unornamented; pereonite 6 with slightly raised transverse ridge posteriorly. Lateral margins of pereonites 6 and 7 slightly upcurved. Pleonite short with posterior midsection projecting dorsally, lateral margins upcurved. Pleotelson anteriorly bulbous, granular and pitted, bearing row of 4 rounded bosses anteriorly and 4 elongate bosses posteriorly; posterior half tapering to rounded apex.

Antennule with peduncular articles decreasing in relative length distally; flagellum of 7 articles, second and fourth articles each bearing 2 aesthetascs, articles 3 and 5 with single aesthetasc. Antenna subequal in length to antennule, fifth article longest; flagellum with 11 articles. Mandible with incisor of 3 cusps, sclerotized lacinia mobilis with 2 cusps; spine row of 4 fringed setae; molar broad with marginal teeth and few setae; palp of 3 articles, article 2 with 3 fringed setae, article 3 with 5 fringed setae distally. Maxilla 1, inner ramus with 4 stout fringed setae; outer ramus with 9 blunt spines, 4 of which faintly dentate. Maxilla 2, inner ramus bearing 6 setae on distomesial margin and 2 setae distolaterally; both lobes of outer ramus with 4 fringed spines. Maxillipedal endite with one coupling hook and single fringed spine on mesial margin, distal margin with 8 stout, fringed setae; palp of 5 articles, each with developed distomesial setose lobe. Pereopod 1 with dense fringe of setules on posterior margins of propodus, carpus, ischium and merus; single stout fringed seta at posterodistal margin of propodus, carpus, and merus. Pereopod 2 markedly more slender and less setulose than pereopods 1 or 3. Pereopods 3–6 with fringe of short setae on posterior margin of propodus, carpus, merus, and posterodistal margin of ischium; long setae as figured on anterior margins of carpus, propodus, merus and ischium. Pereopod 4, ischium indented to receive carpus. Pereopod 7, fringe of setules on posterior margin of propodus and merus; stout dentate spines on posterodistal margins of carpus and merus. Penes unfused, short, stubby, rounded distally. Pleopod 1, 3 coupling hooks on distomesial margin; endopod triangular, exopod elliptical. Pleopod 2, basis with 3 coupling hooks; exopod elliptical and shorter than endopod; endopod with appendix masculina attached basally, extending beyond apex of ramus by one-third of length, with fine setae on anterior half of mesial margin. Pereopod 3, exopod with complete transverse suture in distal fifth; row of fine setae on mesial margins of basis and endopod and lateral margin of exopod. Pereopod 4, both rami membranous, endopod distally narrow. Pleopod 5, both rami membranous, exopod with distal transverse suture and 3 spinulose bosses. Uropodal rami subequal, extending somewhat beyond apex of pleotelson, not meeting in midline; exopod rounded apically; endopod slightly emarginate distally with distomesial edges upturned against pleotelson.

Female: Lacking raised ridges on posterior margins of pereonite 6 and pleonite; sculpturing on pleotelson less distinct than in male; uropodal rami subequal in length to pleotelson, endopod lobed distomesially and strongly upturned against pleotelson.

Remarks.—This second *Paraimene* from Cuba is most closely related to *P. dianae* but differs in the sculpturing of the pleotelson, the length of the uropods, the shape of the epistome, and in the relative length of the appendix masculina. The uropodal endopod differs in shape and is not grooved along the inner margin to fit against the pleotelson as in the male of *P. dianae*. The absence of strong carinae on pereonites 5 and 6 in the latter species helps further to distinguish the new species. *Paraimene charlesae* Kensley & Schotte, 1994, described from Dominica, can be readily identified by three protuberances on each side of the pleotelson in the male. The bifid accessory dactylar spine found in *P. charlesae* and in the type *P. tuberculata* Javed & Ahmed, 1988, from Pakistan is not a consistent feature in the two species from Cuba, although in both of these there is at least one spine placed between the unguis and accessory spine in all pereopods.

The habitat of the *P. tumulus* is similar to that of the type species and of *P. charlesae*, namely, algal turf in the infra-intertidal zone of rocky beaches.

Etymology.—The specific name, used as a noun in apposition, is from the Latin *tumulus*, a raised mound or hillock, and refers to features on the pleotelson.

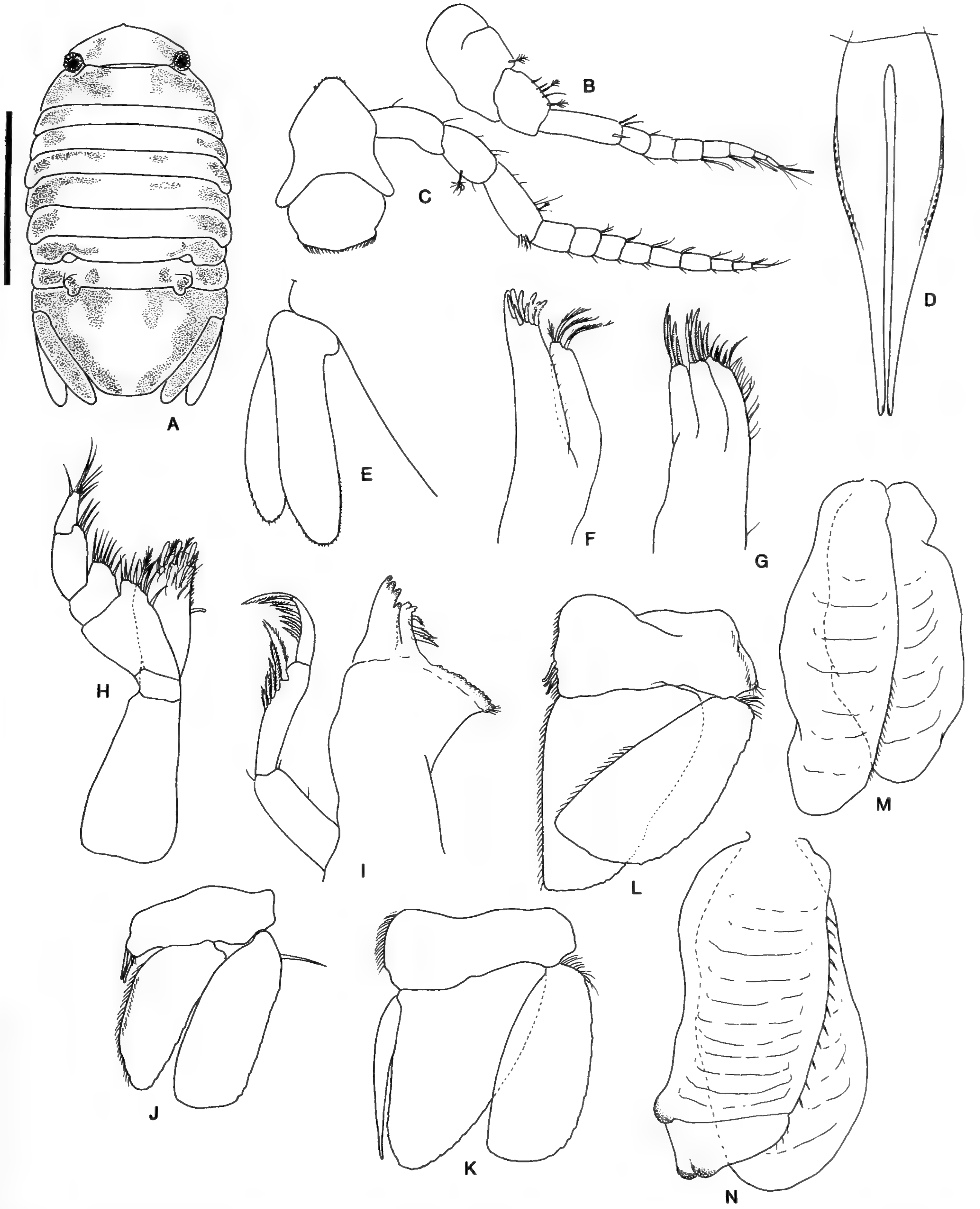

Fig. 14. *Sphaeromopsis mourei* (Loyola e Silva, 1960). A, ♂ Dorsal view, scale = 2 mm; B, Antennule; C, Epistome and antenna; F, Maxilla 1; G, Maxilla 2; H, Maxilliped; Pleopod 1; K, ♂ Pleopod 2; L, Pleopod 3; M, D, Penes; E, Uropod; F, I, Left mandible; J, Pleopod 1; K, ♂ Pleopod 2; L, Pleopod 3; M, Pleopod 4; N, Pleopod 5.

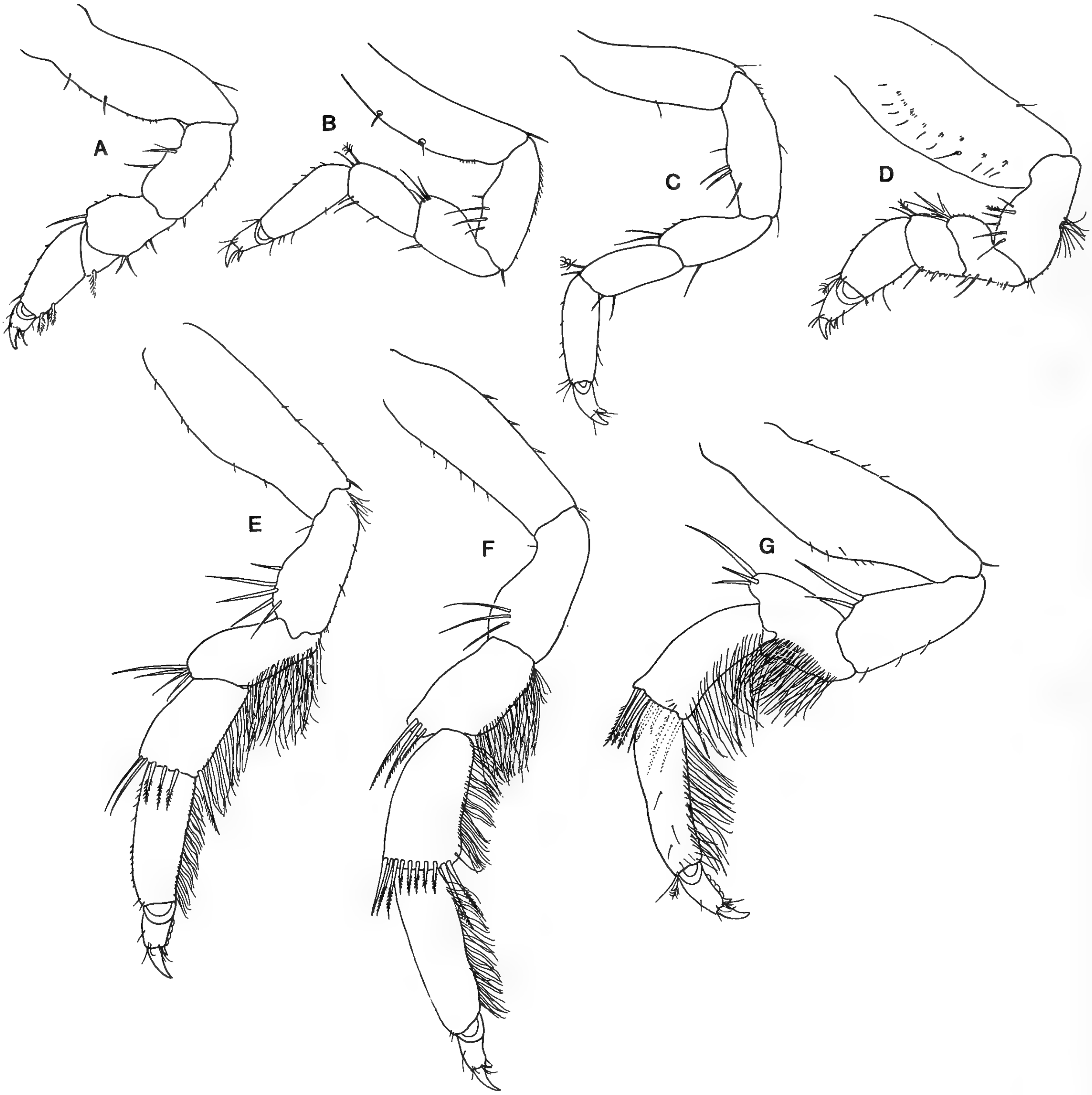

Fig. 15. *Sphaeromopsis mourei* (Loyola e Silva, 1960). A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Pereopod 5; F, Pereopod 6; G, Pereopod 7.

Sphaeromopsis mourei
(Loyola e Silva, 1960)
Fig. 14, 15

Pseudosphaeroma mourei Loyola e Silva, 1960:138, figs. 22, 23.—Menzies & Glynn, 1968:66.—Holdich & Jones, 1973:393.

Sphaeromopsis mourei: Holdich & Harrison, 1981:295.

Material.—USNM 253282, 5 ♂, 2 ovigerous ♀, 2 ♀, 2 juveniles, sta K-CUBA-16, Cayo los Dromedarios near La Isabela, algae and sponges on mangrove roots, 0.5–1 m, 11 Apr 1994.

Description.—Male: Body length approximately 1.9 times width. Cephalon broader than long, smooth, convex. Epistome visible in dorsal view. Frontal lamina with broadly rounded apex and concave lateral margins, somewhat more than twice length of clypeus. Pereonites smooth. Pleon having single free pleonite with two incomplete sutures. Pleotelson very broadly rounded apically, almost truncate, smooth. Pigment of brown chromatophores, densest at margins of tergites and pleotelson, absent in medial a reas, especially of telson.

Antennular basal article 1.5 times length of article 2, both bearing plumose setae; flagellum of 7 articles, articles 4–7 each bearing single aesthetasc. Antenna with peduncle article 3 longest, articles 2 and 3 with plumose setae; flagellum of 9 articles. Mandible with 4 cusps on incisor, spine row with 3 fringed spines; palp with 5 stout, dentate spines on penultimate article, distalmost article with 7 fringed setae. Maxilla 1, inner ramus with 4 fringed setae; outer ramus having 9 blunt spines, innermost 3 dentate. Maxilla 2, inner ramus bearing 2 simple and 3 fringed spines as well as thin marginal setae; outer lobes with 4 and 6 fringed spines respectively. Maxillipedal endite with single coupling hook, distal margin having several plumose and simple setae and 4 stout spines; palp of 5 articles, article 3 shortest, all setose.

Pereopods increasing in length posteriorly. Pereopod 1 with 2 stout, bidentate spines on posterior margin of propodus and single bidentate spine on carpus. Pereopod 2 markedly longer and more slender than pereopods 1 and 3; pereopods 2 and 3 each with single plumose seta on posterior margin of carpus, stiff setae on merus and ishium. Pereopod 3 more setose than previous 2 with many short setae on posterior margin of basis. Pereopods 4–7 each with long, stiff spines on posterodistal margins of ischium and merus; carpus in each with several fringed spines on distal margin; merus, carpus and propodus of each with dense fringe of long, fine setae. Penile rami fused at base, tapering to narrow apices and with small patches of short setae on lateral margins at middle one-third of length. Pleopod 1, basis with 3 coupling hooks; fine setae on and near mesial margin of endopod. Pleopod 2, endopod triangular, appendix masculina attached basally and tapering gradually to very narrow apex, not reaching apex of endopod. Pleopod 3, basis with 3 coupling hooks, both rami undivided and with fringe of fine setae on mesial margins. Pleopod 4, both rami with transverse pleats and setae on outer distal margin of exopod. Pleopod 5, exopod with fine setae on outer margin and 3 spinulose bosses distally. Uropods extending slightly beyond pleotelson, both rami bearing short, fine setae distally; endopod faintly crenulate apically, slightly shorter than exopod.

Female: Tergites as in male; pigment patterns not as pronounced or, largely absent.

Previous records.—Off several beaches in Brazil from Fortaleza in the north to Florianopolis in the south, 6-15 m.

Remarks.—It was thought useful to redescribe and figure this species, as the original description is sometimes difficult to obtain, and given this great range extension of about 5000 kilometers.

Acknowledgments

Several individuals assisted us with collecting and sorting, and in numerous ways helped to make the two field trips on which this paper is based, a scientific success. These included Kristian Fauchald, Diana Ibarzabal, the crew of the R.V. *Ulises*, and especially Dr. Rodolpho Claro, expedition leader from the Institute of Oceanology, Havana. The logistics and financial support for the two trips were arranged by Dr. Michael Smith of the Center for Marine Conservation, Washington, D.C., as part of the U.S./Cuban Scientific Exchange program, supported by the MacArthur Foundation, and the Office of Biodiversity Studies, National Museum of Natural History, Smithsonian Institution. To all of these, our sincere and grateful thanks.

Literature Cited

Bowman, T. E. 1981. *Thermosphaeroma milleri* and *T. smithi*, new sphaeromatid isopod crustaceans from hot springs in Chihuahua, Mexico, with a review of the genus.—Journal of Crustacean Biology 1:105–122.

Bruce, N. L. 1995. The taxonomy and phylogeny of tube-tailed sphaeromatid isopods (Crustacea) with descriptions of new species and a new genus from southern Australia.—Ophelia 43:127–180.

Coineau, N., & L. Botosaneanu. 1973. Isopodes interstitiels de Cuba. Pp. 191–222 *in* Résultats des Expeditions Biospeologiques Cubano-Roumaines à Cuba. Bucarest, Academy of the Socialist Republic of Romania.

Cooke, W. J. 1977. On the occurrence of the commensal asellote *Caecijaera horvathi* Menzies, 1951, in Hawaii.—Crustaceana 33:105–106.

Harrison, K., & D. M. Holdich. 1982. Revision of the genera *Dynamenella, Ischyromene, Dynamenopsis*, and *Cymodocella* (Crustacea: Isopoda), including a new genus and five new species of eubranchiate sphaeromatids from Queensland waters.—Journal of Crustacean Biology 2:84–119.

Hay, W. P. 1903. On a small collection of crustaceans from the island of Cuba.—Proceedings of the United States National Museum 26:429–435.

Holdich, D. M., & K. Harrison, 1981. The sphaeromatid isopod genus *Sphaeromopsis* Holdich & Jones in African, Australia and South American waters.—Crustaceana 41:286–300.

Holdich, D. M., & D. A. Jones. 1973. The systematics and ecology of a new genus of sand beach isopod (Sphaeromatidae) from Kenya.—Journal of Zoology, London 171:385–395.

Javed, W., & R. Ahmed. 1988. *Paraimene tuberculata*, a new genus and species of Isopods (Sphaeromatidae) from Karachi, Pakistan.—Hydrobiologia 169:371–377.

Kensley, B. 1982. Anthuridea (Crustacea: Isopoda) of Carrie Bow Cay, Belize. *In* K. Rützler and I. G. Macintyre, eds., The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, 1: Structure and Communities, pp. 321–352.—Smithsonian Contributions to Marine Sciences 12, 539 pp.

———. 1987. Further records of marine isopods from the Caribbean.—Proceedings of the Biological Society of Washington 100(3):559–577.

———, & M. Schotte. 1987. New records of isopod Crustacea from the Caribbean, the Florida Keys, and the Bahamas.—Proceedings of the Biological Society of Washington 100(1):216–247.

———, & ———. 1989. Guide to the marine isopod crustaceans of the Caribbean. Smithsonian Institution Press, Washington D.C. 308 pp.

———, & ———. 1994. Marine isopods from the Lesser Antilles and Colombia (Crustacea: Peracarida).—Proceedings of the Biological Society of Washington 107:482–510.

Koehler, R. 1885. Description d'un Isopode nouveau, le *Joeropsis brevicornis*.—Annales des Sciences Naturelles (Paris), Zoologie (6)19:1–7.

Kussakin, O. 1962. On the fauna of Janiridae (Isopoda, Asellota) from the seas of the USSR.—Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 30:17–65.

Latreille, P. A. 1803. Histoire naturelle des Crustacés et des Insectes. *In* Volume 5 of G. L. L. de Buffon, 1802–1805, Histoire Naturelle, nouvelle edition, accompagnée des notes. Ouvrage rédigé par C. S. Sonnini, Paris, 14 vols.

Leach, W. E. 1814. Crustaceology. *In* Brewster's Edinburgh Encyclopedia, vol. 7, pp. 383–439.

Loyola e Silva, J. de. 1960. Sphaeromatidae do litoral Brasileiro (Isopoda-Crustacea).—Boletim da Universidade do Parana, Zoologia 4:1–182.

Malyutina, M. V. 1994. *Caecijaera kussakini* sp. n., a new asellote isopod from Vietnam (Crustacea, Isopoda: Janiridae).—Zoosystematica Rossica 3: 27–33.

Menzies, R. J. 1951. A new genus and new species of asellote isopod, *Caecijaera horvathi*, from Los Angeles-Long Beach harbor.—American Museum Novitates 1542:1–7.

———, & P. W. Glynn. 1968. The common marine isopod Crustacea of Puerto Rico: A handbook for marine biologists.—Studies on the Fauna of Curaçao and other Caribbean Islands 27(104):1–133.

Milne Edwards, H. 1840. Histoire naturelles des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux, vol. 3, Paris.

Negoescu, I. 1979. *Cyathura cubana* sp. n. (Isopoda, Anthuridea) from the Caribbean Sea (Cuban waters).—Travaux du Muséum d'Histoire Naturelle Gigore Antipa 20:157–164.

Nordenstam, A. 1933. Marine Isopoda of the families Serolidae, Idotheidae, Pseudidotheidae, Arcturidae, Parasellidae, and Stenetriidae mainly from the South Atlantic.—Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 3(1):1–284.

Ortiz, M., & R. Lalana. 1993. *Caecijaera (Caecijaera) cojimarensis*, nueva especie de isopodo (Asellota, Janiridae) asociado a *Limnoria* sp. (Flabellifera) de Cuba.—Caribbean Journal of Science 29(1/2):44–49.

———, ———, & O. Gómez. 1987. Lista de especies y bibliografía de los isópodos (Crustacea, Peracarida) de Cuba.—Revista de Investigaciones Marinas 8(3):29–37.

Pires, A. M. S. 1981. *Carpias harrietae* (Isopoda, Asellota), a new species from Florida.—Crustaceana 39(1):95–103.

Sars, G. O. 1882. Oversigt af Norges Crustacea.—Forhandlinger i Videnskabsselskabet i Kristiania 1882, 18:1–124.

———. 1899. An Account of the Crustacea of Norway, vol. 2, parts 13–14. Isopoda. Bergen, 270 pp.

Schioedte, J. C., & F. W. S. Meinert. 1879. De cirolanis Aegas simulantibus commentatio brevis.—Naturhistorisk Tidsskrift 12:279–302.

Wagner, H. P. 1990. The stygobiont isopods of the genus *Cyathura* in the Dominican Republic (Crustacea; Isopoda; Anthuridae).—Bulletin Zoologisch Museum, Universiteit van Amsterdam 12(10):145–158.

Wilson, G. D. F., & J.-W. Wägele. 1994. Review of the family Janiridae (Crustacea: Isopoda: Asellota).—Invertebrate Taxonomy 8:683–747.

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Redescription and first record of *Cymbasoma tenue* (Isaac, 1975) (Copepoda: Monstrilloida) in the Mediterranean Sea

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Abstract.—Several male specimens of *Cymbasoma tenue* (Isaac, 1975) were found in zooplankton samples collected at Toulon Bay, on the French Mediterranean coast. This copepod has not been recorded since its original description more than 20 years ago, which was based on material collected in the Bristol Channel, England. *Cymbasoma tenue* is here redescribed based on examination of these specimens and of the type material. The taxonomic analysis of these specimens produced new morphological data for the species. This is the first record of the species in the Mediterranean and a latitudinal extension of its known geographical range.

Monstrilloid copepods are parasitic marine crustaceans which are free-living only during the adult and first naupliar stage; their other immature stages are endoparasites of benthic invertebrates such as molluscs and polychaetes (Hartman 1961, Isaac 1975, Grygier 1994a). Huys & Boxshall (1991) recognized three valid genera: *Monstrilla*, *Monstrillopsis* and *Thaumaleus*. However, the genus *Thaumaleus* Krøyer, 1849 is not valid and, except for the type (*T. typicus* Krøyer, 1849), all the species described under this genus should be included under *Cymbasoma* Thompson, 1888 (Grygier 1994a).

From several surface (0–25 m) plankton samples collected in the Bristol Channel area, Isaac (1974) reported 15 species of Monstrilloida, of which six were new. Among the new species, he described *Cymbasoma tenue* (as *Thaumaleus tenuis*) based on three males caught off Gulland Rock, Padstow, Cornwall, England (approx. 50°35′N, 5°30′E). Since its original description more than 20 years ago, this species has not been recorded again, even around the type locality. Most of the known species of Monstrilloida must be redescribed following to the new upgraded standards on monstrilloid copepod descriptions (Grygier 1994b, Grygier & Ohtsuka 1995). Therefore, Isaac's (1974) brief description of *C. tenue* should be completed with more detail, i.e., descriptions and illustrations of all swimming legs, details of the genital lappets and of the antennular armature, and body proportions.

It should be noted that Grygier (1995) recognized *T. tenuis* as validly proposed in 1974. However, the weak original diagnosis would disallow Isaac's (1974) work as the valid description for this species. Therefore, Isaac (1975) would be then the author and valid date since it was in this work where *T. tenuis* was separated from *T. quadridens* Davis, 1947 by the absence of teeth on the genital lappets and (wrongly) by the absence of hairs on the cephalothorax.

In result of a recent survey (July 1995) of the zooplankton of Toulon Bay on the French Mediterranean coast, several specimens of a monstrilloid copepod were collected and sent to us for identification. The taxonomic analysis of the copepods re-

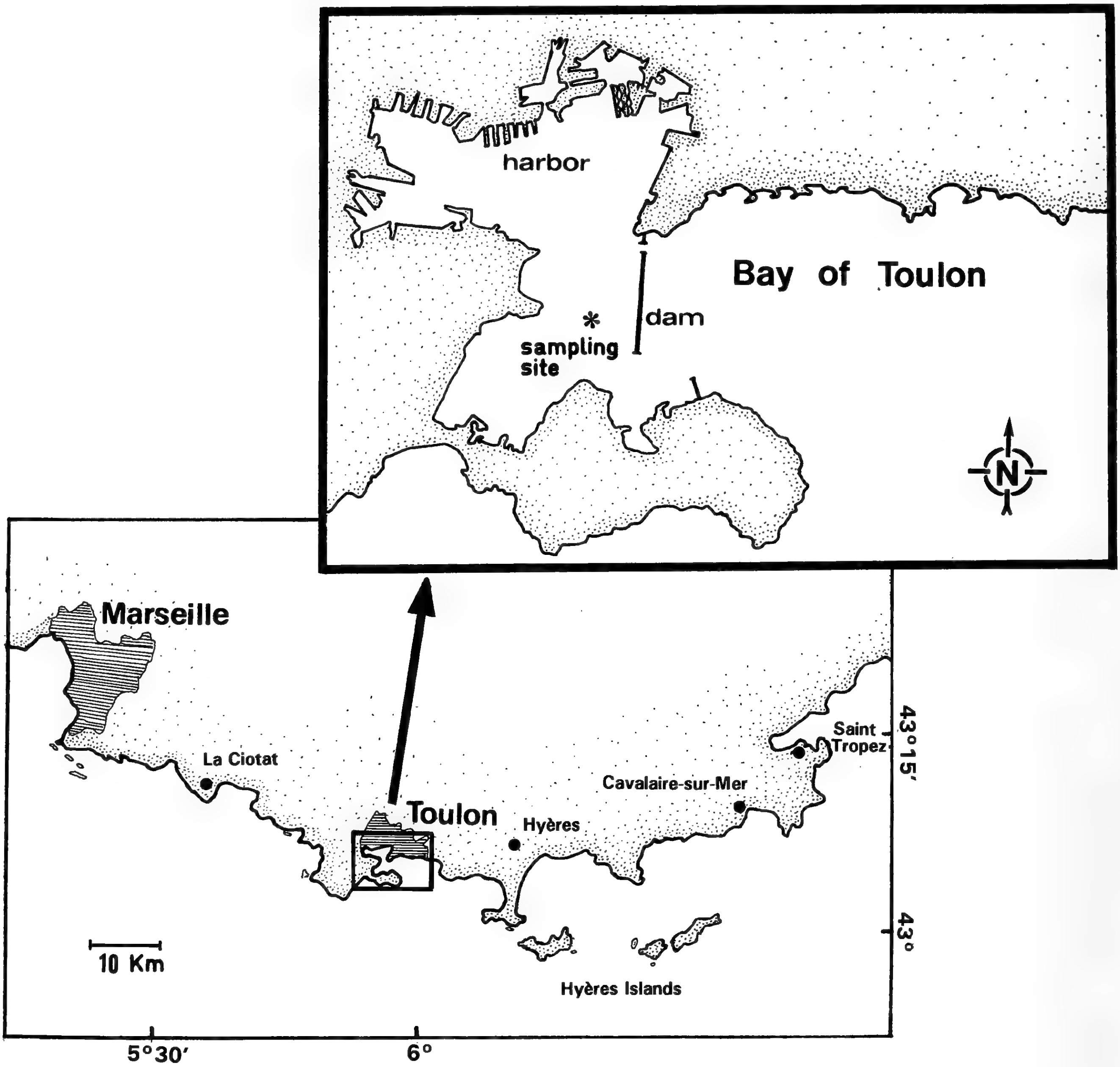

Fig. 1. Study area, showing the locality at which the present specimens were collected.

vealed the presence of three male specimens of *Cymbasoma tenue*, which is here reported for the first time in the Mediterranean, redescribed based on those specimens according to new description standards, and compared with the original description and with the holotype specimen.

Cymbasoma tenue (Isaac, 1975)

Material.—Holotype, adult male from Gulland Rock, Padstow Cornwall, England, deposited at the British Museum of Natural History (BMNH 1972.11.1.7). Three adult males from Toulon Bay, France, sent for deposit to the National Museum of Natural History, Smithsonian Institution, were lost in the mail. An additional male specimen was cataloged as USNM 278220.

New locality and habitat.—Toulon Bay (43°5′N, 6°0′E) is located on the French coast of the Mediterranean Sea (northwestern) (Fig. 1). The continental shelf of the area is narrow, with a mean slope of 2.4% (Poidenot 1993). Zooplankton was collected on 11 July 1995 by vertical hauls (0–22 m) with a standard conical plankton net (0.09 mm mesh size) and preserved in buffered 5% seawater formalin. The monstrilloid copepods were transferred to a 70% ethanol solution. The salinity varied between 33.7 and 33.9 PSU, while the mean water temperature was 22.8°C.

Description.—Male. Mean body length of three analyzed specimens 1.15 mm, measured in dorsal view from anterior end of cephalothorax to posterior edge of anal somite. Cephalothorax 0.54 mm long, representing almost 50% of total body length (Fig. 2A). Oral papilla located less than 30% of way back along ventral surface of cephalothorax (Fig. 2B). Cephalic region, abruptly broadening anterior to oral papilla, posterior part of cephalothorax gradually broadening to same width. Dorsal ocelli present, pigment cups small and widely separated, poorly developed, almost unpigmented, round in dorsal view. Cephalic region in dorsal view with one central cuticular protuberance on forehead between pigment cups (arrow in Fig. 2B) and paired small sensilla on lateral portions of same area. Two strongly chitinized, rounded cuticular processes located posterior to pigmented region of ocelli. Other cuticular features including two concavities and faint ridges on frontal region between oral papilla and antennular base (Fig. 2C).

Mean antennular length of four specimens 0.39 mm, close to 37% of total body length, and *ca.* 75% as long as cephalothorax. Four-segmented, each segment armed with 0-I; 1-V; 2-I; 8-VIII+aes setae (in Arabic numbers), spines (in Roman numbers), and aesthetascs (aes), respectively. Distal antennular segment incompletely fused with third segment, with three subequal, dichotomously branched setae aligned near outer distal end. Following basic setal nomenclature of Grygier & Ohtsuka (1995) for female monstrilloid copepod antennules, two aesthetascs (4aes, 6aes) and three setae (IVv, Vv, Vm) absent in the studied specimens. Length ratio of antennular segments: 20.8: 22.9: 33.3: 22.9 = 100 (Fig. 2D). First pedigerous thoracic somite incorporated into cephalothorax. This and succeeding three pedigers each bearing well developed swimming legs, all with 3-segmented rami and with same armament pattern, except for leg 1 exopod (Fig. 3A–D). Legs 2 and 3 slightly larger (*ca.* 7%) than 1 and 4; exopods longer than endopods in all cases. Coxae of each pair unarmed, joined by intercoxal sclerite slightly longer than wide. Basis separated from coxa posteriorly by diagonal articulation. Outer margin of basis of swimming legs 1, 2 and 4 with a small, thin seta; seta on leg 3 *ca.* 3 times larger and thicker than in the other legs, plumose. These setae were lost in two specimens. Outer distal corner of first and third exopodal segments of legs 1–4 each with short, spinelike seta, about one-ninth as long as segment. All natatory setae lightly and biserially plumose except for seta on outer distal corner of third exopodal segments of legs 1–4, this being plumose along inner side, but bearing row of small denticles along outer margin (Fig. 3A, C, D). Armament formula of swimming legs as:

	Basis	Exopod	Endopod
Leg 1	0-1	I-0; 0-1; I, 2, 2	0-1; 0-1; 1, 2, 2
Legs 2–4	0-1	I-0; 0-1; I, 2, 3	0-1; 0-1; 1, 2, 2

As usual in males, fifth leg absent. Pair of digitiform genital lappets present on genital somite, both appearing elongated, strongly divergent, distally flattened, and almost reaching half-way down last—anal—somite (Fig. 3F). Small, subtriangular protuberance present at medial base of each genital lappet (Fig. 3F).

Urosome consisting of four segments: fifth pedigerous somite (with no appendages), genital somite (with genital complex) and two free somites. From dorsal view, genital somite about as long as preanal urosomites, anterior half expanded ventrally. Anal somite being the longest and widest of the urosome. Ratio of lengths of genital somite and two free posterior somites being: 34.6: 23: 40 = 100 (Fig. 3E).

Furcal rami nearly quadrate, with terminal margin 45% wider than proximal. Approximately 1.2 times wider than long, with three well developed terminal setae of

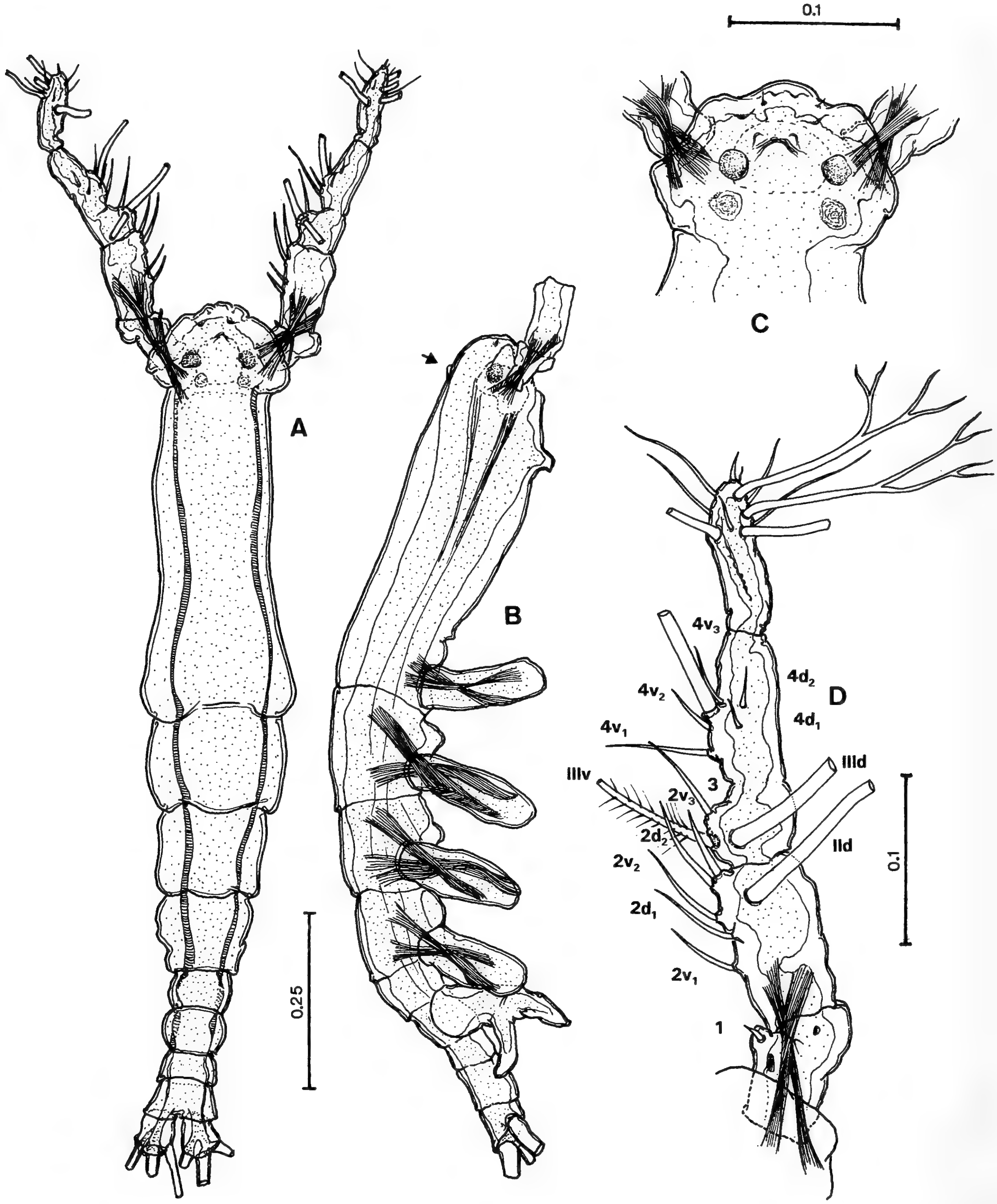

Fig. 2. *Cymbasoma tenue* adult male. A) habitus, dorsal; B) habitus, lateral. C) cephalic region, dorsal. D) right antennule, dorsal. Scales in mm.

which middle one slightly longer than other two, these being equal in length and thickness.

Female: unknown

Discussion.—Previous to this record of *C. tenue*, several other species of *Cymbasoma* have been reported from the Mediterranean (Isaac 1975, Razouls & Durand 1991): *C. claparedii* (Giesbrecht, 1892) (females only, male unknown), *C. longispi-*

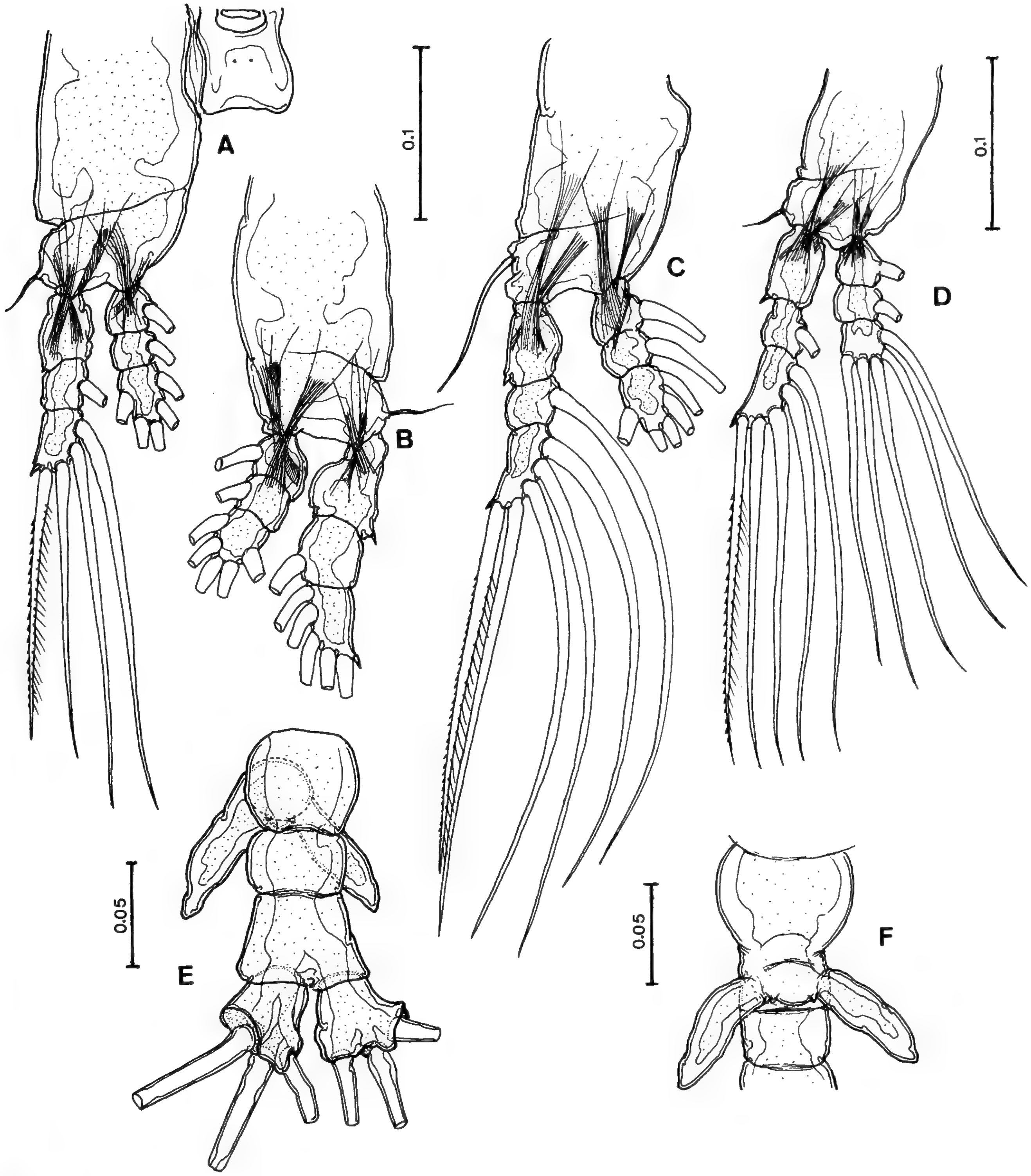

Fig. 3. *Cymbasoma tenue* adult male. A) first leg, posterior; B) second leg, anterior. C) third leg, posterior; D) fourth leg, posterior; E) urosome and furcal rami, dorsal; F) genital complex, genital lappets, ventral. Scales in mm.

nosum (Bourne, 1890), *C. rigidum* Thompson, 1888a, and *C. reticulatum* (Giesbrecht, 1892) (females only, male unknown), *C. thompsoni* (Giesbrecht, 1892), and *C. tumorifrons* (Isaac, 1975). *Cymbasoma herdmani* Thompson 1888b, recorded from off Malta, is considered a synonym of *Monstrilla anglica* Lubbock, while *C. claparedii*, recorded from Naples, is probably a synonym of *C. rigidum* (see Sars 1921). There are some additional undetermined local records of monstrilloids in the Mediterranean, such as a *Thaumaleus* sp from off Capri, reported by LoBianco (1903), or monstrilloids caught from Livorno, Rapallo and San Remo on the Italian coast (Basso et al. 1980). The most recent records of *Cymbasoma* species in Mediterranean waters are those of Lakkis (1984), who found *C. longispinosum* and *C. rigidum* in the Levantine Basin, and Citarella (1986), who found *C. longispinosum* off Marseilles, France.

By direct comparison with the holotype, the male specimens from the Mediterranean easily matched *Cymbasoma tenue* in the general aspect of the body, the general structure of the genital lappets—with a low protuberance between them—and the armature of the antennules (Isaac 1974, 1975). The female of this species remains unknown. This species is morphologically similar to *C. pallidum* (Isaac 1974); males of the two species differ mainly in their size, body proportions and in the structure of the genital lappets, which are very much longer and more slender in *C. pallidum* (Isaac 1975).

The Mediterranean specimens show precise similarities but also some differences with respect to the holotype and the original descriptions and illustrations of *C. tenue*. It is noteworthy to mention that the cephalothorax of the holotype specimen is distorted, some antennular setae are missing, and one rami of the fourth leg is incomplete. The body length is equal in both cases (around 1.1 mm; one of our specimens is slightly larger: 1.24 mm). In both cases the cephalothorax is almost 50% of total body length, the oral papilla is located less than 30% of way back along the ventral surface of the cephalothorax, the antennules are 75% as long as the cephalothorax, and the length ratio of the antennular segments is similar. As in the type material, the Mediterranean specimens bear four-segmented antennules; close to midlength of the third segment there is a constriction which may be the result of an incomplete segmental separation. In monstrilloid copepods the degree of fusion of the antennular segments exhibits a wide range of variation, from a sharp separation (as in the males of *C. longispinosum*, *C. quadridens* or *C. zetlandicum* (T. Scott, 1904)) to an almost complete fusion of the segments (as in *Monstrilla elongata* Suárez-Morales, 1994). The shape of the head is identical in both cases; the cuticular features of the cephalic region could not be compared since they were not originally illustrated.

We found differences between the antennules of the studied specimens and those from the original description. Isaac (1974) reported no bifurcating antennular setae. However, these branched setae are present in the holotype, and are clearly present in our specimens (three along the outer margin of the terminal segment in both cases). Branched and unbranched setae have been observed in the same population of male *Monstrilla reidae* Suárez-Morales, 1992 (pers. obs.), and has been used as a specific diagnostic feature by Grygier & Ohtsuka (1995) for female *Monstrilla*. However, this is not the case of *C. tenue*.

Considering that the setation pattern proposed by Grygier & Ohtsuka (1995) has been designed for female antennules, only the proximal armament will be compared in our male specimens since there are sexual differences in the monstrilloid antennular setation pattern. In the original description (Isaac 1974), the spine on the inner side of the first antennular segment (1) was not illustrated or mentioned. However, a long, slender seta is present in the holotype specimen, it is 2.5 times longer than the spine-like structure described for the Mediterranean material. Setae $2v_1$–$2v_3$ and $2d_1$ and $2d_2$ are present in the holotype specimen and in our material. Seta IId, not illustrated by Isaac (1974), is present only on the left antennule in the holotype. Setae $4d_1$ and $4d_2$ are 50% longer in the holotype than in our specimens, almost reaching the distal margin of the same segment. The single terminal spine on the last antennular segment is twice longer in the holotype than in the Mediterranean specimens. On the other hand, none of the setae or aesthetascs missing in our specimens according to Grygier and Ohtsuka's (1995) pattern, were illustrated in the original description, which supports the idea that the present analysis completes the antennular armature set of the male of this species.

The urosomal somites were illustrated by Isaac (1974); the anal somite appears very thin and long, with approximate relative lengths of these somites being (from the figure): 24: 17: 57 = 100. However, proportions of the holotype specimens and those of the Mediterranean differ from Isaac's illustrations (holotype, 35: 23: 45 = 100; our specimens, 34.6: 23: 40 = 100).

Isaac (1974) illustrated only the fourth swimming leg. All the swimming legs of *C. tenue* are here described and illustrated for the first time. The genital lappets in both cases are identical in most respects; however, the Mediterranean specimens show a low, subtriangular protuberance in the base of each genital lappet, a structure which was not previously described for the species. Differences at this level (genital complex) are taxonomically relevant (McAlice 1985). This is a relevant new structure to be considered useful for the diagnosis and recognition of this species since several species of the genus *Cymbasoma* share this type of male genital lappets (*C. pallidum*, *C. tumorifrons* Isaac, *C. similirostratum* Isaac, and *C. quadridens*.

Key for the Mediterranean species of *Cymbasoma* (males)

1A. With constriction on anal somite, genital lappets with serrated posterior margins .... *C. rigidum*
1B. Without constriction on anal somite, genital lappets not serrated 2
2A. Genital lappets extended more than ⅓ of anal somite 3
2B. Genital lappets short, barely reaching anterior margin of preanal somite .... *C. longispinosum*
3A. Genital lappets long, tapering distally and ending in sharp tips .. *C. tumorifrons*
3B. Genital lappets distally rounded 4
4A. With subtriangular protuberances on basal portion of each lappet. Cephalic portion wider than body ...... *C. tenuis*
4B. Without such protuberances. Cephalic portion not wider than body .... *C. thompsoni*

Acknowledgments

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Literature Cited

Basso, M. P., M. G. Cevasco, N. della Croce, & P. Picone. 1980. Caratteristiche ecologiche e popolamento zoplanctonico in ambienti portuali del Mar Ligure e Alto Tirreno. Universitá de Genova, Cattedra di Idrobiologia e Pescicoltura.—Facolta di Scienze Fisiche, Matematiche e Naturali. Rapporto Tecnico 12: 2 p.

Bourne, G. C. 1890. Notes on the genus *Monstrilla*, Dana.—Quarterly Journal of Microscopical Science 30:565–578.

Citarella, G. 1986. Les Copépodes des eaux portuaires de Marseille (Méditerranée nord-occidentale).—Syllogeus 58:276–282.

Davis, C. C. 1949. A preliminary revision of the Monstrilloida, with descriptions of two new species. Transactions of the American Microscopical Society 68:245–255.

Giesbrecht, W. 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna und Flora des Golfes von Neapel 19:1–831.

Grygier, M. J. 1994a [dated 1993]. Identity of *Thaumatoessa* (=*Thaumaleus*) *typica* Krøyer, the first described monstrilloid copepod.—Sarsia 78:235–242.

———. 1994b. Nomenclature, redescription, and new record from Okinawa of *Cymbasoma morii* Sekiguchi, 1982 (Monstrilloida).—Hydrobiologia 292/293:23–29.

———, & S. Ohtsuka. 1995. SEM observation of the nauplius of *Monstrilla hamatapex*, new species, from Japan and an example of upgraded descriptive standards for monstrilloid copepods.—Journal of Crustacean Biology 15:703–719.

Hartman, O. 1961. A new monstrilloid parasitic in capitellid polychaetes in southern California.—Zoologischer Anzeiger 167:325–334.

Huys, R., & G. A. Boxshall., 1991. Copepod evolution. The Ray Society, London, United Kingdom, 468 pp.

Isaac, M. J. 1974. Copepoda Monstrilloida from south-west Britain including six new species.—Journal of the Marine Biological Association of the United Kingdom 54:127–140.

———. 1975. Copepoda, sub-order: Monstrilloida.—Fiches Identification du Zooplancton 144/145: 10 pp.

Krøyer, H. 1849. Karcinologiske Bidrag (Fortsættelse).—Naturhistorisk Tidsskrift. Nyt Hæfte 2:561–609, pl. VI.

Lakkis, S. 1984. On the presence of some rare copepods in the Levantine Basin.—Crustaceana Supplement 7:288–304.

LoBianco, S. 1903. Le pesche aissali eseguite da F.A. Krupp col yacht Puritan nelle adiacensze di Capri ed in altre località del Mediterraneo.—Mittleilungen aus der Zoologischen Station zu Neapel 16(1–2):109–128.

Martin Thompson, P. K. 1976 [dated 1973]. Occurrence of *Cymbasoma longispinosum* (Copepoda: Monstrilloida) from the Indian seas.—Journal of the Marine Biological Association of India 15:616–620.

McAlice, B. J. 1985. On the male of *Monstrilla helgolandica* Claus (Copepoda, Monstrilloida).—Journal of Crustacean Biology 5:627–634.

Poidenot, F. 1993. Le Canyon de Toulon: morphologie et sédimentation (Méditerranée Nord-Occidentale). Thése Doct. Océanologie. University of Aix-Marseille II, 182 pp.

Razouls, C., & J. Durand. 1991. Inventaire des Copépodes planctoniques méditerranéens.—Vie Milieu 41(1):73–77.

Sars, G. O. 1921. An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. VIII. Copepoda Monstrilloida & Notodelphioida. The Bergen Museum, Bergen, 91 pp.

Suárez-Morales, E. 1993. *Monstrilla reidae*, a new species of monstrilloid copepod from the Caribbean Sea off Mexico.—Bulletin of Marine Science 52:717–720.

Thompson, I. C. 1888a. Copepoda of Madeira and the Canary Islands, with descriptions of new genera and species.—Journal of the Linnean Society London, Zoology 20:145–156, pls. X–XIII.

———. 1988b. Second report on the Copepoda of Liverpool Bay.—Proceedings of the Liverpool Biological Society 2:63–71.

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Amboleberis cubensis, a new species of myodocopine ostracode from the vicinity of Cuba (Crustacea: Ostracoda: Cylindroleberididae)

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Abstract.—A new species of myodocopine ostracode, *Amboleberis cubensis,* in the Family Cylindroleberididae collected near Los Dromedarios Key, off the north coast of Cuba, is described and illustrated.

The new species described herein was collected near Los Dromedarios Key, which is off the north coast of Cuba, during a benthic survey of non-decapod crustaceans conducted by the First Joint Cuba-USA Expedition, 1994, in which the National Museum of Natural History, USA, the Centro de Investigaciones Marinas, Universidad de la Habana, Cuba, and the Institute of Oceanology of the Ministry of Environmental Technology and Science, Cuba, participated.

For definition of lettering system for appendage bristles see Skogsberg (1920:188) and Kornicker (1985:2). Letters used in identifying sclerites in the protopodite of the 2nd antenna are explained in Kornicker (1994:189).

The following abbreviations are used in illustrations and legends: am., central adductor muscle attachments; epip., epipodial bristle; fu., furca; gird., girdle; im., inner margin of infold; iv., inside view; lv., lateral view; mls., medial longitudinal sclerite of protopodite of 2nd antenna; mv., medial view; ov., outside view; pr., posterodorsal process; Y-scl., Y-sclerite. Arrows on illustrations indicate anterior.

Suborder Myodocopina Sars, 1865
Cylindroleberididae Müller, 1906

This family contains three subfamilies: Cylindroleberidinae Müller, 1906; Cyclasteropinae Poulsen, 1965; and Asteropteroninae Kornicker, 1981. Two species in the Asteropteroninae have previously been described from Cuba (Kornicker 1981). A new species of the Cyclasteropinae from the vicinity of Cuba is described herein. Members of the Cylindroleberidinae are no doubt present in Cuban waters although, so far as we know, they have yet to be reported in the literature.

Cyclasteropinae Poulsen, 1965

This subfamily contains three tribes: Cyclasteropini Poulsen, 1965, Cycloleberidini Hartmann, 1974, and Tetraleberidini Kornicker, 1981. Only the Tetraleberidini are known from Cuba.

Tetraleberidini Kornicker, 1981

This tribe contains two genera: *Tetraleberis* Kornicker, 1981, and *Amboleberis* Kornicker, 1981. *Tetraleberis* is unknown in the western Atlantic whereas *Amboleberis* is common (Kornicker 1981:166).

Amboleberis Kornicker, 1981

Amboleberis Kornicker, 1981:166.

Type species.—*Asterope americana* Müller, 1890.

Including the new species described herein from Cuba, *Amboleberis,* contains

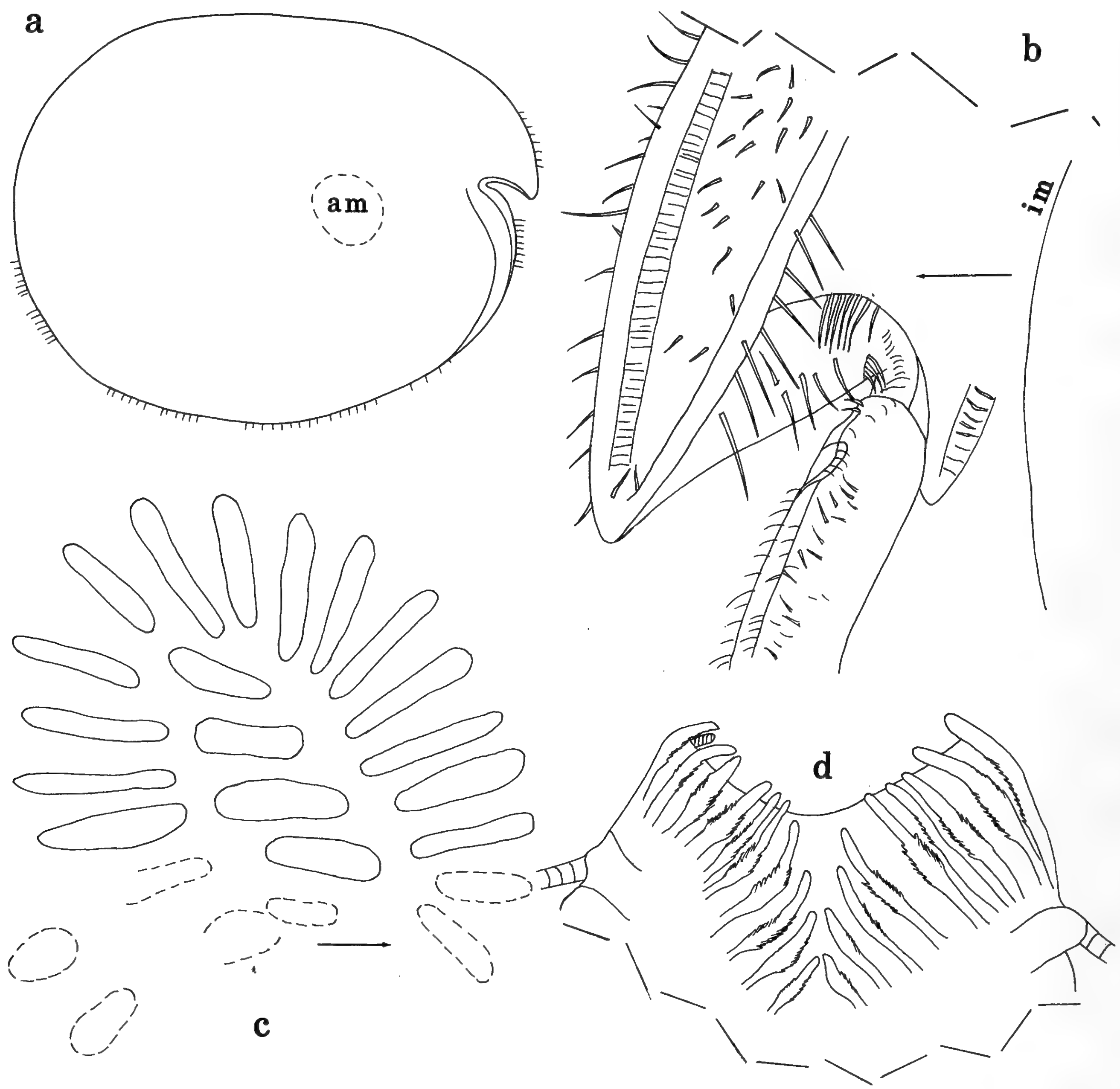

Fig. 1. *A. cubensis* holotype, adult female: a, Outline of complete specimen from right side, length 1.56 mm; b, Anterior of right valve, iv; c, Detail of central adductor muscle attachments of right valve, ov; d, Terminus of 7th limb.

three species: *A. americana* (Müller, 1890), *A. antyx* Kornicker, 1981, and *A. cubensis,* new species. *Amboleberis americana* has been collected in the Gulf of Mexico, and in the Atlantic and Pacific Oceans in the vicinity of North, Central, and South America (Kornicker, 1986:111); and *A. antyx* has been collected in the vicinity of Madagascar, Indian Ocean (Kornicker 1981:181). Known depth range for the genus is from 0.6 to 97.5 m in benthos, and rarely in plankton (Kornicker 1986:111).

Material.—In addition to the holotype of the new species, two specimens of *A. americana* were examined for comparative purposes: USNM 157148, ovigerous female from Panama (Pacific side), and USNM 157587, from Anclote anchorage, Florida.

Amboleberis cubensis, new species
Figs. 1–6a

Etymology.—The species is named for the collecting site.

Holotype.—Dissected adult female on

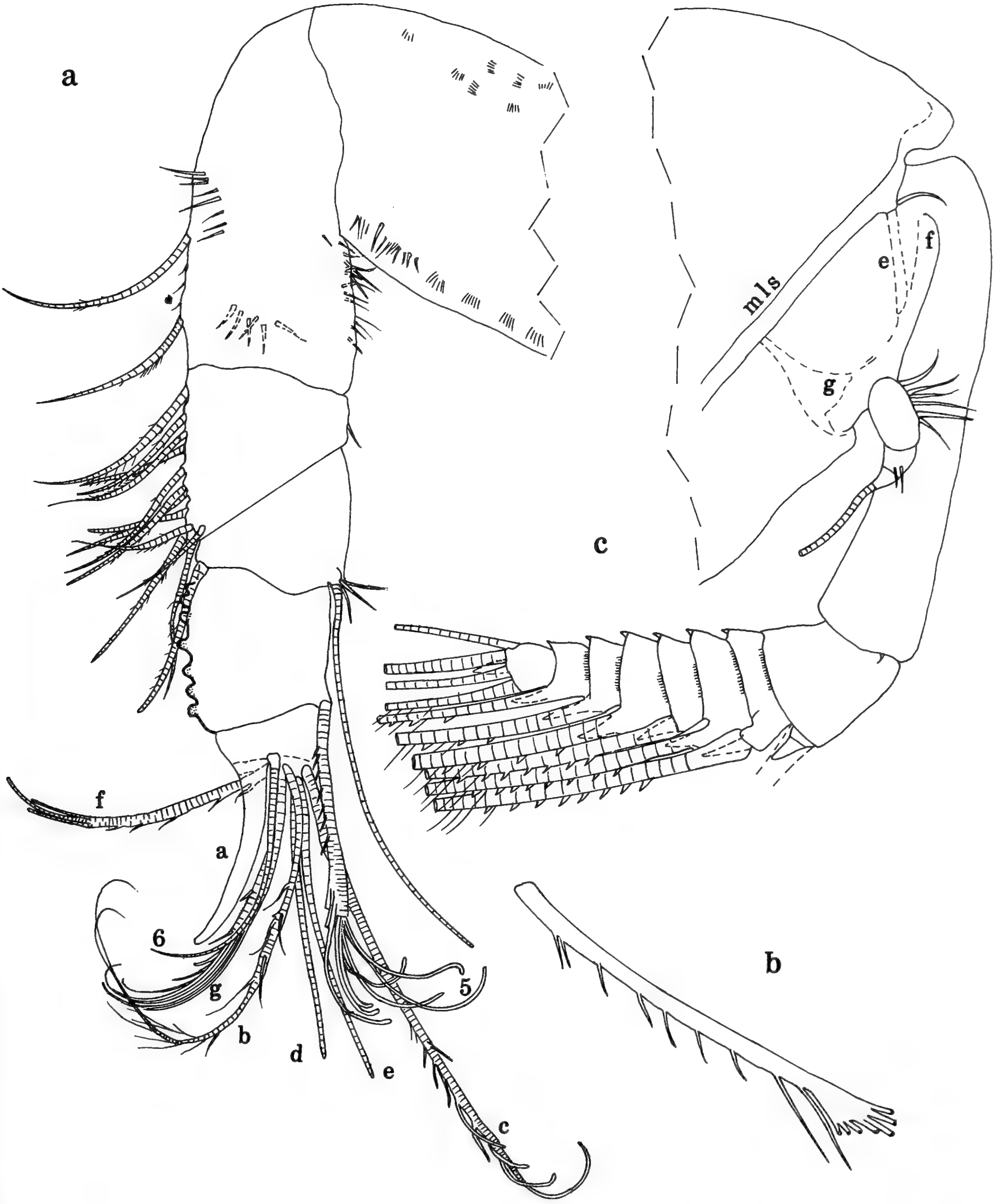

Fig. 2. *A. cubensis* holotype, adult female: a, Right 1st antenna, mv; b, Detail of sensory bristle shown in "a" (only proximal part of 7 terminal filaments shown); c, Left 2nd antenna, mv.

slide and in alcohol deposited in the invertebrate collection of the Centro de Investigaciones Marinas, Universidad de la Habana, Cuba. Unique specimen.

Type locality.—Cayo los Dromedarios (Los Dromedarios Key), leeward side of key, near La Isabela, Archipelago Sabana-Camagüey, off north coast of Cuba.

Collection data.—Unique specimen collected 11 April 1994 in net swept through

Fig. 3. *A. cubensis* holotype, adult female: a, Left mandible (coxale endite broken off), mv; b, Left lamella of furca, lv; c, Part of Bellonci organ.

Thalassia bed; *Halimeda* and sponges present in area. Water depth 0.6–1.2 m.

Description of adult female.—Carapace oval in lateral view, with deep incisur near midheight of anterior margin (Fig. 1a). Curved vertical ridge present with dorsal end just posterior to inner end of incisur and ventral end intercepting ventral margin (generic character). Lateral surface with few long bristles and many pores.

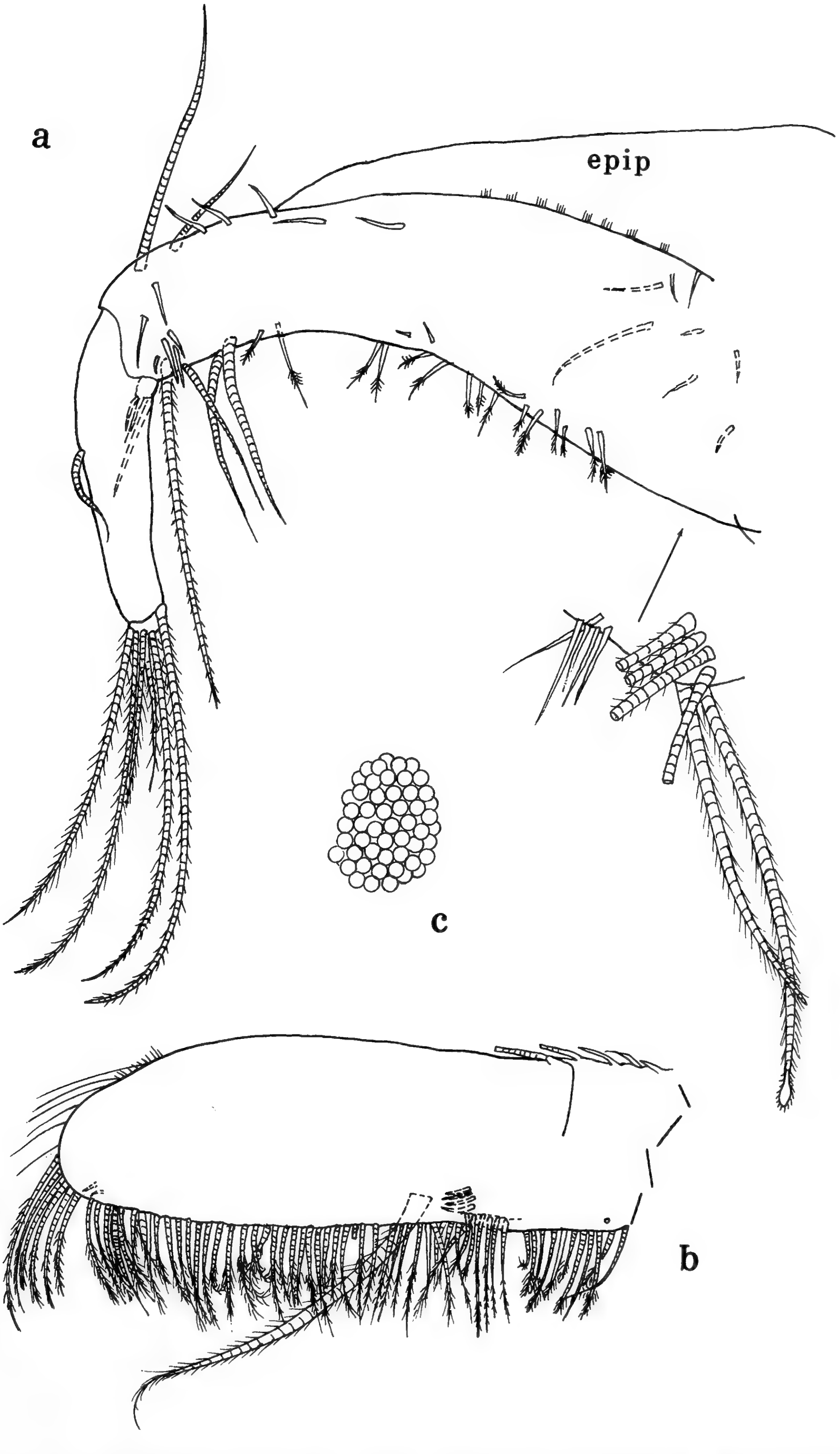

Fig. 4. *A. cubensis* holotype, adult female: a, Right maxilla (dashed proximal bristles of basale indistinct and approximate), with detail of endites, mv; b, Comb of right 5th limb, mv; c, Left lateral eye.

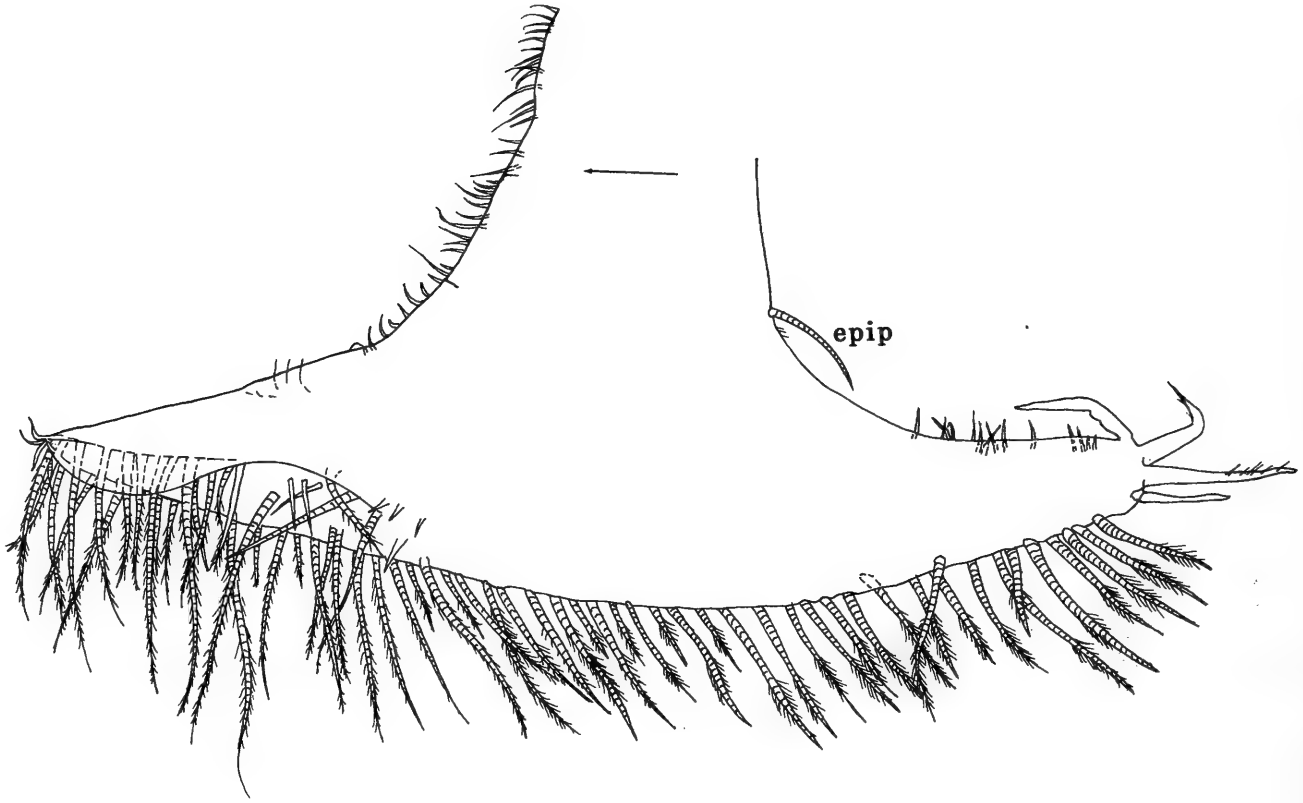

Fig. 5. *A. cubensis* holotype, adult female: left 6th limb, lv.

Infold: Typical for genus (Fig. 1b).

Central adductor muscle attachments (Fig. 1a, c): Comprising about 25 elongate attachments.

Carapace size: Holotype, length 3.2 mm, height 2.5 mm; height 78.1% of length.

First antenna (Fig. 2a, b): 1st joint with groups of very short spines near dorsal margin and groups of longer spines near ventral margin. 2nd joint: ventral and dorsal margins spinous; dorsal margin with 2 long distal bristles; lateral surface with 6 short distal bristles (these are dashed in Fig. 2a). 3rd joint with 12 long dorsal bristles and 1 short ventral bristle. 4th joint with 4 ventral bristles (3 short, 1 long (about 3× length of 5th joint)) and 1 long terminal dorsal bristle. 5th joint; dorsal margin with 7 or 8 nodes; ventral sensory bristle with 7 short proximal filaments separated by short space from 2 filaments about 3× length of proximal filaments and then 7 long terminal filaments (Fig. 2a, b). 6th joint with long terminal medial bristle. 7th joint: a-claw bare, longer than 5th joint: b-/and c-bristles each with 9 marginal filaments (distal 2 longer than others). 8th joint: d-/and e-bristles about ⅔ length of c-bristle, both bare with blunt tips; f-bristle bent dorsally, tip missing on holotype, with 9 filaments on remaining part; g-bristle about same length as c-bristle, with about 9 filaments.

Second antenna (Fig. 2c): Protopodite with short distal medial bristle. Endopodite 3-jointed: 1st joint with 6 short bristles; 2nd joint shorter than 1st, with 2 distal bristles; 3rd joint short with long terminal filament. Exopodite: 1st joint with minute medial terminal bristle; bristles of joints 3–8 with natatory hairs and stout ventral spines; joints 2–8 with stout basal spines; 9th joint with stout lateral spine and 4–5 terminal bristles (2 with stout ventral spines).

Mandible (Fig. 3a): Coxale endite lost. Basale: endite with about 11 long bristles (triaenid and end types) and 5 ventral dwarf bristles; ventral margin with 8 or 9 triaenid bristles (ventral margin folded over in Fig. 3a); dorsal margin with about 16 short bristles and 2 long terminal bristles. Exopodite reaching just past distal end of dorsal margin of 1st endopodial joint, with 2 subter-

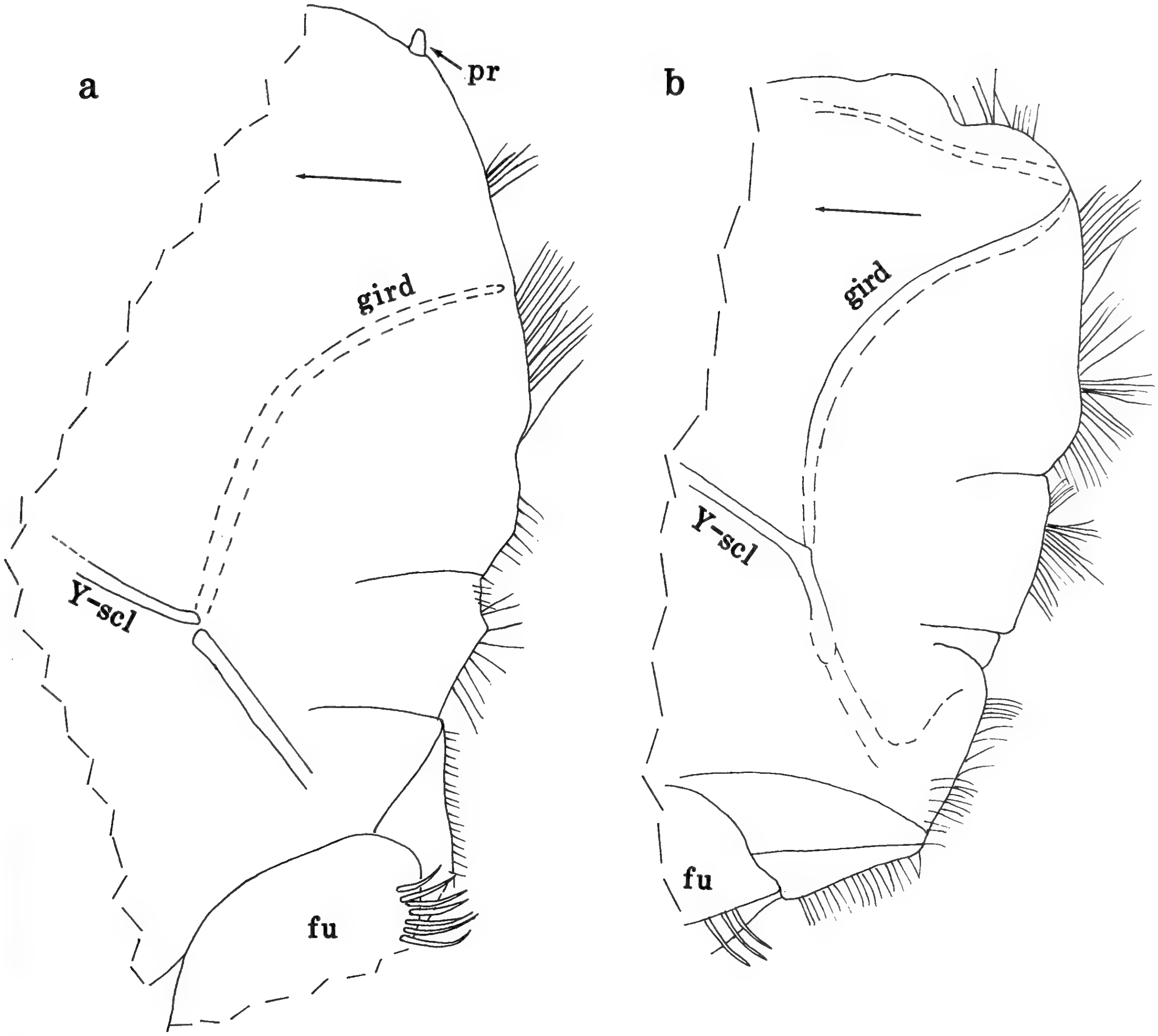

Fig. 6. a, *A. cubensis* holotype, adult female, posterior of body from left side (note small thumb-like process (pr)). b, *A. americana* (Müller), USNM 157148, adult female from Pacific, posterior of body from left side.

minal bristles and hirsute tip. 1st endopodial joint with 6 ventral bristles. 2nd endopodial joint: ventral margin with 2 subterminal and 2 terminal bristles; dorsal margin and medial surface near dorsal margin with numerous long and short bristles. 3rd endopodial joint broken off.

Maxilla (Fig. 4a): Epipodite triangular. Endites I and II fused, with 11 bristles (6 long, 5 shorter). Basale: medial surface with 7 proximal bristles and 6 distal bristles; lateral side with short proximal bristle; dorsal margin with proximal spines and about 9 distal bristles (2 long, remainder short); ventral margin with 18 short bristles followed by 3 longer bristles and a very long terminal bristle. Exopodite small with 3 bristles (2 short, 1 long). Endopodite ½ length of basale: 1st joint with short anterior alpha-bristle and long beta-bristle; 2nd joint with 5 terminal bristles (2 short, 3 long).

Fifth limb (Fig. 4b): Dorsal margin of comb with 5 small proximal bristles; anterior edge of comb smoothly rounded and hirsute; exopodial bristles consisting of long stout spinous bristle, 4 minute bristles ventral to base of stout bristle, and 6 small bristles (with several long hairs near tip) close to ventral edge of comb near midlength.

Sixth limb (Fig. 5): With 1 epipodial

bristle; anterior margin with 2 distinct sutures; anterior edge of stem and ventral margin of skirt with numerous bristles; posterior end of skirt with 4 plumose bristles (all hairs not shown); posterior extension of skirt with numerous spines; tip of lateral flap with 2 bristles.

Seventh limb (Fig. 1d): Each limb with about 64 bristles, about same number on each side; each bristle with 5–7 bells; terminus with opposing combs, each with 18–20 teeth.

Furca (Fig. 3b): Each lamella with 3 stout claws followed by 1 slender bristle, a fourth stout claw, and then 7 slender bristles; ventral margin of lamellae with many small spines.

Bellonci organ (Fig. 3c): Typical for genus, with striae near midlength and narrow tip.

Posterior of body (Fig. 6a): Hirsute, with small thumb-like posterodorsal process.

Number of eggs: Holotype with 57 eggs in marsupium. Length of typical egg 0.32 mm.

Comparisons.—The new species *A. cubensis* differs from *A. americana* (Müller, 1890) in having a thumb-like node on the posterodorsal corner of the body (compare Fig. 6a and 6b). The dorsal margin of the 5th joint of the 1st antenna of the unique female *A. cubensis* bears 7–8 nodes compared to 4–6 for *A. americana,* but variability of former is not known. The dorsal margin of the mandibular basale of *A. cubensis* bears about 16 short bristles compared to 7 or 8 for *A. americana.* The 1st antenna of *A. cubensis* differs from that of *A. antyx* Kornicker, 1981, in having nodes along the dorsal margin of the 5th joint, and in not having teeth on the a-bristle of the 7th joint.

Acknowledgments

The senior author wishes to thank Elizabeth Harrison-Nelson (Smithsonian Institution) for general assistance during a stay at the U.S. National Museum of Natural History. The unique specimen described herein was collected with a net by Marilyn Schotte (Smithsonian Institution). We thank the personnel aboard the R/V *Ulises* for their participation. The illustrations were drawn by the senior author using a camera-lucida.

Literature Cited

Hartmann, G. 1974. Die Ostracoden des Untersuchungsgebiets, Part 3: Zur Kenntnis des Eulitorals der afrikanischen Westküste zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostküste von Südafrika und Moçambique unter besonderer Berücksichtigung der Polychaeten und Ostracoden.—Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 69:229–520.

Kornicker, L. S. 1958. Ecology and taxonomy of Recent marine ostracodes in the Bimini area, Great Bahama Bank.—Publications of the Institute of Marine Science (The University of Texas) 5: 194–300.

———. 1981. Revision, distribution, ecology, and ontogeny of the ostracode subfamily Cyclasteropinae (Myodocopina: Cylindroleberididae).—Smithsonian Contributions to Zoology 319:1–548.

———. 1985. Sexual dimorphism, ontogeny, and functional morphology of *Rutiderma hartmanni* Poulsen, 1965 (Crustacea: Ostracoda).—Smithsonian Contributions to Zoology 408:1–28.

———. 1986. Cylindroleberididae of the western North Atlantic and northern Gulf of Mexico, and zoogeography of the Myodocopina (Ostracoda).—Smithsonian Contributions to Zoology 425:1–139.

———. 1994. Ostracoda (Myodocopina) of the SE Australian Continental Slope, part 1.—Smithsonian Contributions to Zoology 553:1–200.

Müller, G. W. 1890. Neue Cypridiniden.—Zoologische Jahrbücher 5:211–252.

———. 1906. Die Ostracoden der Siboga-Expedition. Leiden: E.J. Brill, 40 pp.

Poulsen, E. M. 1965. Ostracoda-Myodocopa, 2: Cypridiformes—Rutidermatidae, Sarsiellidae, and Asteropidae.—Dana Report 65:1–484.

Sars, G. O. 1865. Oversigt af Norges marine Ostracodes.—Fordhandlinger i Videnskabs-Selskabet I Christiania 7:1–130. [Preprint: Serial published 1866.]

Skogsberg, T. 1920. Studies on marine ostracods, I: Cypridinids, Halocyprids, and polycopids.—Zoologiska Bidrag fran Uppsala, (supplement) 1:1–784.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(1):115–127. 1997.

Macrothrix smirnovi, a new species (Crustacea: Anomopoda: Macrothricidae) from Mexico, a member of the *M. triserialis*-group

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Abstract.—*Macrothrix smirnovi*, new species, is described from a small reservoir located at a transitional zone between neartic and neotropic regions in Mexico. It resembles taxa related to *M. triserialis*, mainly the South-American *M. superaculeata*, but parthenogenic females are characterized by differences in spinulation of the antennae. Trunk limb II has a unique lobe carrying a stout conical seta densely ciliated at its distal portion located at the external surface of the endopod, near to the insertion of scrapers 4 and 5. The postabdomen is also distinct. The ephippium has a structure similar to *M. rosea*. Adult males have a postabdomen fairly similar to females and a copulatory hook with one crescentic ridge at the tip of an irregular margin which gives a spoon-like appearance to this portion.

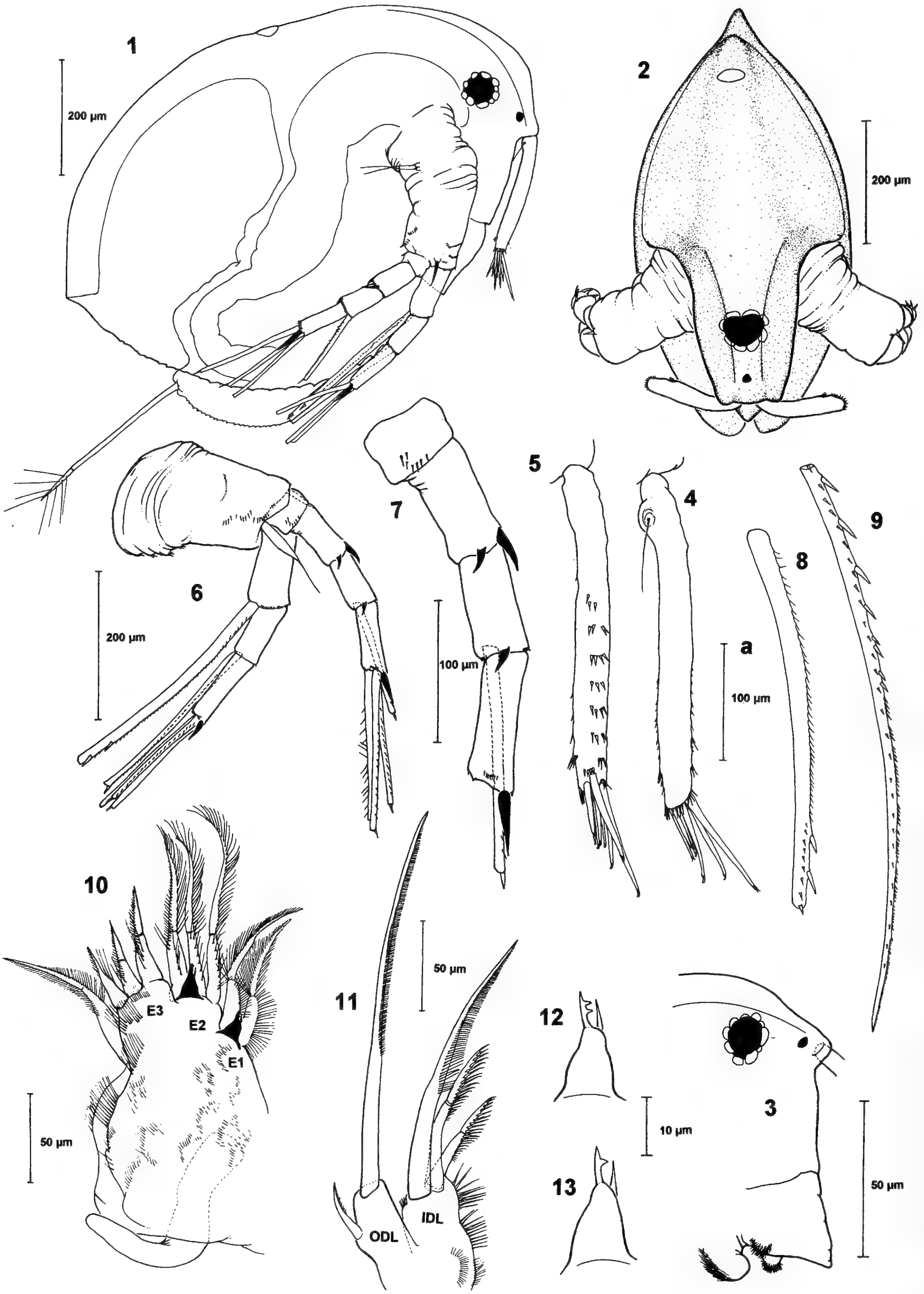
Recently, new concepts about diversity in tropical freshwater zooplankton indicate that at minimum the same number of species of cladocerans (ca. 50 per lake) are found in tropical as in temperate systems (Dumont 1994). In addition, the statements of Frey (1982a, 1988a) about non-cosmopolitanism in cladoceran species were confirmed (Frey 1988b), mainly on chydorids. On the other hand, if temperate regions were the most surveyed for their freshwater fauna while tropical zones generally were ignored until the last decade, many new species will remain to be described from tropical zones. Dumont (1994), based on data published by different authors, estimates a future increase at about 25% in the number of known cladoceran taxa. Most new descriptions will be from the tropics. This paper mainly deals with a new macrothricid cladoceran from central Mexico which is located at a transitional zone between neartic and neotropic regions.

Samples were collected from the littoral zone of water bodies, with a 50 μm-mesh plankton net and were fixed with sugar-formaldehyde (Haney & Hall 1973). The paratype material of *M. superaculeata* (Smirnov) (deposited at the Instituto Nacional de Pesquisas de Amazonia, Brazil INPA-CR 3035) and mature parthenogenetic females of *M. triserialis* s.l. from Malaysia, Nepal, Nigeria, Nicaragua and Mexico, *M. paulensis* (Sars) from Brazil, *M. rosea* (Jurine) from Russia, *M. capensis* (Sars) from South Africa and Australia and *M. odiosa* (Gurney) from Malaysia also were studied.

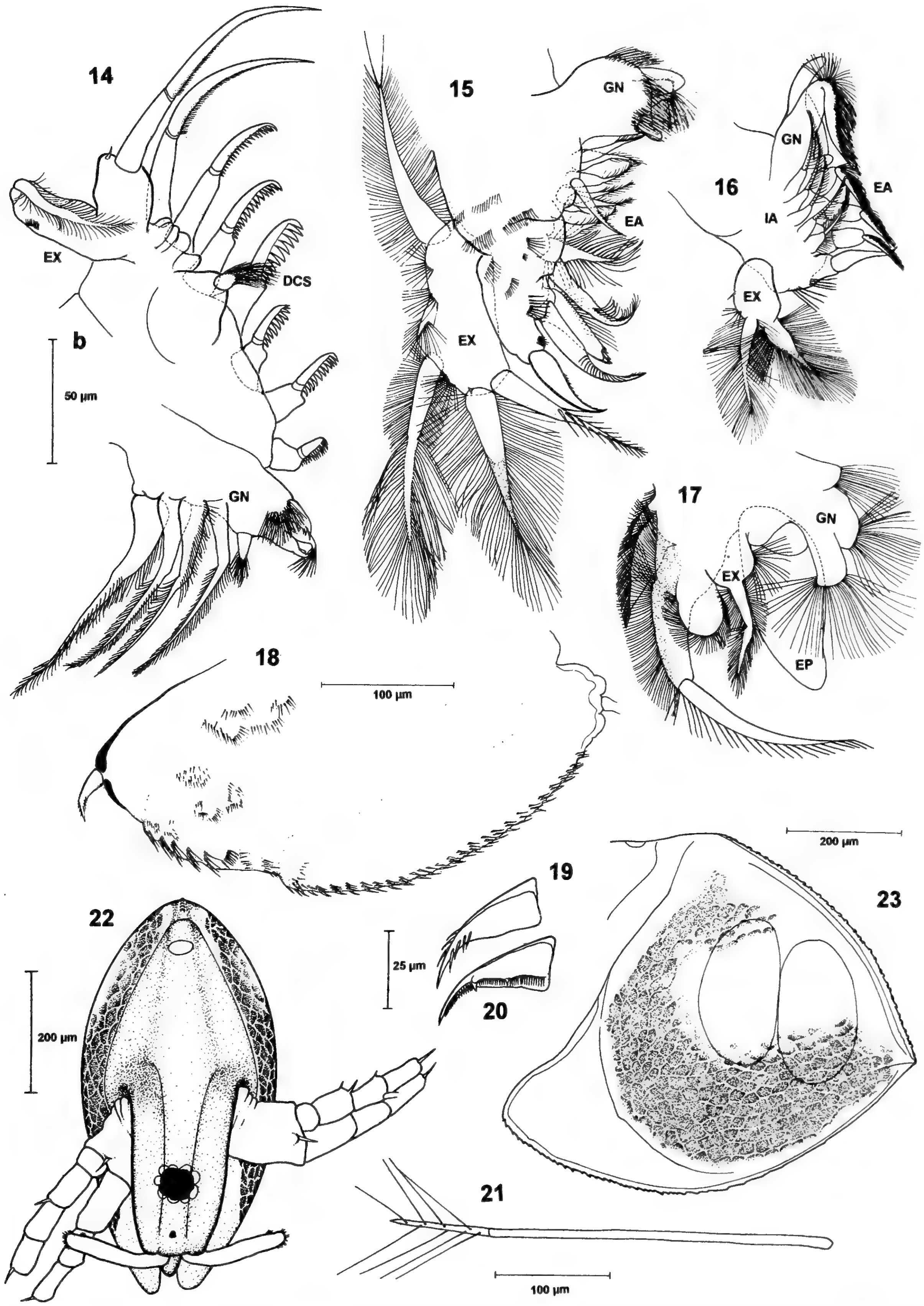
All measurements were made according to Smirnov (1971). Structures were dissected with tungsten needles and mounted in a mixture of glycerin-formaldehyde for the fine analysis. Drawings were made with a camera lucida attached to a microscope Nikon Labophot-2.

Macrothrix smirnovi, new species
Figs. 1–35

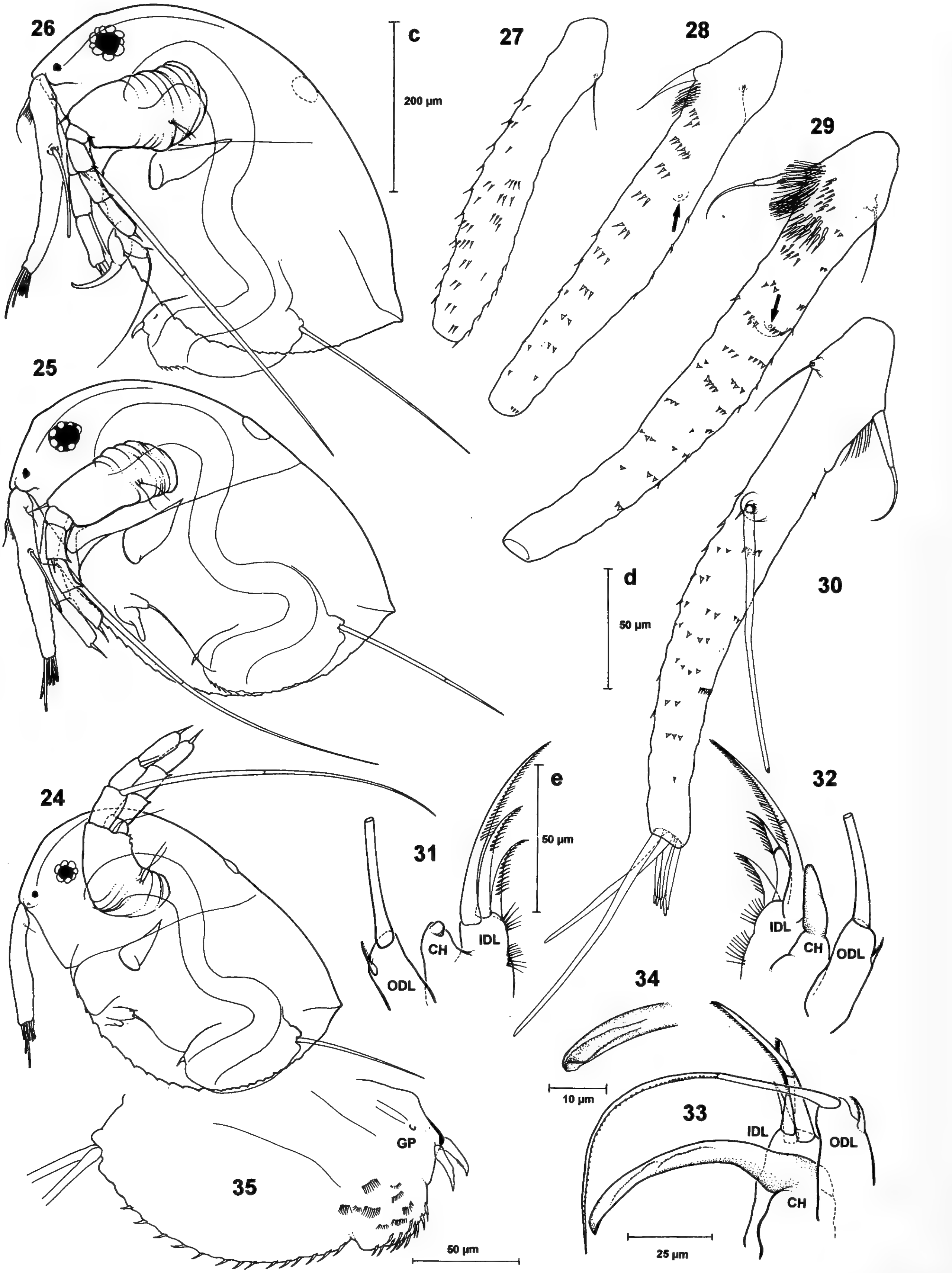
Material.—Holotype: One adult ovigerous female (total length 0.8 mm, height 0.5 mm), The Natural History Museum (BMNH), London, England, 1995.1290, 16 Aug 1995. Allotype: One adult male (total



Figs. 1–13. *Macrothrix smirnovi*, new species from kilometer 28 on the highway Jilotepec-Ixtlahuaca, State of Mexico, Mexico. Parthenogenetic female. 1, lateral view (distal segments of antennal setae are omitted); 2, frontal view of mature female; 3, ventral margin of the head and labrum; 4, AI lateral side; 5, AI medial side; 6, AII medial view (distal segments of setae are omitted); 7, antennal exopod, showing the spine armature; 8, proximal segment of seta on first endopod of AII; 9, distal segment of seta on first endopod of AII; 10, left trunk limb I, medial (ODL and IDL are omitted); 11, ODL (outer distal lobe or exopod) and IDL (inner distal lobe or endite 4) of trunk limb I; 12, inner spine of endite 1 on trunk limb I; 13, inner spine of endite 2 on trunk limb I. Scale bar "a" is for Figs. 4, 5, 8 and 9. Abreviations: E1, endite 1; E2, endite 2; E3, endite 3.



Figs. 14–23. *Macrothrix smirnovi*, new species from kilometer 28 on the highway Jilotepec-Ixtlahuaca, State of Mexico, Mexico. All are parthenogenetic female except Figs. 22 and 23 which are ephippial females. 14, left trunk limb II, lateral; 15, right trunk limb III, medial; 16, right trunk limb IV, lateral; 17, left trunk limb V, medial; 18, lateral view of postabdomen; 19, terminal claw of postabdomen, lateral; 20, terminal claw of postabdomen, medial; 21, seta natatoria of postabdomen; 22, frontal view of ephippial female; 23, lateral view of ephippial region of a sexual female, showing the slough line. Scale bar "b" is for Figs. 14, 15, 16 and 17. Abreviations: EX, exopod; EN, endopod; GN, gnathobase; DCS, densely ciliated seta; IA, inner armature; EA, external armature; EP, epipodite.



Figs. 24–35. *Macrothrix smirnovi*, new species from kilometer 28 on the highway Jilotepec-Ixtlahuaca, State of Mexico, Mexico. Males. 24, lateral view of instar-I male; 25, lateral view of instar-II male; 26, lateral view of mature male; 27, AI of instar-I male, medial (aesthetascs are omitted); 28, AI of instar-II male, medial (aesthetascs are omitted) arrow indicates point of insertion of external, medial seta; 29, AI of instar-II male, medial (aesthetascs are omitted), arrow indicates point of insertion of external medial seta; 30, AI of instar-II male, lateral; 31, part of trunk limb I of instar-I male; 32, part of trunk limb I of instar-II male, showing the

length 0.48 mm, height 0.32 mm) BMNH 1995.1291, 16 Aug 1995. Paratypes: One ephippial female, BMNH 1995.1292, 16 Aug 1995. All mounted on slides in glycerine jelly sealed with depict mounting medium. One adult ovigerous female, mounted on a slide in glycerine jelly sealed with DePeX mounting medium and five parthenogenetic females in 4% formaldehyde solution, with a drop of glycerol added, National Museum of Natural History, Washington, D.C., U.S.A., USNM 274176, 29 Aug 1995. Five parthenogenetic females in 4% formaldehyde solution, with a drop of glycerol added, Zoological Museum of Moscow University, ZMMU 4010, 14 Aug 1995; one adult ovigerous female mounted on a slide in glycerine jelly sealed with DePeX mounting medium and five parthenogenetic females in 4% formaldehyde solution, with a drop of glycerol added, Instituto Nacional de Pesquisas da Amazônia, Manaos, Amazonia, Brazil, INPA-CR 569 and INPA-CR 570. One slide each of instars I, II and III of males and one ephippial female mounted in glycerine jelly sealed with DePeX mounting medium; 10 parthenogenic females in 4% formaldehyde solution, with a drop of glycerol added, Museo de Zoología, Universidad Nacional Autónoma de México, Campus Iztacala, Mexico. UNAM-Cl 1047 to UNAM-Cl 1051.

All remaining specimens and ephippia of both populations, including two dissected ovigerous females and one dissected male of each instar, mounted on slides in glycerol sealed with DePeX mounting medium, are deposited at the Museo de Zoología, Universidad Nacional Autónoma de México, Campus Iztacala, Mexico.

Type locality and habitat.—A small reservoir located at kilometer 28 on the highway Jilotopec-Ixtlahuaca, State of Mexico. The geographical coordinates are 19°49′14″N, 99°41′50″W at 2740 m above sea level. At the time of sampling, we recorded a water temperature of 14°C (air temperature 19°C), conductivity 135 mS/cm and pH 7.0. No other macrothricid species were found at the time of collection. The date of collection was 3 Dec. 1993.

Second locality: A temporary pond located at kilometer 44 on the highway Toluca-Atlacomulco, State of Mexico. The approximate coordinates are 19°38′54″N, 99°47′24″W at 2540 m above sea level. The date of collection was 3 Dec 1993.

Etymology.—The species is named for Dr. Nikolai N. Smirnov, from the Russian Academy of Sciences, as a tribute to his work in Cladocera.

Diagnosis.—This species is characterized by the arrangement of antennal armature, which is one spine on the distal edge of segments 2 and 4 from the endopod branch, plus an accessory spine on segments 2 and 3, about a half length of the other spines. A distinctive lobe carrying a stout, conical seta is found on endopod external surface of trunk limb II. The exopod of trunk limb V has only one seta. The preanal postabdominal spinules subequal in size are arranged in a stripe of several rows. The distal segment of postabdominal seta natatoria is three to four times shorter than the proximal segment. Males are characterized by an ontogenetic development over the three instars; the last instar is mature. Copulatory hook on trunk limb I is strong with a crescentic ridge at the tip. The postabdomen is slightly shorter and its shape is as in female. The antennula has a characteristic pattern of setae and spines proximally on the medial surface. It has two ba-

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enlarging copulatory hook; 33, part of trunk limb I of mature male, showing the highly modificated setae on ODL and IDL; 34, detail of tip copulatory hook on trunk limb I of mature male; 35, lateral view of postabdomen of mature male. Scale bars: "c" is for Figs. 24, 25 and 26; "d" is for Figs. 27, 28, 29 and 30; "e" is for Figs. 31 and 32. Abreviations: ODL, Outer distal lobe; IDL, inner distal lobe; CH, copulatory hook; GP, genital pore.

sal sensory setae and a long seta attached at the middle region of the external surface. Ephippial female with two ephippial eggs; about the same shape in lateral view as parthenogenetic female. The ephippial surface has a mesh-like pattern and a dorsal margin with a row of sclerotized rounded papillae.

Measurements.—Mature parthenogenetic females: Total length of the body from 0.70 to 1.05 mm, height from 0.48 to 0.75 mm (n = 31).

Males: Instar I, length from 0.37 to 0.4, height from 0.24 to 0.26 (n = 3); instar II, length from 0.45 to 0.52, height from 0.27 to 0.32 (n = 25); mature, length from 0.45 to 0.55, height from 0.29 to 0.45 (n = 13). All measurements are in mm.

Description of parthenogenetic female.—Shape and shell: Body ovoid (length : maximum height = 1.45–1.60 mm). Dorsal margin is curved from the supraocular region to the posterior-dorsal angle, with a slight depression in the vicinity of the head pore (Fig. 1); a pointed keel at the top of the shell is evident, clearly shown from a frontal view of the animal (Fig. 2). The dorsal margin of the shell is without serration. The ventral margin is deeply serrated with two rows of movable spines which are inserted at the submarginal edge. The external row of sparse needle-like spines increases in length distally and are outwardly directed. The inner row of bilaterally spinulated spines is inwardly directed, with every two of these followed by one spine of the external series; close to the middle region, the proximal member of the spinulated spines starts becoming stout and longer, while the second decreases in size toward the posterior angle. The entire surface of the shell has dots and is striated with a polygonal pattern.

Head: Evenly rounded with a slight supraocular bulge, tapering to the rostral region. The frontal part of the rostrum is trilobed with a medial large lobe and two lateral, blunt tips (Fig. 2), widening from the tip of rostrum onwards. The lateral ridges begin from the rostral apex running above the ocellus and the eye until it reaches the dorsal margin of the headshield. The head pore is large and subcircular. The ventral margin of the head is even, slightly convex with a transversal squamose pattern. The labrum is cuneiform and continuous with the ventral margin of the head (Fig. 3). The labral apex is blunt. Compound eye is located close to the middle distance between the dorsal and the ventral edges. The ocellus is close to the apex of rostrum, from 4.75 to 5.6 times smaller than compound eye.

First antenna (Figs. 4, 5) rod-shape (body length : antennule length = 3.4–3.8) inserted subapically, barely dilated distally, reaching over half-way to the labrum tip. One basal sensory seta is located ventrolaterally. Distally with a row of relatively long spinules near the lateral side of aesthetascs insertion. The medial surface has 7 to 9 transverse rows of small spines on the two distal thirds. Lateral and anterior surface armed with several rows of minute scale-like spinules plus a subapical group of spines on the posterior side. Nine aesthetascs, unequal in length (longest member : shortest member = 2.0–2.2) with a bifurcated tip, the longest one is 2.6–3.0 times shorter than the antennular length.

Second antenna: Stout and long (Fig. 6). Coxa massive, the basal region appears annulated with several folds and provided with a row of tiny denticles at the ventral side; the middle region presents two ventrolateral, soft sensory setae and the distal one is made up of ventrolateral margin armed with some rows of sclerotized spinules. The external surface of the distal portion has a spine used for burrowing and a longer soft seta at the medial face extended well beyond the end of the second exopod segment. Swimming setae 0-0-1-3/1-1-3, spines 0-2-1-1/0-0-1. All exopod setae carry spines at the distal septum except for the innermost apical member. The exopod is characterized by one spine on the distal edge of segments 2 and 4, as in all the Macrothricidae taxa (Smirnov 1992), plus an accessory, internal curved spine on segments 2 and 3, both subequal in length (Fig. 7). The spine is attached to the second segment (2nd segment : spine = 2.2–3.2) which is about 1.8 to 3.0 times longer than the other one. The surface of all antennal segments includes rows of fine scale-like spinules.

The longest antennal seta (Figs. 8, 9) is on the first endopod segment, and is bisegmented (distal segment: proximal segment = 1.2–1.6) stout, sclerotized and long (body length : seta length = 1.2–1.4). Its convex margin is provided with a series of fine setules along the three proximal quarters of the first segment, followed by a row of stout spines, two or three of which are subequal in length and are attached to the proximal joint (Fig. 8). The remaining row of spines runs along the second segment, decreasing in size gradually toward the tip. Beyond the middle third of the seta, these spines form groups of different number. There is a row of sparse spinules that continues along the next segment on the external surface of distal quarter of the first segment (Fig. 9).

Trunk limb I (Fig. 10): The exopod (ODL) is slender, bearing a long apical seta unilaterally having fine setules along its distal portion, and a short lateral seta (Fig. 11). Endite 4 (IDL) has three setae unequal in length, the longest one with a pattern similar to seta of ODL, the other two setae posses a row of stout setules, increasing moderately in size distally (Fig. 11). The posterior surface of IDL is provided with groups of strong setae. There are four setae different in length on endite 3, two of them are more sclerotized and bisegmented. Endite 2 has three bisegmented setae, setulated along the distal portion and with a row of sparse stout setules through the proximal joint. Endite 1 presents two fine plumose setae (Fig. 10). The inner spines on endite 1 and 2 have two and one teeth respectively on a pointed apex and one lateral spinule (Figs. 12, 13).

Trunk limb II (Figs. 14): The exopod is reduced, with an apical soft seta bilaterally setulated. The endopod has a row of eight spine-scrapers, six similar in structure, with an enlarged base, and distally with a pecten of strong, sclerotized teeth. Scraper 4 has the largest and strongest pecten. Scrapers 7 and 8 are long with an armature similar to the seta of ODL from trunk limb I. There is a lobe carrying a stout conical seta densely ciliated on its distal portion, located at the external surface of the endopod, near the insertion of scrapers 4 and 5. The gnathobase presents a filtering comb composed of four short setae which are different in structure and with four long plumose setae.

Trunk limb III (Fig. 15): The exopod carries four setae. The two outermost are fine and bilaterally setulated, the third one is densely setulated in the distal portion. The last one is strong and provided with two rows of spiniform setules. The lateral surface of exopod is covered with some groups of needle-like setae. Endopod with a distalmost seta stout, sclerotized, with a hook-like shape and proximally followed by five setae, all of them different in structure. Setae of the external armature are straight, finely ciliated in the distal portion. The gnathobase is rounded and it has a setose outgrowth on the external surface and two blunt papillae.

Trunk limb IV (Fig. 16): There are two apical setae on the exopod, the outermost is bilaterally setulated, the other one is densely setulated at the distal portion. The medial armature consists of five equal setae; the lateral row bears four setae, the distal one is stout and spiniform, the remaining ones are strongly hairy. There is also a tubular sensillum between the gnathobase and the proximal endopod. The gnathobase is reduced, composed of a setose furry-like seta and a finger-like lobe.

Trunk limb V (Fig. 17): Exopod suboblong, reduced to a small flap, with one fine setulose seta. The endopod has a rounded hairy flap and three setae remarkably different in size, the two outermost are reduced and strongly ciliated; the third one is the longest, bisegmented, unilaterally setulated along its distal portion. The gnathobase is composed of three well defined lobes, each one is armed with a series of long setae. The epipodite is large and subovoid.

Postabdomen (Fig. 18): Large, subovoid in lateral view (body length : postabdomen length = 2.8–3.4). The ventral margin is straight, somewhat convex with one or two groups of minute spinules. The dorsal margin is asymmetrically convex, non-bilobed, however, the preanal region is well differentiated from the rest of postabdomen (preanal portion : anal-postanal portion = 1.65–1.90). The preanal region has a dorsal stripe of needle-like spinules arranged in several transversal rows (ca. 25–30) which are subequal in length. The anus is bordered by 5 to 7 groups of larger spinules on each side with lateral surface covered with crescent rows of fine setae. The postanal portion has no setae. The claw is heavily sclerotized, evenly curved with a lateral face armed by two rows of small spinules on both concave and convex margins (Fig. 19). The medial side is provided with a row of three continuous pectens, obliquely arranged (Fig. 20) The two most proximal are composed of fine setae distributed along two thirds of the claw length, with a large and sclerotized member between them. The distal pecten is provided with a series of short, stout spinules, hardly sclerotized, the proximal member is stouter and longer than its companions. The setae natatoria arise from a sclerotized heel located at the proximal portion of the postabdomen (Fig. 21). The distal segment is shorter than the proximal one (proximal segment : distal segment = 3.0–4.0), having long, bristle-like setae.

Description of ephippial female and ephippium.—Female with two ephippial eggs is about the same shape in lateral view as parthenogenetic female (Fig. 22). The major difference is in cross section (Fig. 23) in which the pointed dorsal median keel of the parthenogenetic female is replaced by a broadly rounded median ridge. Dorsal profile of shell is higher than in parthenogenetic female, the maximum height is near the anterior slough line; the egg locule is well developed on each side. The shell surface of ephippial region is finely granulated with mesh-like pattern, weak and diffuse at egg locule and dorsal region. Dorsal margin with one row of chitinous rounded papillae. Slough line evidenced by a simple line that follows closely below the ephippium, so the entire anterior ventral portions of shell are lost after molting except for a small postero-ventral portion left in the ephippium. Portion of shell that sloughs has no punctae, meshes or pigmentation. Most of ephippial region is yellowish brown, mainly around the dorsal and the egg locule regions.

Description of males.—Two different prereproductive instars (Figs. 24, 25) and only one mature instar (Fig. 26). The functional male has a height somewhat lower than in female (length : height = 1.50-1.80). There are some appreciable ontogenetic changes over the three instars in shape of head. The rostrum of adults is directed more anteriorly than in immature instars, so the general outline of body has an attenuated ovoid aspect in lateral view. The two immature instars have a general shape similar to females (length : height of instar I and II = 1.45-1.70).

Antennula in instar I has a basal sensory seta and the setulation of internal surface is about as in female (Fig. 27). In instar II the antennula increases in size, and it has an additional sensory seta near its base, which arises from a rod-like projection, proximal to a characteristic group of long setae on the proximal internal portion (Fig. 28). In the adult male, the antennula is highly modified and is curved inwardly (Figs. 29, 30). The two basal sensory setae are well developed. One originates at the anterior margin and the other is located behind the former and close to the posterior margin. The latter is long and thin while the first is thicker and arises from a rod-like projection. On the external surface near the middle of antennular length (Fig. 30), there is a long soft seta (antennular length : seta length = 2.0-2.4). It is evident from instar II. Proximally, on the medial surface, close to the rod-like projection, there is a group of long hair-like setae and three groups of spinules, the distal and proximal ones are made up of sparse minute members, while the medial one has long and stronger spinules (Fig. 29). Nine aesthetascs in all instars; instars I and II aesthetascs with bifurcated tips as that in female, but in instar III this character is lost or barely visible. There are two aesthetascs 2.25 to 3.3 times longer than the others, these latter ones are subequal in length (Fig. 30).

Trunk limb I with typical instar sequence of development of copulatory hook (Figs. 31–33); adults with a long, stout free portion, with one crescentic ridge at tip of irregular margin that gives a spoon-like appearance to this portion (Fig. 34). IDL of adult male with three setae shorter than in female, the shortest one modificated as a spine-like seta, naked and hardly sclerotized. ODL with a large seta provided with small tubercle-like setules along its distal portion (Fig. 33).

Postabdomen (Fig. 35) roughly similar in shape to that of female although smaller; ventral margin tends to be irregular, in part because of the presence of genital pores, which in mature male open near ventral midline at a notch, located about two basal postabdominal claw lengths from tip. The postabdominal claw is the same as in the female, except that it is relatively longer and somewhat stouter.

Differential diagnosis and relationship.—*Macrothrix smirnovi* is a member of the *M. triserialis*-group. It shares with this species-group the general shape of the body, structure of the antennulae, the postabdomen, and the largest seta of the antenna. *M. triserialis* Brady was described from Sri Lanka. Fryer (1974) and Smirnov (1992) mentioned that *M. triserialis* is a species with wide and complex distribution, but their conclusions were based on only general morphological aspects. Sometimes, finer scaled morphology has been used (e.g., Fryer 1974, Dumont & Van de Velde 1977, Korinek 1984), but the differences observed were considered as variations within a single species rather than differences between species. Through detailed morphological comparisons Smirnov (1976, 1992) and Brandorf et al. (1982) distinguished three separated geographically isolated species from this taxa-group: *M. gauthieri* from Africa, *M. superaculeata* from Brazil and *M. flabelligera* from Australia. In addition *M. rosea* (Jurine) is mentioned by Dumont & Van de Velde (1977) as a possible synonymy of *M. triserialis.*

This species differs from *M. triserialis* s. str. mainly because it lacks the two stout, hook-like spines on IDL of limb I, clearly shown by Fryer (1974: fig. 69) and pointed out by Korinek (1984); instead of hooks, these spines are not curved and they seem to be less strong, both armed with rows of setules (Fig. 11). The combination of characters suggests a closer relationship of this new species to *M. superaculeata* (Smirnov) described from Brazil and *M. rosea* (Jurine) from Central Europe than to the other species of the group. Parthenogenetic females can be easily distinguished from both related taxa, mainly because of the antennal formula, the structure and armature of postabdomen and some fine details of trunk limbs (Table 1). *M. smirnovi*, *M. capensis* (Sars), *M. paulensis* (Sars) and *M. gauthieri* Smirnov have accessory spines on the antennal exopod, but *M. capensis* can be distinguished by a hump-like protuberance on the ventral part of the head and the preanal region with very small spinules. *M. paulensis* and *M. gauthieri* as well as *M. odiosa* Gurney and *M. sioli* (Smirnov) differ from *M. smirnovi* because of the large spines along the antennulae and the structure of postabdomen (Brandorf et al. 1982, Smirnov 1992).

Detailed morphology of mature males also shows evident differences among *M. triserialis*-group species. There are no descriptions of *M. triserialis* males on populations from type locality (Sri Lanka), the

Table 1.—Comparison of *Macrothrix smirnovi,* new species with the related *M. superaculeata* (Smirnov) and *M. rosea* (Jurine).

		Mature parthenogenetic female	
Character	*Macrothrix smirnovi,* new species	*M. superaculeata*[a]	*M. rosea*[a]
Shell	Dorsal edge has no serration.	Dorsal edge has very fine serration.	Dorsal edge has no serration.
Head	Ventral margin even with a slightly transverse squamose pattern (Fig. 3).	Ventral margin with transversal step-like ridges each one armed with a spine.	Ventral margin with a slightly transverse squamose pattern.
Antennulae	Posterior side with a subapical group of 2–3 spinules (Fig. 5).	Both posterior and anterior sides with a group of 2–3 strong and sclerotinized spinules	No subapical strong spinules.
Antennae	Spines 0-2-1-1/ 0-0-1 (Figs. 6, 7).	Spines 1-2-1-1/ 0-0-1	Spines 0-1-0-1/ 0-0-1
	Largest seta has two to three spines subequal in length proximal to its joint (Fig. 8), and a series of several spines decreasing in size toward the tip on the distal segment (Fig. 9).	Largest seta has a small and a large spine proximal to its joint, and a large and several small spines distally of its joint.	Largest seta with two larger spines in the area of the joint between its proximal and distal segments, distally followed by several small spines.
Trunk limb I	Endite 4 (ODL) with three seta of different length; the shortest two with a row of setules, increasing moderately in size distally (Fig. 11).	Those setae with a row of setules increasing distinctively in size distally.	Those setae with a row of setules increasing distinctively in size distally.
	Inner spines on endites 1 and 2 having two and one teeth respectively on the pointed apex and one lateral spine (Figs. 12, 13).	Both inner spines with two teeth on pointed apex and one lateral spinule.	Both inner spines with one tooth on pointed apex; two and one lateral spinules respectively.
Trunk limb II	Distinctive lobe carrying a stout conical seta, densely ciliated on its distal region, located near scrapers 4 and 5 (Fig. 14).	No such lobe and seta.	No such lobe and seta.
	Scrapers 4 and 5 with teeth of same length (Fig. 14).	Scraper 4 and 5 with a subapical larger tooth followed by a tuft of small spinules.	Scraper 4 and 5 with a subapical larger tooth followed by a tuft of small spinules.
Trunk limb V	Exopod with one seta (Fig. 17).	No information.	Exopod with two setae.
Postabdomen	Preanal region with rows of small spinules subequal in size (Fig. 18).	Such rows of spinules are strong increasing in size proximally.	Such rows of spinules are small and fine only the most proximal rows are relatively stronger and larger.
Postabdominal setae natatoria	Proximal segment 3.0–4.0 times as long as distal segment (Fig. 21).	Proximal segment 11.0–16.5 times as long as distal segment.	Three times as long as distal segment.

Table 1.—Continued.

Character	Mature males		
	Macrothrix smirnovi, new species	*M. superaculeata*[a]	*M. rosea*[a]
Copulatory hook	Strong, having one crescent ridge at tip giving to this portion a spoon-like appearance (Fig. 34).	Strong, carrying three subapical transversal crests.	Slender, tapering with only one subapical lamella.
Postabdomen	Shape somewhat similar to that in female (Fig. 35).	Extending distally into tubular projection, with scale-like subapical denticulate plate and basal sensillum.	Distal end of postabdomen conical without subapical scale-like plate and without basal sensillum.
Antennula	There are no clusters of spinules instead there are a group of long hairs-like setules and three groups of spinules proximally on the inner surface (FIg. 28).	Inner side covered with heavily sclerotinized clusters of strong spinules.	Antennular clusters of spinules not arranged in scales, less sclerotinized.
	Two basal sensory setae, one of which arises from a rod-like projection, and a long soft seta at the middle region (Fig. 30).	Two basal sensory setae.	One basal sensory seta and a long soft seta at the middle region.
		Ephippium	
	Finely granulated with a mesh-like pattern. Heavily sclerotinized. Dorsal margin with only one row of rounded papillae. Yellowish brown color (Fig. 23).	Sculpture of rounded cells. Feebly sclerotinized. Yellow color.	With thick lamellae of reticulation, surface coarsely granulated. Heavily sclerotinized. Dorsal margin with one to two rows of rounded papillae. Dark brown color.

[a] Information on mature males and ephippium obtained from published data in Korinek (1984).

only published data available is the *M. elegans* Sars. The description, which is a young synonym of *M. triserialis* according to Smirnov (1992), is featured by a long cylindrical distal part of postabdomen, no claws and a copulatory hook of trunk limb I with three transversal crests at tip. There are no described males of the related *M. superaculeata* from the type locality, but Korinek (1984) analyzed a population from Cuba that he assigned to this taxon, where males may be distinguished by the presence of three transversal crests at tip of copulatory hook and postabdomen, extending distally into a tubular projection, with a subapical scale-like plate and without any claws. *M. rosea* males are also different since there are a conical postabdominal distal part (Werner 1927) with terminal claws (Korinek 1984) and a slender copulatory hook tapering distally with only one subapical lamella.

Macrothrix rosea resembles the ephippial structure and reticulation of *M. smirnovi*, which is characterized by a mesh-like pattern on the surface and differs because the dorsal margin of the former has only one row of rounded papillae whereas *M. rosea* includes from one to two rows. However, the sculpture is markedly different in *M. superaculeata* which possesses rounded cells; it is feebly sclerotized and lightly colored (Korinek 1984).

There are five species of this genus reported from Mexico including *M. smirnovi* as well. The Mexican cladoceran fauna, as was monographed by Frey (1982b), included only two species: *M. laticornis* (Jurine) and *M. rosea* (Jurine). Recently, this number has increased because of the record of *M. triserialis* s.l. (Ciros & Elias 1995) and by the description of *M. mexicanus* (Ciros et al. 1995). However, it is worthwhile to point out that current knowledge of the taxonomy and geographical distribution of *Macrothrix* in this region is still scarce and some old reports should be analyzed with caution.

It is possible, according to the improvement in research on macrothricid cladocerans, that some species known in the past as cosmopolitan would be geographically restricted as was demonstrated by Frey for diverse chydorids. This statement is vindicated because macrothricids are the cladocerans most closely related to chydorids (Frey 1988). Future analysis should be based on larger samples containing ephippial females, males and females in all instars.

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Literature Cited

Brandorff, G. O., W. Koste, & N. N. Smirnov. 1982. The composition and structure of rotiferan and crustacean communities of the lower Rio Nhamundá, Amazonas, Brazil.—Studies on Neotropical Fauna and Environment 17:69–121.

Ciros-Perez, J., & M. Elias-Gutierrez. 1995. Nuevos registros de cladóceros (Crustacea: Anomopoda) en México.—Revista de Biología Tropical 44:297–304.

———, M. Silva-Briano, & M. Elias-Gutierrez. 1995. A new species of *Macrothrix* (Anomopoda: Macrothricidae) from central Mexico.—Hydrobiologia 319:159–166.

Dumont, H. J. 1994. On the diversity of the Cladocera in the tropics.—Hydrobiologia 272:27–38.

———, & I. Van de Velde. 1977. Cladocères et Conchostracés récoltés par le professeur Th. Monod dans la moyenne du Niger en décember 1972 et janvier 1973.—Bulletin de L'Institute Francais D'Afrique Noire 39:75–93.

Frey, D. G. 1982a. Questions concerning cosmopolitanism in Cladocera.—Archiv für Hydrobiologie 93:484–502.

———. 1982b. Cladocera. Pp. 177–186 *in* S. H. Hulbert & A. Villalobos-Figueroa, eds., Aquatic biota of Mexico, Central America and the West Indies. Aquatic Biota SDSU Foundation Vol XV, San Diego University Press, 529 pp.

———. 1986. The non-cosmopolitanism of chydorid Cladocera: implications for biogeography and evolution. Pp. 237–256 *in* R. H. Gore and K. L. Heck, eds., Crustacean biogeography. Balkema, Rotterdam.

———. 1988a. Are there tropicopolitan macrothricid Cladocera?—Acta Limnologica Brasiliensia II: 513–525.

———. 1995. Changing attitudes toward chydorid anomopods since 1769.—Hydrobiologia 307: 43–55.

Fryer, G. 1974. Evolution and adaptive radiation in the Macrothricidae (Crustacea: Cladocera): a study in comparative functional morphology and ecology.—Philosophical Transactions of Royal Society, London Biological Sciences B 269:137–274.

Haney, J. F., & D. J. Hall. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera.—Limnology and Oceanography 18:331–333.

Korinek, V. 1984. Cladocera. *in* Hydrobiological survey of the lake Bangwelulu Luapula river basin. Scientific results 13, fasc 2, Cercle hydrobiologique de Bruxelles, Bruxelles, 117 pp.

Sars, G. O. 1901. Contributions to the knowledge of the freshwater Entomostraca of South America, as shown by artificial hatching from dried material. Part I: Cladocera.—Archiv for Mathematik og Naturvidenskab Kristiania 23:1–102.

Smirnov, N. N. 1971. Chydoridae of the world's fauna. Fauna of the USSR. New series No. 101. Crustacea. 1(2), Leningrad, 531 p. (English transl. by A. Mercado. Israel Program for Scientific Translations, Jerusalem, 1974).

———. 1976. Macrothricidae and Moinidae fauna mira. Fauna SSSR, novaya seriya, N 112. Rkoobraznye T.I,3 Leningrad, Nauka. 237 pp.

———. 1992. The Macrothricidae of the world. SPB Academic Publishing, The Hague, 143 pp.

Werner, C. F. 1927. Wachstum und Formentwicklung der Cladocere *Macrothrix rosea*.—Wilhem Roux Archiev Entwicklungsmechanik Organismen 109:241–252.

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Some deep-sea Pycnogonida from the Argentine slope and basin

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Abstract.—Five stations from the Argentine Slope and Basin in the South Atlantic resulted in a rich collection of thirteen pycnogonid species, the majority new to that area of the Atlantic Ocean. Ten of the thirteen species are from the family Nymphonidae and four of these are new: *Heteronymphon caecigenum*, *Nymphon centrum*, *N. dentiferum*, and *N. vacans*. Distributions are given for all species along with pertinent remarks. The new species are described, illustrated, and compared with likely congeners. One additional species, *Nymphon scotiae*, is illustrated to contribute to knowledge of its morphology where the type figures were diagramatic and not entirely accurate.

This small collection was omitted from a previous report on deep-sea pycnogonids from the North and South Atlantic Basins (Child 1982) because it was not known to exist at that time and did not come to my attention until many years later. It consists of five additional stations made by the *Atlantis II*, of the Woods Hole Oceanographic Institution, in the South Atlantic off Argentina. None of these stations is duplicated in the previous report listed above. Seventeen species were listed in the first report from the Argentine Basin with six species and one genus described as new of the seventeen (35% new). It was noted (Child 1982: 1) that Argentine Basin fauna is poorly known.

Knowledge of the Basin's fauna is only slightly improved with the addition of the thirteen species listed in this report, four of which are described as new (31%) and four additional species recorded for the first time herein from the Argentine Basin. The new species are; *Heteronymphon caecigenum*, *Nymphon centrum*, *Nymphon dentiferum*, and *Nymphon vacans*. Known species recorded for the first time in the Argentine Basin and slopes are; *Nymphon longicollum* Hoek, *N. inferum* Child, *N. scotiae* Stock, and a questionable specimen of *Colossendeis scoresbii* Gordon. The other five species are either cosmopolitan deep water species or have apparently invaded this basin from nearby deeps or Subantarctic deep-seas.

Family Ammotheidae Dohrn, 1881
Genus *Cilunculus* Loman, 1908
Cilunculus acanthus Fry & Hedgpeth, 1969

Cilunculus acanthus Fry & Hedgpeth, 1969:126–127, figs. 207–209.—Stock, 1978:197 [key].—Child, 1982:9; 1994a: 34.

Material examined.—Slope E of Cabo San Antonio, Argentina, 36°55.7′S, 53°01.4′W, 2707 m, sta. 245A, epibenthic sled, 14 Mar 1971, 1 ♂ with eggs, 1 ♂, 5 ♀, 4 juv.

Distribution.—The species is apparently confined to the Scotia Sea and Argentine basin, based on what few records there are of captures. The type was collected in the Drake Passage. This capture extends the distribution of *C. acanthus* a little to the north in the Argentine Basin where it has been reported (Child 1982) and adds nothing new to a known depth range of 2450–2818 m.

Remarks.—This is a rare species, but perhaps only scarce because of the few deep-sea collections which have come from the Argentine basin. It is rare in the Scotia Sea where many more trawl samples have been made and from which many pycnogonids are known. Members of this genus are more commonly found in temperate regions.

The distinctive truncate conical cement gland tube and delicate slender dorsomedian tubercles easily identify this species among the many rather plain Subantarctic pycnogonids known from the Scotia Sea.

Family Austrodecidae Hodgson, 1907
Genus *Pantopipetta* Stock, 1963
Pantopipetta longituberculata (Turpaeva, 1955)

Pipetta longituberculata Turpaeva, 1955: 324–327, fig. 2.

Pantopipetta brevicaudata Stock, 1963: 336–338, figs. 9, 10a.—Hedgpeth & McCain, 1971:219, fig. 1E, 220, table 1, 222 [key], 223–225, figs. 3, 4, table 3.

Pantopipetta longituberculata-complex.—Stock, 1981:465–466 [text].

Pantopipetta longituberculata.—Child, 1982:49–50 [literature]; 1994b:88–89, fig. 17.

Material examined.—Basin E of Mar del Plata, Argentina, 38°16.9′S, 51°56.1′W, 4382–4402 m, sta. 242, epibenthic sled, 13 Mar 1971, 27 specimens. Slope E of Cabo San Antonio, 36°55.7′S, 53°01.4′W, 2707 m, sta. 245A, epibenthic sled, 14 Mar 1971, 30 specimens. Basin E of Valdez Peninsula, 43°33.0′S, 48°58.1′W, 5208–5223 m, sta. 247, epibenthic sled, 17 Mar 1971, 30 specimens. Basin E of Mar del Plata, 37°40.9′S, 52°19.3′W, 3906–3917 m, sta. 256, epibenthic sled, 24 Mar 1971, 16 specimens. Basin E of Cabo San Antonio, 37°13.3′S, 52°45.0′W, 3305–3317 m. sta. 259, epibenthic sled, 26 Mar 1971, 14 specimens.

Distribution.—This species is fairly common in very deep waters of the Pacific and Atlantic basins, and appears to be common in the Argentine basin. It has been found as far south as the South Shetland Islands of the Antarctic. It has one of the broadest depth ranges of any known pycnogonid: 567–6700 m.

Family Colossendeidae Hoek, 1881
Genus *Colossendeis* Jarzynsky, 1870
Colossendeis ?scoresbii Gordon, 1932

Colossendeis scoresbii Gordon, 1932:18–21, figs. 5c, 6b, 6b′, 6c, 6c′, 7a, b.—Child, 1995b:90, fig. 8.

not *Colossendeis megalonyx scoresbii* Fry & Hedgpeth, 1969:18 [key], 32, 33, figs. 7, 8, 17–20, 23.

Material examined.—Basin E of Mar del Plata, Argentina, 38°16.9′S, 51°56.1′W, 4382–4402 m, sta. 242, epibenthic sled, 13 Mar 1971, 1 specimen.

Distribution.—The species is only known from a few stations generally north of the Falkland Islands in 128–303 m. This specimen extends this distribution to the northeast and into very much deeper waters.

Remarks.—This small specimen is possibly not *C. scoresbii* due to the gross depth differences in this capture and those of the type specimens and the records of Child (1995b:90). This specimen also apparently lacks eyes. They are not discernable in the rather tall ocular tubercle. The ninth palp segment is shorter than usual for *C. scoresbii*, and the tarsus and propodus are longer in relation to the long claw of the *Atlantis II* specimen. It is closer to *C. scoresbii* than to any other known species.

It has similarity to *C. angusta* Sars in the short proboscis, although *C. angusta* has a shorter proboscis in relation to trunk length. The ninth palp segment of *C. angusta* is also longer. It is as long as the terminal segment while the ninth segment of this *Atlantis II* specimen is shorter than the tenth. This specimen is possibly a new species but in light of the great variation known to most species in this large genus, this single specimen must remain as a doubtful record of

C. scoresbii until more specimens are collected from this position in the South Atlantic.

Family Nymphonidae Wilson, 1878
Genus *Heteronymphon* Gordon, 1932
Heteronymphon caecigenum, new species
Fig. 1

Material examined.—Basin E of Valdez Peninsula, Argentina, 43°33.0′S, 48°58.1′W, 5208–5223 m, sta. 247, epibenthic sled, 17 Mar 1971, 1 ♀, holotype, USNM 234719; 1 ♂, 4 ♀, 1 juv., paratypes, USNM 234720.

Distribution.—Known only from the Argentine basin, in 5208–5223 m.

Description.—Size moderately small, leg span about 22 mm. Trunk fully segmented. Trunk and lateral processes smooth, glabrous, segments fully articulated, well separated by intervals equal to their diameters or slightly greater. Lateral processes slightly longer than their diameters. Ocular tubercle and eyes lacking, but hump containing lateral sensory papillae at anterior of cephalic segment suggests a low ocular tubercle. Oviger implants large, placed just anterior to but not touching first lateral processes. Neck short, not as long as wide, moderately expanded at anterior. Proboscis typical, gradually tapering to rounded oral surface, not as long as chelifore scapes. Abdomen short, distally a truncate cone with laterodistal pair of short setae.

Chelifores slender, scapes slightly longer than proboscis, armed laterally and distally with row of short setae. Chela palm as long as fingers, armed with many short lateral and ventral setae. Fingers robust, sharply curved distally, armed with 13 short recurved teeth on movable finger and ten similar teeth on immovable finger.

Palp segments moderately short, only slightly longer than chelifore scapes, typical for genus. Second segment short, only 0.6 as long as third, the longest segment. Fourth slightly shorter than second, fifth 0.25 longer than fourth, distal three segments with few very short distal and ventral setae.

Oviger (female) fourth segment subequal to fifth, sixth about 0.6 as long as fifth, all with few short lateral setae increasing in numbers on distal segments. Strigilis distal segments increasingly shorter than those more proximal, each armed with three-four short ectal setae and short endal denticulate spines in formula 6: 5: 5: 6, with terminal claw lacking teeth, hardly longer than distal denticulate spine. Spines with four lateral lobes per side.

Legs moderately slender, with few short dorsal and ventral setae, only three-four dorsal setae longer than segment diameters. Second tibia the longest segment, with first tibia slightly longer than femur. Tarsus about 0.75 length of propodus, both slightly curved, armed with row of very short sole spines and few short dorsal setae. Claw half propodal length, robust, moderately curved, auxiliaries lacking.

Male characters: slightly smaller size, femoral cement glands not evident, oviger fifth segment almost twice length of fourth.

Measurements (holotype in mm):—Trunk length, 2.46; trunk width across 2nd lateral processes, 1.1; proboscis length, 0.83; abdomen length, 0.63; third leg, coxa 1, 0.32; coxa 2, 1.0; coxa 3, 0.41; femur, 1.78; tibia 1, 2.03; tibia 2, 2.59; tarsus, 0.83; propodus, 1.08; claw, 0.53.

Etymology.—The name (Latin, caecigenus, meaning born blind) refers to the lack of any evidence of eyes in the new species.

Remarks.—This is the third known blind species in the genus *Heteronymphon*, the first being *H. profundum* Turpaeva, 1956, and second, *H. abyssale* (Stock, 1968). The latter species was moved from the genus *Nymphon* (Turpaeva, 1970:1723) because the sensory papillae commonly associated with an ocular tubercle are situated at the extreme anterior of the cephalic segment, suggesting that an ocular tubercle would be found there had one existed in *H. abyssale*. Most members of this genus live in deep waters and have inconspicuous or not fully formed eyes which are unpigmented as befits a lack of need for eyes in those habitats.

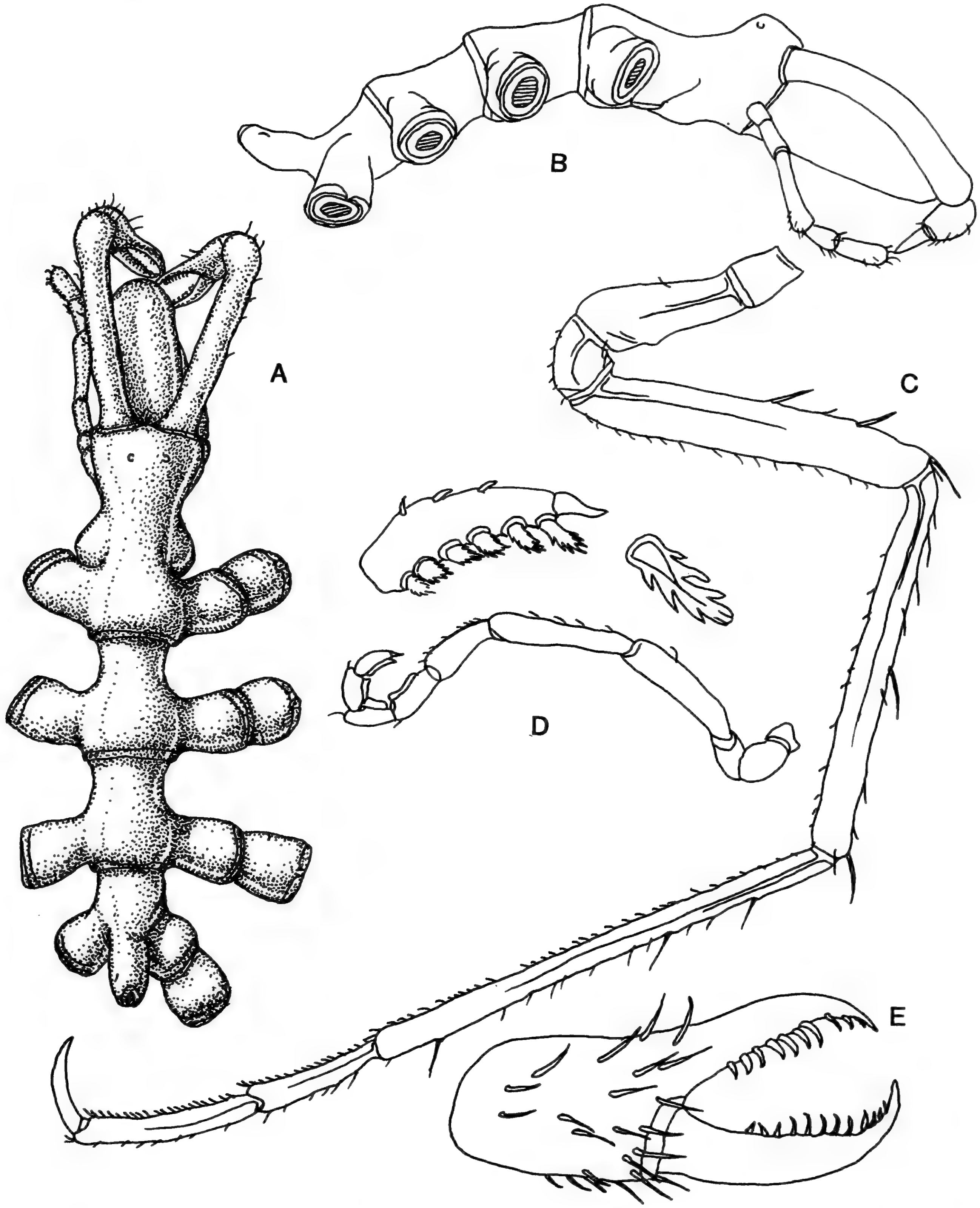

Fig. 1. *Heteronymphon caecigenum*, new species, holotype: A, Trunk, dorsal view; B, Trunk, lateral view; C, Third leg; D, Oviger, with enlargements of terminal segment and denticulate spine; E, Chela.

This new species and the two previously known have progressed to a fully blind status, going beyond the partly formed but unpigmented eyes of other species. The principal difference between this genus and the genus *Nymphon* is the placement of the ocular tubercle and its associated sensory papillae. These are found in the extreme anterior of species in the genus *Heteronymphon* but are further posterior in species of

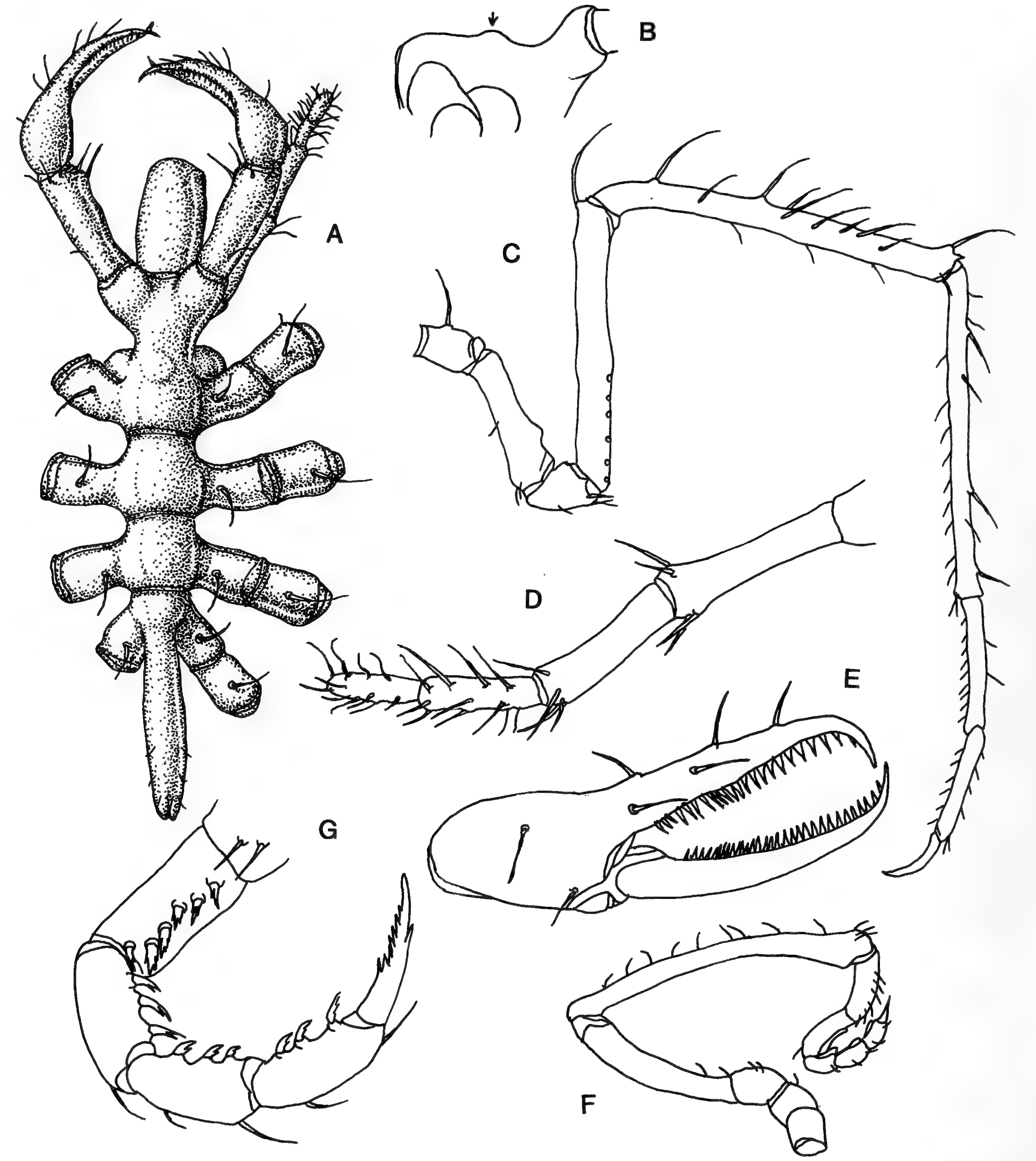

Fig. 2. *Nymphon centrum*, new species, holotype: A, Trunk, dorsal view; B, Ocular tubercle from right side; C, Third leg; D, Palp; E, Chela; F, Oviger; G, strigilis, enlarged.

Nymphon. Where there are no eyes and the ocular tubercle is only a morphological suggestion, the sensory papillae must exist in the location where there would be an ocular tubercle if one existed. With these three species, the papillae are anterior as in the other members of *Heteronymphon*, strong evidence that they belong in that genus.

Genus *Nymphon* Fabricius, 1794
Nymphon centrum, new species
Fig. 2

Material examined.—Slope E of Cabo San Antonio, Argentina, 36°55.7′S, 53°01.4′W, 2707 m, sta. 245A, epibenthic sled, 14 Mar. 1971, 1 ♂ holotype, USNM

234715; 3 ♂ with eggs, 6 ♂, 7 ♀ ovig., 4 ♀, 10 Juv. paratypes, USNM 234716.

Distribution.—Known only from the type-locality in 2707 m.

Description.—Size moderately small for genus, leg span 23.5 mm. Trunk fully segmented, unadorned. Lateral processes slightly longer than their diameters, separated by intervals equal to their diameters or less, each armed with single long mediandorsal spine, spines often missing. Oviger attachment lobes against first lateral processes, filling most of short neck. Ocular tubercle a slight bulge only, directly dorsal to oviger bases, sensory papillae not evident. Proboscis short, slightly tapering distally. Abdomen very long, extending well beyond first coxae of fourth leg pair, slightly inflated medially, armed with six short dorsolateral setae.

Chelifores large with wide cylindrical scapes armed with fringe of distal setae and one proximolateral seta. Chelae only moderately curved inward, palm shorter than fingers, armed with two-three setae. Fingers strongly curved distally, overlap at tips, armed with 33 short pointed teeth on movable finger and 24 slightly larger pointed teeth and six-seven ectal setae on immovable finger. Palps moderately short. Second segment longest, with few distal setae, third segment about 0.75 length of second, with few distal setae, fourth/fifth subequal, shorter than third, armed with many scattered setae longer than segment diameters.

Oviger segment four well curved, longer than first three combined. Fifth almost twice length of fourth, slightly curved, armed with row of scattered ectal setae as long as segment diameter. Sixth segment short, armed with similar row of ectal setae. Strigilis segments increasingly short distally, armed with ectal setae and few denticulate spines in formula 6: 3: 3: 3:, the spines with one or two lateral lobes. Terminal claw slightly curved, longer than terminal segment, armed with seven endal teeth and one distal ectal tooth.

Legs long, slender. First coxae with long middorsal spines matching those of the lateral processes. Second coxae longer than usual, about 2.5 times length of first and third. Femora with small dorsodistal tubercle bearing long spine. Cement glands proximoventral, with five-six tiny internal bulbs each with external pore. First tibiae the longest of major segments, armed with several dorsal and lateral tubercles bearing long spines, with few other shorter spines. Second tibiae with shorter spines only and row of short ventral setae. Tarsus slightly longer than propodus, both armed with row of short sole spines. Claw well curved, about half length of tarsus. Auxiliaries lacking.

Female characters: size slightly larger except for ovigers in which segment four is subequal to segment five. Strigilis with few more denticulate spines.

Measurements (holotype in mm).—Trunk length, 2.64; trunk width across 2nd lateral processes, 1.46; proboscis length, 0.91; abdomen length, 1.3; third leg, coxa 1, 0.46; coxa 2, 1.03; coxa 3, 0.44; femur, 2.01; tibia 1, 2.52; tibia 2, 2.34; tarsus, 0.95; propodus, 0.82; claw, 0.46.

Etymology.—The name (Latin: centrum, a noun in apposition, meaning center or the midpoint of a circle,) refers to the large middorsal spines placed centrally on each lateral process and first coxa.

Remarks.—A member of the *N. australe*-group (Child 1995a), this new species compares with those few species of the group that are blind and uniunguiculate. It fits into the group key (Child 1995a:6–7) next to *N. compactum* Hoek, and has some similarities with *N. hampsoni* Child, also from the Argentine basin, and *N. inornatum* Child, from the Antarctic Weddell Sea. It is probably closest to *N. compactum*, but has a very different oviger morphology from that species. The fifth oviger segment of *N. compactum* is distally inflated and the sixth segment is much longer than that of this new species. The chelifore scapes of *N. compactum* are much longer and the chelae have many more teeth than in this species. *N. centrum* also has middorsal lateral process spines which, although common in this group, are almost always in groups or only placed dorsodistally. *N. hampsoni* has similar lateral process spines, but they are in pairs and placed dorsodistally. It also has an ocular tubercle mound with conspicuous sensory papillae, longer chelifores, an oviger similar to that of *N. compactum*, and it has vestigial auxiliary claws.

This new species has a general habitus similar to that of *N. inornatum*. However, that species has an ocular tubercle almost twice as long as its diameter, palps with differing segment lengths, legs with more and longer major segment spines, and other small differences.

Nymphon dentiferum, new species

Fig. 3

Material examined.—Basin E of Mar del Plata, Argentina, 37°40.9′S, 52°19.3′W, 3906–3917 m, sta. 256, epibenthic sled, 24 Mar 1971, 1 ♀ holotype, USNM 234721; 1 ♀ ovig., 4 juveniles, paratypes, USNM 234722. Basin E of Valdez Peninsula, Argentina, 43°33.0′S, 48°58.1′W, 5208–5223 m, sta. 247, epibenthic sled, 17 Mar 1971, 15 ♀, 5 juveniles, paratypes, USNM 234723.

Distribution.—Known from its type-locality, off Mar del Plata, Argentina, in about 3900 m, the new species was also collected E of the Valdez Peninsula in about 5200 m.

Description.—Moderate sized, leg span about 48 mm. Trunk ovoid, fully segmented, lateral processes separated by about their diameters, moderately short, glabrous. Neck long in relation to most other *Nymphon* species, oviger implants halfway between first lateral processes and chelifore insertion, anterior to rounded hump representing ocular tubercle which is just anterior to first lateral processes. Sensory papillae of ocular tubercle prominent, on elevated surface, nipple-shaped. Proboscis cylindrical, very slightly inflated at tip, lips flat. Abdomen short, not extending to tip of first coxae of fourth leg pair, armed with four short dorsodistal setae.

Chelifores large, scapes short cylinders armed with two lateral setae distally. Chelae long, slender, palms slightly longer than scapes, fingers longer than palms, well curved, overlap at tips, armed with 26 slender sharp teeth on movable finger, 17 longer curved teeth on immovable finger, and one short seta at movable finger base. Palps rather long in relation to proboscis, slender, very lightly armed with few short setae, third segment slightly longer than second, fifth about 0.25 longer than fourth, distal two segments longer in combination than third. Oviger (female) fourth segment little longer than third which has small lateral bulge proximal to midpoint. Sixth segment about 0.6 length of fifth. Strigilis segment seven slightly longer than eighth which is subequal to ninth and tenth. Denticulate spines in formula 8: 5: 5: 6. Spines very short except for one distal spine of each segment which is twice longer than those more proximal, with more lateral serrations. Terminal claw longer than terminal segment, slender, well curved, armed with ten very long sharp teeth.

Legs robust, moderately long, major segments armed with rows of slender dorsal and lateral setae, some longer than segment diameters. Second coxae distally inflated, with large prominent ventrodistal sex pores. Femora of ovigerous female moderately swollen in proximal 0.75 of their lengths. Second tibiae longest, more slender than first tibiae or femora. Tarsus about 0.6 propodus length, both of equal diameter, slender, curved, armed with row of very short ventral spines and row of slightly longer dorsal setae. Claw long, slender, slightly curved, about 0.25 as long as tarsus.

Male characters unknown.

Measurements (holotype in mm).—Trunk length, 5.71; trunk width across 2nd lateral processes, 3.32; proboscis length, 2.46; abdomen length, 0.86; third leg, coxa 1, 0.97; coxa 2, 1.84; coxa 3, 0.96; femur,

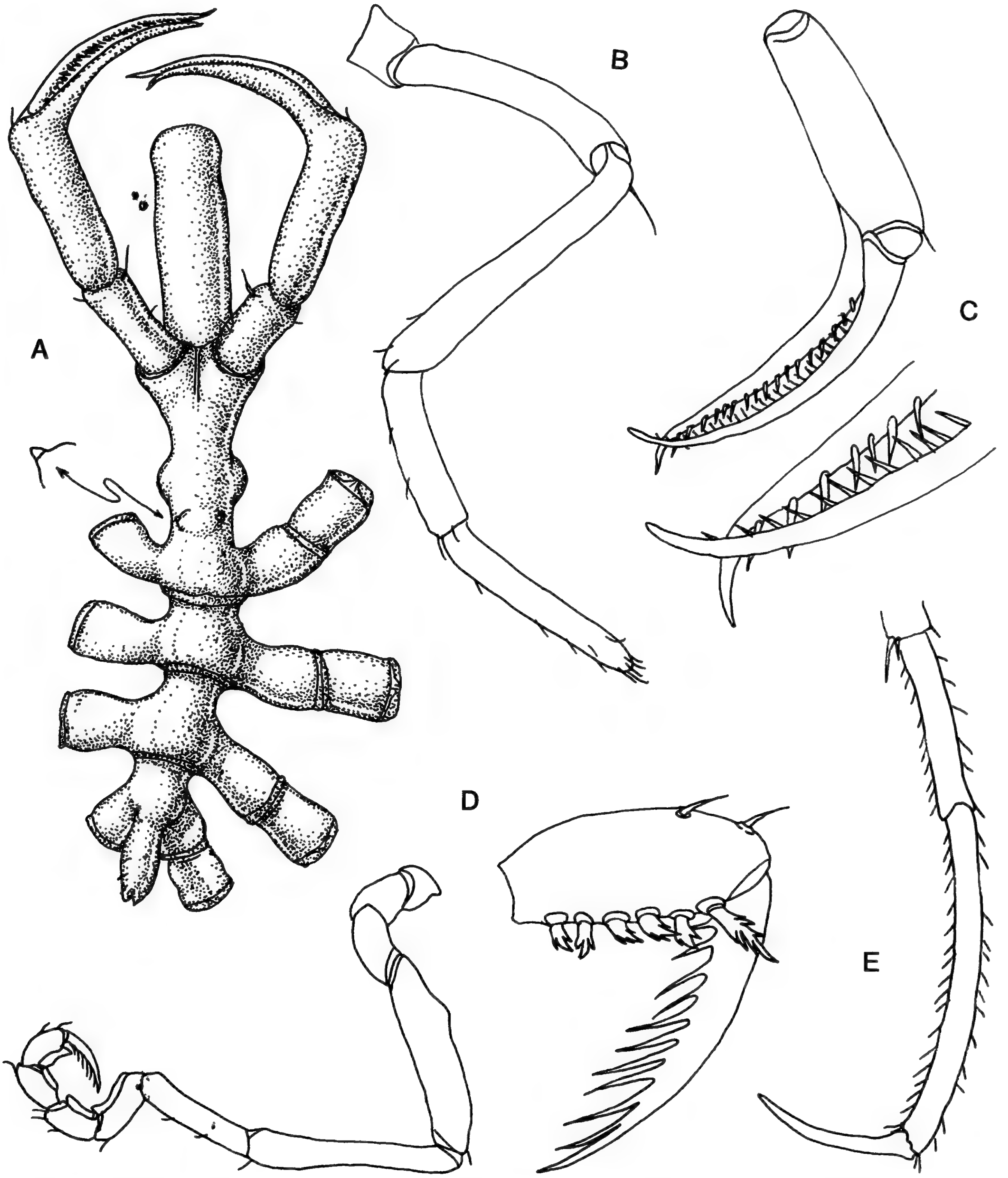

Fig. 3. *Nymphon dentiferum*, new species, holotype: A, Trunk, dorsal view, with enlargement of sensory papilla; B, Palp; C, Chela, with enlargement of finger tips; D, Oviger, with enlargement of terminal segment and claw; E, Distal leg segments, enlarged.

5.14; tibia 1, 4.5; tibia 2, 6.09; tarsus, 1.01; propodus, 1.74; claw, 0.24.

Etymology.—The name (Latin: *dentiferum*, diminutive of dens, a tooth or denticle) draws attention to the enlarged terminal denticulate spine on each of the four strigilis segments which is an unusual character in the genus *Nymphon*.

Remarks.—The strigilis of at least one species of *Nymphon* (*N. floridanum*, in Child, 1979:33) was seen to be used as an instrument for cleaning appendages and an enlarged distal spine might offer some advantage in this scraping function. This cleaning or scraping function was shown experimentally by Prell (1910:13, fig. 5B) with specimens of *Nymphon leptocheles* Sars, 1891.

The proboscis, trunk, and abdomen of this species are very like those of *N. hadale* Child, particularly in the neck length, placement of the oviger bulges, and the sensory papillae representing the vestigial ocular tubercle. The appendages are each quite different from *N. hadale*. The chelifore scapes of the new species are much shorter than those of *N. hadale*, and the chelae fingers of that species have many more teeth than the fingers of *N. dentiferum*. The combined length of the distal two palp segments of *N. hadale* is shorter than the third segment while the two are much longer than the third in the new species. The oviger strigilis of *N. dentiferum* has a very enlarged distal denticulate spine on each segment while those of *N. hadale* are more or less equal in size.

Nymphon inferum Child, 1995a

Nymphon inferum Child, 1995a:40–42, figs. 12A–F.

Material examined.—Slope E of Cabo San Antonio, Argentina, 36°55.7′S, 53°01.4′W, 2707 m, sta. 245A, epibenthic sled, 14 Mar 1971, 1 ♀.

Distribution.—This species was known only from Subantarctic and Antarctic waters among the island groups on both sides of the Scotia Sea. The nearest specimens to the above record are from South Georgia Island. All are deep-sea and range from 2450 to 3873 m. The Cabo San Antonio record marks a lengthy range extension to the north but adds nothing to its known depths.

Remarks.—It is not surprising to find some of the Antarctic species with ranges extending into the South Atlantic. There will probably be some which extend into the South Pacific, but deep-sea collections from that distant region are as rare as are the species known from there.

This relatively giant species (comparable only to *N. charcoti* of Antarctica in that respect) is difficult to confuse with any other from the Scotia Sea and South Atlantic region. It is blind, uniunguiculate, and with a leg span of 160+ millimeters, its size surpasses any other *Nymphon* known among species with these characters.

Nymphon laterospinum Stock, 1963

Nymphon laterospinum Stock, 1963:322, 323, fig. 1; 1978a:211, 212, fig. 9a–d.—Child, 1982:42–43.

Material examined.—Argentine Basin E of Cabo San Antonio, 37°13.3′S, 52°45.0′W, 3305–3317 m, sta. 259, epibenthic sled, 26 Mar 1971, 25+ specimens.

Distribution.—This distinctive species is known from the North and South Atlantic basins on both sides of the Mid-Atlantic Ridge and has a wide depth range of 1894–4715 m. The above record is very near another *Atlantis II* capture in nearly the same depth.

Remarks.—The tall slender lateral process tubercles of this species along with its characters of uniunguiculate claws and blind ocular mound serve to differentiate it from all other deep water *Nymphon*, at least in the South Atlantic.

Nymphon longicollum Hoek, 1881

Nymphon longicollum Hoek, 1881:40–41, pl. 3, figs. 1–3, pl. 15, fig. 11.—Gordon, 1944:18, table 2, 19 [key].—Stock, 1965: 22 [list, key].—Child, 1995a:43.

Material examined.—Argentine basin E of Mar del Plata, 38°16.9′S, 51°56.1′W, 4382–4402 m, sta. 242, epibenthic sled, 13 Mar 1971, 3 ♀, 4 Juv. Same locality, 37°40.9′S, 52°19.3′W, 3906–3917 m, sta. 256, epibenthic sled, 24 Mar 1971, 1 ♀, 1 Juv.

Distribution.—This species was known only from the Chilean basin for more than one hundred years until many more specimens were collected in the Subantarctic islands of the South Atlantic and from the Antarctic in the Weddell and Ross Seas. It was also found on the southern New Zealand slope in 2612 m (Child 1995a:43). It is therefore known in many Southern Hemisphere localities in a wide depth range of 508–4069 m. These records extend its range to the north of the Subantarctic localities, into the Argentine basin and increase its known depth slightly to 4402 m.

Remarks.—The tall, erect, conical, blind ocular tubercle serves as a good recognition character for this species. It is conspicuous, broad based, and its shape is not found on any other known Southern Hemisphere *Nymphon.*

Nymphon longicoxa Hoek, 1881

Nymphon longicoxa Hoek, 1881:38–39, pl. 2, figs. 1–5, pl. 15, figs. 8, 9.—Child, 1995a:43–44 [literature].

Material examined.—Slope E of Cabo San Antonio, Argentina, 36°55.7′S, 53°01.4′W, 2707 m, sta. 245A, epibenthic sled, 14 Mar 1971, 2 ♀ without legs.

Distribution.—This species has been recorded from south of New Zealand to the SE Pacific, Scotia Sea, Ross Sea, and South Atlantic off Argentina. It has a known wide depth distribution of 318–3000 m.

Remarks.—A diagnosis of the species has been provided by Child (1995a:44). These specimens are without legs, but there can be little doubt in their identification. There is a small rounded ocular tubercle which may or may not have eyes. The palps are typical of the species; very slender, long, and delicate. The lateral processes are glabrous, the proboscis has the three bumps arranged radially around its distal circumference, and the oviger bases are well anterior to the first lateral processes and crowd most of the neck lateroventrally. There are very many chelae finger teeth. The tarsus and propodus are variable but usually subequal in length although it is impossible to tell from these legless specimens.

Nymphon scotiae Stock, 1981
Fig. 4

Nymphon stocki Turpaeva, 1974:282, fig. 1 [preoccup.:Utinomi, 1955:10].

Nymphon scotiae Stock, 1981:458 (footnote).

Material examined.—Slope E of Cabo San Antonio, Argentina, 36°55.7′S, 53°01.4′W, 2707 m, sta. 245A, epibenthic sled, 14 Mar 1971, 2 ♂ with eggs, 9 ♂, 19 ♀, 24 juveniles.

Distribution.—This species was described from two specimens collected in the Scotia Sea in 2960–2980 m. It has not been captured since until the present record in the Argentine basin. This record places it well north but near the same longitude and in a similar depth.

Remarks.—This is a slender graceful species which is only recorded with new material for the second time. Illustrations are provided herein for this rare species because the only figures of its unique characters are not readily available, are diagramatic and slightly inacurate.

Nymphon typhlops (Hodgson, 1915)

Chaetonymphon typhlops Hodgson, 1915: 144; 1927:327–329, fig. 6.

Nymphon typhlops.—Gordon, 1944:19 [key].—Stock, 1965:22 [key].—Child, 1995a:20–21.

Nymphon spicatum Child, 1982:46–48, fig. 15.

Material examined.—Slope E of Cabo San Antonio, Argentina, 36°55.7′S, 53°01.4′W, 2707 m, sta. 245A, epibenthic sled, 14 Mar 1971, 2 ♀, 4 Juv.

Distribution.—This species was described from Antarctic specimens and the few other specimens known were collected either in Antarctic waters or in the Argentine slope and basin. The specimen described by Child (1982) as *N. spicatum* was

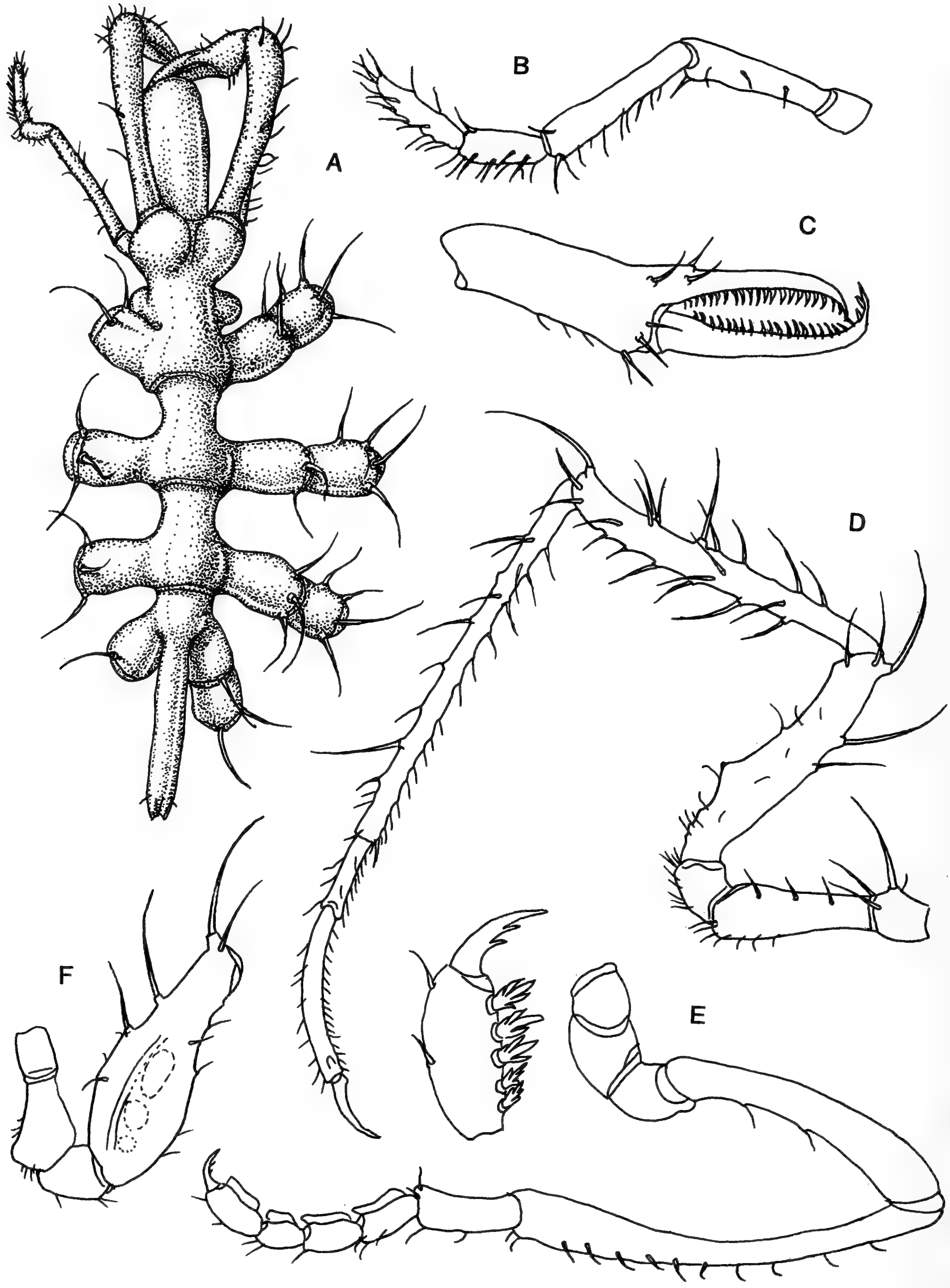

Fig. 4. *Nymphon scotiae* Stock. male: A, Trunk, dorsal view; B, Palp; C, Chela; D, Third leg; E, Oviger, with enlargement of terminal segment and claw. Ovigerous female: F, Proximal leg segments.

collected just slightly to the SE of the specimens in hand but in deeper waters. The known depth range for this species is 2450–3822 m.

Remarks.—This is another of the blind deep-sea species that either has vestigial auxilliary claws or none at all. The Argentine specimens all appear to lack auxiliaries and have a few small differences from the type specimens. The ocular tubercle is variable in its length and it appears to be directed slightly toward the posterior in most but not all specimens. The paired dorsomedian trunk spines are often broken off or missing. The distal two palp segments are slightly longer in the types, the strigilis has several more denticulate spines, the chelae fingers a few more teeth, and the propodal claw is flanked by tiny auxiliaries.

Nymphon vacans, new species
Fig. 5

Material examined.—Slope E of Cabo San Antonio, Argentina, 36°55.7′S, 53°01.4′W, 2707 m, sta. 245A, epibenthic sled, 14 Mar 1971, 1 ♀, holotype, USNM 234717; 2 ♂, 5 ♀, 7 juv. paratypes, USNM 234718.

Distribution.—Known only from the type locality in 2707 m.

Description.—Size moderate, leg span about 36 mm. Trunk fully segmented, glabrous. Lateral process length about 1.5 times their diameters, separated by slightly less than their diameters, armed with two long dorsodistal spines except for second lateral processes which have three. Neck short, crowded with oviger implants. Very slight bulge of ocular tubercle placed dorsally and slightly posterior to oviger bulges, sensory papillae evident laterally, eyes entirely lacking. Proboscis a cylinder with slight distal constrictions, oral surface flat. Abdomen of moderate length, tapering distally to tiny tip, extending almost to distal rim of fourth leg first coxae, armed with four short dorsodistal setae.

Chelifores large, scapes cylindrical, slightly longer than proboscis, with slight inward curve, armed with lateral and distal setae of varying lengths. Chelae long, slender, palm about 0.75 length of fingers, armed with short scattered setae. Fingers curved sharply at tips which overlap, immovable finger armed with short ectal setae and about 30 short teeth of varying sizes. Movable finger without setae, with about 37 teeth similar to those of immovable finger. Palps with many short setae increasing in numbers on distal segments. Second segment slightly longer than third, fourth and fifth subequal in length, combined length longer than either second or third segment.

Oviger (female) fourth segment slightly longer than fifth, sixth about 0.75 length of fifth, both with short lateral setae. Strigilis segments each shorter than last, each armed with ectal setae and endal denticulate spines in formula 8: 6: 4: 5:, spines slender, with three lateral lobes. Terminal claw slightly shorter than terminal segment, armed with six endal teeth.

Legs moderately spinose, few spines longer than segment diameters. Second tibiae the longest segments, with first tibiae very slightly shorter and femora shortest of major segments. Propodus about 0.8 as long as tarsus, both slender, armed with dorsal row of short setae and ventral row of very short sole spines. Claw about half propodal length. Auxiliaries lacking.

Male characters: size slightly smaller, oviger fourth segment quite curved, fifth about 0.3 longer, almost straight, slightly swollen distally. Fewer denticulate spines, each with only two lateral lobes. Cement glands and pores not evident.

Measurements (holotype in mm).—Trunk length, 3.55; trunk width across 2nd lateral processes, 1.8; proboscis length, 1.97; abdomen length, 1.0; third leg, coxa 1, 0.6; coxa 2, 1.18; coxa 3, 0.88; femur, 3.17; tibia 1, 3.86; tibia 2, 3.89; tarsus, 1.64; propodus, 1.3; claw, 0.66.

Etymology.—The name (Latin: *vacans*, meaning empty, void, or clear) refers to the slight bulge of the ocular tubercle which is devoid of eyes.

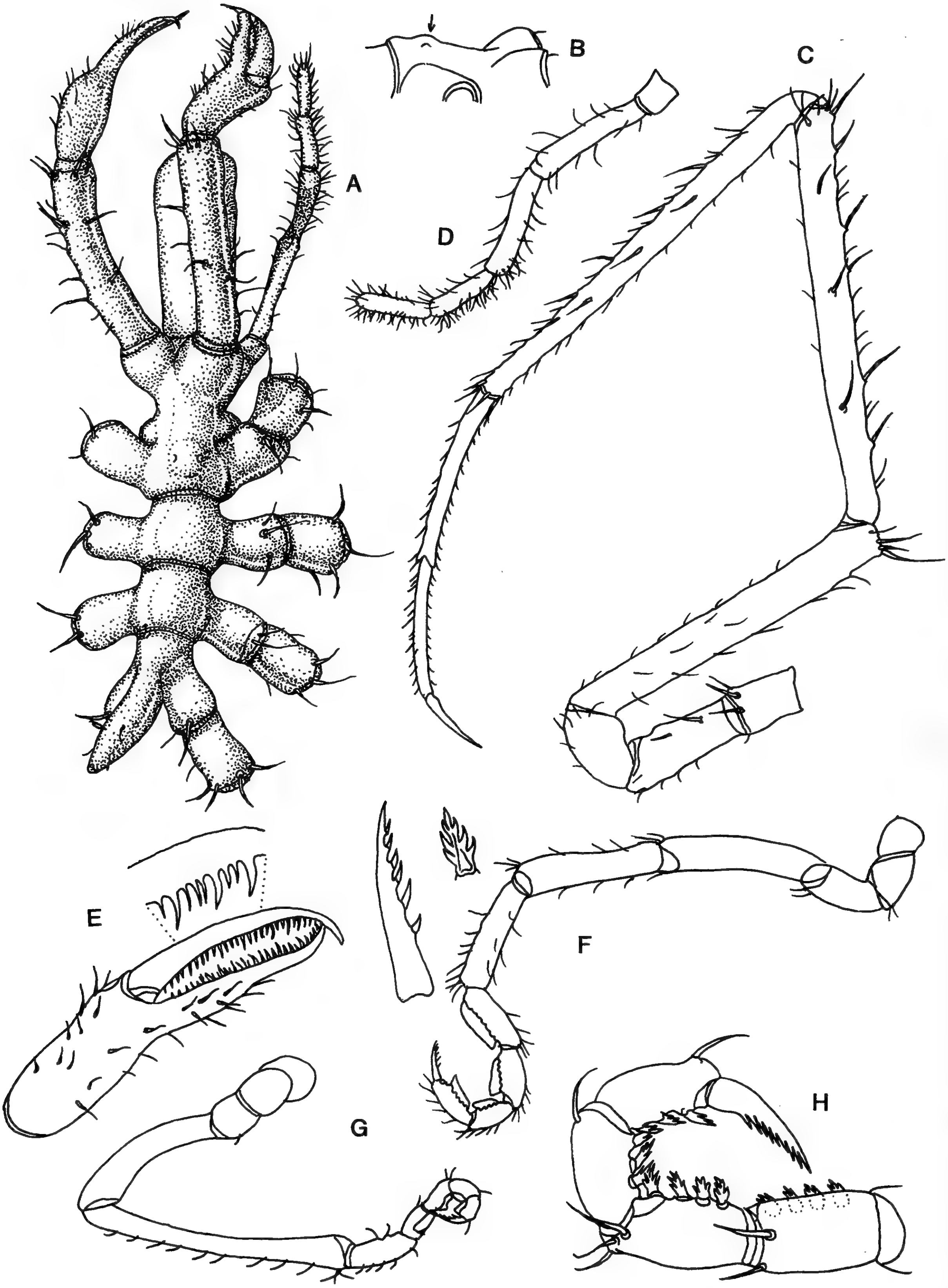

Fig. 5. *Nymphon vacans*, new species, holotype: A, Trunk, dorsal view; B, Ocular tubercle from right side; C, Third leg; D, Palp; E, Chela, with enlargement of several teeth; F, Oviger, with enlargement of denticulate spine and terminal claw. Male: G, Oviger; H, Strigilis, enlarged.

Remarks.—The habitus of this species is superficially quite close to that of *N. centrum*, discussed elsewhere in this report, and to *N. hampsoni* Child, *N. compactum* Hoek, and indeed to most members of the *N. australe*-group of related species (Child 1995a). The similarities with *N. centrum* occur in the trunk habitus of the same shape with long spines on the lateral processes, although the spines are placed differently on each species. The many small differences are in the proboscis and chelifore scape lengths; long in *N. vacans* and much shorter in *N. centrum*. The abdomen of this new species is shorter than that of *N. centrum*, and its palp segments are longer than those of the latter species.

Nymphon vacans agrees with *N. hampsoni* in lateral process length and placement, the dorsolateral spination, proboscis and chelifore length, and with other similarities in legs and palps. The major differences occur in the short male ovigers with club-shaped fifth and sixth segments in *N. hampsoni* and also in *N. compactum*. The ovigers of *N. vacans* have much longer fifth segments in relation to the fourth, and they are only slightly inflated distally and the sixth segment is much shorter in relation to the fifth. The other major difference between all of these species is in abdominal length. This varies with each species and is longest in *N. centrum* and decreases in length from *N. hampsoni*, then *N. vacans*, and is shortest in *N. compactum*.

Nymphon species indeterminate

Material examined.—Basin E of Mar del Plata, Argentina, 38°16.9′S, 51°56.1′W, 4382–4402 m, sta. 242, epibenthic sled, 13 Mar 1971, 1 ♀, 2 Juv. Same locality, 37°40.9′S, 52°19.3′W, 3906–3917 m, sta. 256, epibenthic sled, 24 Mar 1971, 1 juv.

Remarks.—The female from sta. 242 is badly damaged and the other specimens are too immature for identification.

Acknowledgments

I wish to thank Joel W. Hedgpeth for relinquishing his right to describe this collection and for contributing it to me for examination and report. All specimens are deposited in the National Museum of Natural History, Smithsonian Institution.

Literature Cited

Child, C. A. 1982. Deep-sea Pycnogonida from the North and South Atlantic basins.—Smithsonian Contributions to Zoology 349:1–54.

———. 1994a. Antarctic and subantarctic Pycnogonida I. The family Ammotheidae.—Biology of the Antarctic Seas XXIII. Antarctic Research Series 63:1–48.

———. 1994b. Antarctic and subantarctic Pycnogonida II. The family Austrodecidae.—Biology of the Antarctic Seas XXIII. Antarctic Research Series 63:49–99.

———. 1995a. Antarctic and subantarctic Pycnogonida III. The family Nymphonidae.—Biology of the Antarctic Seas XXIV. Antarctic Research Series 69:1–68.

———. 1995b. Antarctic and subantarctic Pycnogonida IV. The families Colossendeidae and Rhynchothoraxidae. Biology of the Antarctic Seas XXIV.—Antarctic Research Series 69:69–111.

Dohrn, A. 1881. Die Pantopoden des Golfs von Neapel und der Angrenzenden Meeresabschnitte.—Flora und Fauna des Golfes von Neapel 3:1–252.

Fabricius, J. C. 1794. Entomologia Systematica Emendata et aucta 4:416–417. Hafniae.

Fry, W. G., & J. W. Hedgpeth. 1969. Pycnogonida, 1. Colossendeidae, Pycnogonidae, Endeidae, Ammotheidae. Fauna of the Ross Sea 7.—Memoirs of the New Zealand Oceanographic Institute 49: 1–139.

Gordon, I. 1932. Pycnogonida.—Discovery Reports 6:1–138.

———. 1944. Pycnogonida.—Reports of the British, Australian and New Zealand Antarctic Research Expedition (ser. B) 5(1):1–72.

Hedgpeth, J. W., & J. C. McCain. 1971. A review of the pycnogonid genus *Pantopipetta* (family Austrodecidae, emend.) with the description of a new species. Pp. 217–229 *in* G. A. Llano and I. G. Wallen, eds., Biology of the Antarctic Seas, IV.—Antarctic Research Series 17:217–229.

Hodgson, T. V. 1907. Pycnogonida.—National Antarctic Expedition 1901–1904. 3(Zoology and Botany):1–72.

———. 1915. The Pycnogonida collected by the

Gauss in the Antarctic regions, 1901–3; preliminary report.—Annals and Magazine of Natural History ser. 8, 15(85):141–149.

———. 1927. Die Pycnogoniden der Deutschen Südpolar-Expedition 1901–03.—Deutsche Südpolar-Expedition, Ser. II, Zool. 19:303–358.

Hoek, P. P. C. 1881. Report on the Pycnogonida dredged by HMS *Challenger* 1873–76.—Reports of the Scientific Results of Exploring Voyage of HMS *Challenger* 3(10):1–167.

Jarzynsky, T. 1870. Praemissus catalogus Pycnogonidarum, inventarum in mari Glaciali, ad oras Lapponiae rossicae et in mari Albo, anno 1869 et 1870.—Annales de la Société des Naturalistes de St. Pétersbourg 1:319–320.

Loman, J. C. C. 1908. Die Pantopoden der Siboga-Expedition.—Siboga Expeditie Monographie 40:1–88.

Prell, H. 1910. Beiträge zur Kenntnis der Lebensweise einiger Pantopoden.—Bergens Museums Aarbok (N.R.), 1909 (10):1–30.

Stock, J. H. 1963. South African deep-sea Pycnogonida with descriptions of five new species.—Annals of the South African Museum 46(12):321–340.

———. 1965. Pycnogonida from the southwestern Indian Ocean.—Beaufortia 13(151):13–33.

———. 1968. Pycnogonida collected by the *Galathea* and *Anton Bruun* in the Indian and Pacific Oceans.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 131:7–65.

———. 1978. Abyssal Pycnogonida from the northeastern Atlantic Basin, Part I.—Cahiers de Biologie Marine 19:189–219.

———. 1981. Abyssal Pycnogonida from the Walvis Basin, southern Atlantic.—Cahiers de Biologie Marine 22:453–471.

Turpaeva, E. P. 1955. [New Species of Sea Spiders (Pantopoda) from the Kurile-Kamchatka Trench].—Trudy Instituta Okeanologii P. P. Shirshov, Akademiya Nauk SSSR 12:323–327. [In Russian]

———. 1956. [Pantopoda of the genus *Heteronymphon* from the northwest part of the Pacific Ocean.]—Byulleten Moskovskovo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii, 61(2): 67–72. [In Russian]

———. 1970. Belonging of *Nymphon abyssale* Stock to the genus *Heteronymphon.*—Zoologicheskii Zhurnal 49(11):1723–1725. [In Russian + English title]

———. 1974. [The pycnogonids of the Scotia Sea and surrounding waters.]—Trudy Instituta Okeanologii P. P. Shirshov, Akademiya Nauk SSSR 98:277–305. [In Russian]

Utinomi, H. 1955. Report on the Pycnogonida. collected by the Soyo-Maru Expedition made on the continental shelf bordering Japan during the years 1926–1930.—Publications of the Seto Marine Biological Laboratory V(1):3–42.

Wilson, E. B. 1878. Synopsis of the Pycnogonida of New England.—Transactions of the Connecticut Academy of Arts and Sciences 5:1–26.

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Syllides eburneus, a new species, with notes on other members of the genus (Polychaeta: Syllidae) from the coast of New England and New Brunswick

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Abstract.—*Syllides eburneus* new species, is described from the subtidal zone of the southern Gulf of Maine and the intertidal zone of the northern part. Morphological data obtained from living individuals of *Syllides convoluta* Webster & Benedict, 1884, *S. benedicti* Banse, 1971, *S. longocirrata* (Örsted, 1845), and *S. setosa* Verrill, 1882 occuring in the region are presented to clarify discrepancies which have arisen from the use of fixation artifacts encountered in preserved specimens. The role of protraction and retraction in the location of the foregut in specific setigers is discussed. *Syllides setosa* Verrill, 1882 is accepted as a valid species, whose morphology has been misinterpreted.

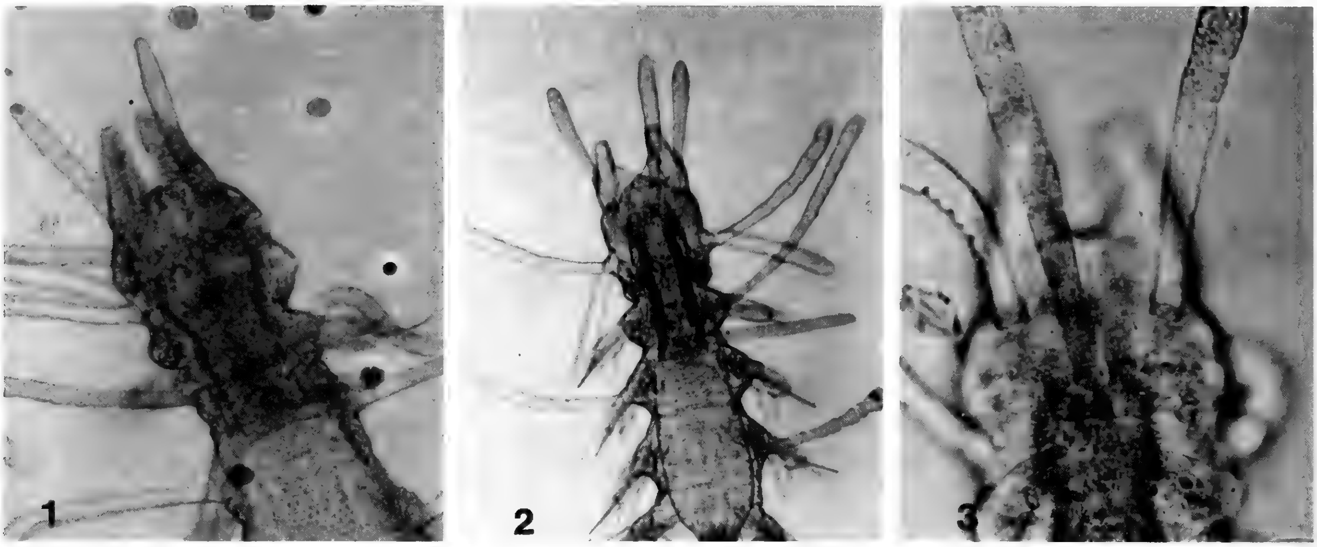
The polychaete genus *Syllides* is commonly encountered in sandy interstitial environments in which there is little indication of anaerobic conditions, although there may be some silt or finely fragmented algal debris. Living individuals can be readily identified, and while many of the identifying characters can not be seen or clearly observed in preserved animals setation frequently is distinctive. *Syllides convoluta* Webster & Benedict, 1884, *S. benedicti* Banse, 1971, and *S. longocirrata* (Örsted, 1845) are found in the intertidal zone of the Gulf of Maine. *S. longocirrata* and *S. setosa* Verrill, 1882 (usually as *S. japonica* Imajima, 1966) have also been recorded from depths of 20–40 m, in environmental surveys in the region. A previously undescribed species has been encountered at depths of 7–30 m in Nahant Bay, Massachusetts, frequently in large numbers, and in the intertidal interstitial community in the Northern Gulf of Maine.

Materials and Methods

Specimens were obtained from sand collected for meiofaunal studies. Intertidal samples were dug from coarse sand beaches with a garden trowel at low tide level during periods of extreme low tide. The subtidal samples were taken from the piles of sand kicked out from under rocks by lobsters digging retreats at depths of 7–40 m. Sediment was washed with fresh sea water and decanted onto 153 μm screens from which animals were removed for sorting. The sediment was then extracted with 7.5% $MgCl_2$, and decanted onto the screens from which the animals were washed into fresh sea water. Specimens of the new species from the intertidal were not numerous, 3–8 per 8-ounce bag of sand. Subtidal samples yielded 15–35 individuals per 8 ounces, the largest numbers occuring at depths of 20 m. All measurements were obtained from living specimens.

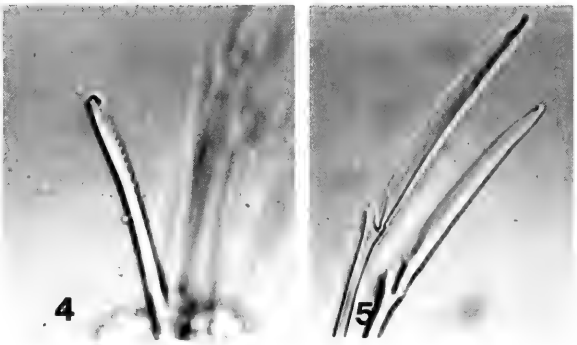
Syllides eburneus new species
Figs. 1–5, 7

Diagnosis.—Small species attaining body length of less than 5 mm, up to 30 setigers. Prostomium hemispherical, slightly broader than long, projecting anteriorly beyond bases of lateral antennae. With two



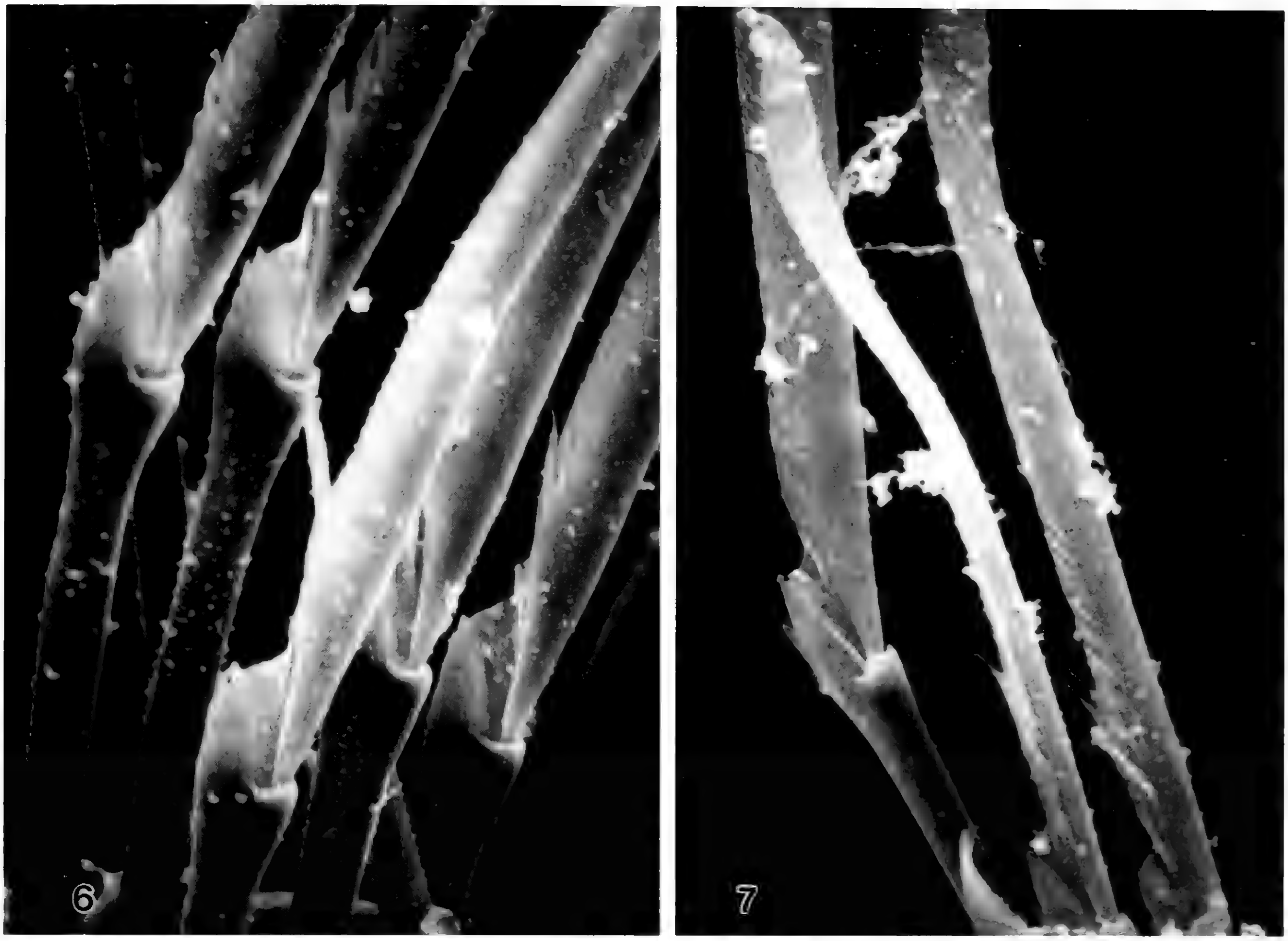
Figs. 1–3. *Syllides eburneus* new species. Slightly compressed living specimens. 1, Optical section at level of posterior eyes, dorsal view; 2, Optical section of foregut region of immature specimen, ventral view; 3, Surficial dorsal view.

pairs of eyes, one pair at bases of lateral antennae, second pair approximately same size as anterior pair, at posterior ventrolateral corners of prostomium. Tentacular segment with many large greenish vacuoles. Antennae, tentacular cirri, and dorsal cirri of first three setigers, pseudoarticulate; dorsal cirri of following setigers with up to 14 articles, large ivory white vacuoles in each article. Antennae, tentacular cirri and dorsal cirri about same length, caudal cirri longer. Palps approximately same length as prostomium. Ventral papilla of palp digitiform. Pygidial stylus 16 μm long, with a stereocillium at either side of the tip. Ventral cirrus of each parapod digitiform, extending slightly beyond setal lobe. Aciculum tapered slightly to rounded apex; a thin, curved, pointed aciculum also present in parapods of reproductive setigers. Simple setae denticulated on convex surface toward hemispherical apex (Fig. 4), usually only one per setiger, one or two thin, pointed, simple setae in last three setigers. Falciger blades unidentate, three to six in each parapod, in three distinct sizes, large blades ~48 μm long, serrated at base, medium blades ~36 μm long, shortest blades ~14 μm long. Apex of shafts of falcigers sometimes with a subapical tooth. Shafts of falcigers and simple setae of first three setigers thinner than those of following setigers. Capillary (swimming) setae begin on setiger 10. Lips of pharynx nipple-like with large vacuole in base. Pharynx/proventriculus length ratio ~1:1.4, proventriculus width/length ratio ~1:1.9; ventriculus in 5 with no apparent caeca. Muscles of proventriculus thin, lattice-like, approximately 35 rows posterior to proventricular organ, muscles not in rows anterior to organ. Gonads begin in setigers 7–9; 1–2 yolky, pink ova, 65 μm diameter, per gonad; sperm 8 μm long, pear-shaped with pointed acrosome constituting about one-tenth of that length.



Figs. 4, 5. *Syllides eburneus* new species. 4, Apical end of simple seta; 5, Falciger blades and apices of shafts.

Etymology.—Latin *eburneus*, like ivory or ivory colored, from Latin *ebur*, ivory;



Figs. 6, 7. 6, *Syllides setosa.* Apices of shafts and bases of blades of falcigers. SEM ×4000; 7, *Syllides eburneus* new species, Apices of shafts, and bases of blades of falcigers, SEM ×3600.

referring to the ivory colored vacuoles in the dorsal cirri.

Holotype.—USNM 054107. Massachusetts; Nahant Bay, North side of Egg Rock. Coarse shelly sand; 10 m depth. 12 Sep. 1976.

Paratype.—USNM 054108. Same location and date.

Observations.—Antenna and tentacular cirri of living sexual individuals were 0.19–0.22 mm long. The dorsal cirri were up to 0.5 mm long with as many as 14 articles; the terminal article bearing scattered stereocilia at its apex, and each of the other articles with a ring of such cilia apically, and a single stereocilium in the middle of the posterior surface as is characteristic of other species of the genus. Caudal cirri tend to coil and attain lengths of 1.9 mm. They consist of a few long articles, rarely more than eight, usually six. Ventral cirrus (Fig. 2) of each parapod 57–76 μm long. The digitiform palpal papilla was 12–17 μm long with a few stereocilia scattered over the margin of the apex and was directed medially from the ventral edge of each palp near the palpal base. This structure is characteristic of *Syllides* species and was referred to by Webster & Benedict (1884) as a "short conical cirrus" in their description of *S. convoluta* and as "small projecting papillae" in the (1887) description of *S. longocirrata.* It appears to be a sensory structure incapable of use in food manipulation. The palps of preserved members of the genus usually form a funnel in front of the prostomium with the palpal papilla directed inward, but in the living state, they frequently flatten so that the papillae project laterally. Greenish vacuoles (gold or amber in transmitted light), concentrated in a collar behind the tentacular cirri (Fig. 3), are characteristic of the genus. Frequently such vacuoles are also present behind the posterior eyes in the prostomium. The nuchal organs are present in a sulcus anterior to the collar. The thickened backs of the blades of the falcigers hook at the tip, but a subapical tooth is absent; the shafts are rather simple with the apical end extending as a single pointed prong sometimes with a subapical tooth (Figs. 5, 7) and the articular side with a flat termination that may be slightly elevated to either side. The ivory-white contents of the vacuoles in the antennae and dorsal cirri become transparent after a few days in specimens maintained in sea water, but can be used for preliminary identification while sorting fresh samples. The presence of two pairs of eyes (Fig. 1) is a primary character for the species (A posterior dorsal pair is absent), but in immature specimens, with fewer than 20 setigers, only the anterior pair of eyes (corresponding to ocelli) are pigmented. Gonads occurred from setiger 7–9 through 23–25 in specimens collected in October and November, with swimming setae beginning in setiger 10. The species seems to be an annual, breeding in late autumn and early winter. Intertidal specimens, collected in January and February at Liberty Point, Robbinston, Maine and Pagan Point, St. Andrews, New Brunswick, have consistently had fewer than 12 setigers.

Remarks,—The anterior pair of eyes of *S. eburneus* are always pigmented and relatively large, compared with the ocelli of most other species, and the posterior pair can be located on small immature specimens even though they may not be pigmented, but both pairs are pigmented and obvious in sexual individuals. *Syllides edentula* (Claparède, 1868), a Mediterranian species in which the dorsal cirri are not articulate, was described as having two pairs of eyes and the specimens from the Galapagos, tentatively identified as that species by Westheide (1974) only one pair. Westheide's specimens consisted of up to 12 setigers and some specimens were sexual. It would appear that the Mediterranean *S. edentula* and that from the Galapagos are not conspecific. Preserved specimens of *S. convoluta*, in which the eyes have lost pigmentation, and preserved *S. eburneus* are difficult to distinguish without comparative material. Both species belong to the group of *Syllides* species in which the proventriculus is located in setiger 5, simple setae do not taper to a point, and when sexual, measure 3–5 mm. The two species are very similar. Variability of characters used to distinguish different species may "in reality simply represent intraspecies variability" as noted by Reish (1977), but the eye pattern and the pigment in the dorsal and caudal cirri is a constant found in intertidal and subtidal *S. eburneus*. These characters are not restricted to populations and appear to the author to signify separate species.

Protractors and retractors of the foregut occur as muscle stays running from the body wall to attachment points on the pharynx and proventriculus of syllid polychaetes as illustrated and described by Malaquin (1893). The fine stays involved with eversion of the pharyngeal tip are weakly developed in the genus *Syllides*, while the protractors attached to the base of the pharynx and proventriculus are strongly developed and draw back the body wall so that the proventriculus comes to occupy many or even all of the anterior setigers. The number of setigers occupied by the various regions of the foregut is not a fixed character, and in preserved specimens varies according to degree of contraction of the anterior body region. The stays (retractors) at the base of the proventriculus tend to fix the posterior location of the organ although it may be pressed into the ventricular setiger. Such compression against the intestine may bulge the ventriculus giving the impression that ventricular caeca are present. The ratio of length of pharynx to proventriculus can be affected by the amount of eversion or expansion (Fig. 1) of the pharynx, but the relative lengths are of use in distinguishing some sympatric species in which setation is closely similar such as *S. benedicti* and *S. convoluta*. The proventricular organ is an eliptical epidermal gland containing a strongly azanophilous secretion which tends to harden and fracture in histological preparations. The intestine is fixed in position anteriorly, and thus, the ventriculus occurs in a specific setiger. The ventriculus occurs in setiger 5 of *S. convoluta* and *S. eburneus* and setiger 8 of *S. benedicti* and *S. longocirrata*.

Syllides eburneus is sympatric with *Ophryotrocha gracilis* Huth, 1934, *Schistomeringos caecus* (Webster & Benedict, 1884), and an eyeless species of *Protodorvillea* which are primarily subtidal species in the southern Gulf of Maine but are also commonly encountered in the intertidal of the northern part of the region.

Other Syllides *species from the Gulf of Maine*.—The method of collection of substrate does not allow for distinction between epipsammic and mesopsammic species. The various species of *Syllides* maintain themselves in the interstitial environment by wrapping around grains of sand, thus, few are encountered in the sea water rinses, and extraction with $MgCl_2$ is required. Substrate containing *S. benedicti* or *S. convoluta* routinely yielded 10–30 specimens per 8 ounce sand sample, thus over 100 individuals of each of these species have been examined and measured since the start of this study.

Syllides convoluta has been the most frequently encountered member of the genus in intertidal coarse sand between the southern shore of Cape Cod, Massachusetts and Georgetown, Maine. When freshly collected, the gut is dark purple to black in color, but in individuals maintained in clean sea water, it becomes reddish brown to tan. Fig. 3 of Banse (1971) is drawn from the syntype slides of *S. convoluta*. The membrane-like hood covering the tips of the acicula and simple setae is not apparent as a result of the clearing and mounting of these specimens. The apices of these structures in fresh, unfixed specimens tend to be round as a result of the constriction of the shaft near the apex and the visible presence of the hood over the tip, producing a ball-like shape. Ridges in the wall of the hood (forming the apex in Banse's fig. 3b in which the hood is not apparent) are evident under high magnification. The ridges in the wall of the hood of the aciculum are weakly produced as in Banse's fig. 3a, making the ball-like appearance of the apex more pronounced. (Oil immersion is required to see these ridges in *S. eburneus* and even then, they are frequently not apparent due to the smaller diameter of the distal ends of setae and acicula in this species.)

Syllides benedicti Banse, 1971 is the dominant intertidal interstitial member of the genus North of Georgetown, Maine. Fig. 6h of Banse (1971) shows a "basal spur" which is actually the thickened margin of the cutting edge of the blade of *S. benedicti*. Beyond this thickened region, the edge is very thin. Serrations are not evident on any of the blades. There are four blade sizes, usually two small (15–20 μm long), one or two medium (27–29 μm), two with thickened ridge on blade (56–58 μm), and two or three large (64–70 μm). San Martin *et al.* (1985) ascribed material from the playa de Toja of Spain to *S. benedicti*; however, although the serrations on the blades could be interpreted as intraspecific variation, the length of the largest falciger blades, and the pharynx/proventriculus length ratio, indicate a distinct and different species. The simple setae of *S. benedicti* are similar to those of *S. convoluta* and *S. eburneus*. Ability to see the ridges at the apex is a factor of the relative diameter of that region, and thus, the ridges are pronounced in *S. benedicti*, obvious in *S. convoluta* and almost indiscernible in *S. eburneus*. The gut of freshly collected specimens of *S. benedicti* has been brown or tan. The muscle stays anchoring the intestine of *S. benedicti* originate in setiger 9. Gonads sometimes were observed in setigers 10 and 11, but in most sexual individuals first occurred in 12. Ova were pink.

In the type description of *Syllides setosa* Verrill, 1882, the "dark colored" pharynx is described as "apparently unarmed, but sometimes showing a pale, oblong spot, that might be taken for a feeble tooth." Hartman (1942) reported that the type material could not be found, however a portion of a specimen from the "surface, July 26, 1883" and identified by Verrill as *S. setosa* (USNM 10080) is available and was examined for the present paper. Emerton's drawing of *S. setosa* (Hartman, 1944 Pl. 24, fig. 11) shows a structure in the pharynx that has been interpreted as a tooth by various workers in spite of Verrill's statement. From time to time, Verrill mentioned in his papers that drawings accompanying some of his papers had to be corrected [apparently as a result of artistic license on the part of the illustrator as has been noted by Banse (1969) for the figure of *Acrocirrus leidyi* Verrill, 1882 in Hartman (1944), and is evident in the dorsal cirri, setae and setation, absence of palps etc, in Emerton's figure of *S. setosa*]. Palps are not present, the articles of the dorsal cirri are few in number, the basal article is almost half the total length of the cirrus, and capillary setae begin on setiger 8 in Emerton's figure. Verrill further stated that "simple long setae begin singly on the eighth or ninth setigerous segment; fascicles of capillary setae appear on the eighteenth segment in our largest example." Verrill described some polychaete species from the drawings as noted by Hartman (1944) and it is possible that he may have used Emerton's figure and inadvertedly recorded eighteen instead of 8 in his description. However, neither 8 nor 18 seem to be correct. He stated that the description of *S. setosa* was "from life." At the end of the description, he mentions collecting specimens about 3 mm long "perhaps distinct from the above" with capillary setae beginning "on the tenth body segment." Banse (1971) noted that the simple setae of the specimens which he examined began in the first setiger and the capillary setae in the tenth as in the Nahant Bay individuals. The benthic specimens from Nahant Bay have been taken routinely since 1976 between March and November at which time divers could be safely employed. Specimens with gonads have ranged in length from 3.2–11.5 mm. Morphological differences which could not be accounted for by size (age or growth) were not evident in any of the more than forty specimens which were measured or examined. Careful measurements using a calibrated ocular micrometer have yielded no measurable differences other then total length and breadth. Verrill's statement that the smaller epitokes might belong to a different species may be correct, however, it is possible that the species lives and grows through more than one reproductive episode or season, adding setigers after the initial spawning. The heavily pigmented pharynx is very black in specimens over six mm long which might be an indication of aging. The simple setae of *S. setosa* are geniculate, flexing at the origin of the denticulations. The denticulated side terminates below the apical tooth in such a way that the apex often appears to be bidentate. The denticulated side is thin, much like the cutting edge of the falcigers and the thickened back hooks at the tip forming the apical tooth. The cutting edges of the falcigers are very thin, but ridges resulting in fine denticulation are modified producing two or three "basal spines" (Fig. 6). Subapical spines on the shafts of the falcigers are not distinctly visible with light nor Nomarski microscopy, but are demonstrable with SEM (Fig. 6). Imajima (1966) figured strong subapical serrations on the falciger shafts of *S. japonicus* and comparable serrations are obvious on the Pacific coast specimen (USNM 45264) from Lopez Island, Washington identified by Banse (1971), and are distinctly figured by Westheide (1974) for *S. japonica edentula* and by San Martin et al. (1985) for *Syllides* sp A. The notoacicula of *S. setosa* taper gently toward the apex which is expanded as a mushroom-like cap in dorsal and ventral view, but is flexed in lateral view. A slender accessory aciculum occurs adjacent to the notoaciculum in each parapod from setiger 10 through the intestinal region. Single slender, tapered neuroacicula with rounded apices also occur in these parapodia. Intact dorsal cirri consist of up to twenty articles. The proventriculus is anchored in setiger 8, which is occupied by the ventriculus. Perkins (1981) furnished a table of characters recorded for the "*S. japonicus*" complex of species. He concluded that possibly five species were present, and that *S. japonicus* Imajima 1966 "perhaps should not be a member of the genus," with which I concur, since Imajima specifically stated that "a subterminal middorsal tooth" was present in the pharynx. Unfortunately, this has never been confirmed. The sperm of *S. setosa* differ from those of other species in the present study in that the head is almost round, total length of head, about 4 μm and diameter slightly over 3 μm with a small pointed acrosome.

Syllides longocirrata has only been encountered in the intertidal of the Gulf of Maine at Pagan Point, along the seaward side of the causeway to Ministers Island, and at Joe's Point, St. Andrews, New Brunswick, in 25 years of routine meiofaunal sampling and has been associated with *S. benedicti* and *S. eburneus* at both locales. It falls into the same size range as *S. benedicti* and *S. setosa,* from which it can be readily distinguished by the distribution and morphology of the simple setae.

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Literature Cited

Banse, K. 1969. Acrocirridae n. fam. (Polychaeta Sedentaria).—Journal of the Fisheries Research Board of Canada 26:2595–2620.

———. 1971. A new species, and additions to the descriptions of six other species of *Syllides* Örsted(Syllidae: Polychaeta).—Journal of the Fisheries Research Board of Canada 28:1469–1481.

Claparède, E. 1868. Les annélides chétopodes du golfe de Naples.—Mémoires de la Société de Physique et d'Histoire naturelle de Genève 19:313–584.

Hartman, O. 1942. A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University.—Bulletin of the Bingham Oceanographic Collection 8:1–98.

———. 1944. New England Annelida. Pt.2. Including the unpublished plates by Verrill with reconstructed captions.—Bulletin of the American Museum of Natural History 82:327–344.

Imajima, M. 1966. The Syllidae (polychaetous annelids) from Japan (III). Eusyllinae.—Publications of the Seto Marine Biological Laboratory 14: 85–116.

Malaquin, A. 1893. Recherches sur les Syllidiens. Morphologie, anatomie, reproduction, développement.—Mémoires de Société des Sciences et Arts, Lille, pp. 1–477.

Perkins, T. H. 1981. Syllidae (Polychaeta), principally from Florida, with descriptions of a new genus and twenty-one new species.—Proceedings of the Biological Society of Washington 93:1080–1172.

Reish, D. J. 1977. The role of life history studies in polychaete systemtics. Pp. 461–476 *in* D. J. Reish and K. Fauchald, Essays on polychaetous annelids in memory of Dr. Olga Hartman. Allan Hancock Foundation, University of Southern California, Los Angeles.

San Martin, G., G. González, & E. López-Jamar. 1985. Aspectos sistemáticos y ecológicos sobre de las algunas especies de Sílidos (Polychaeta:Syllidae) de las costas gallegas.—Boletín del Instituto Español de Oceanografía 2:27–36.

Verrill, A. E. 1882. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England, and of some additions to the fauna of Vineyard Sound.—American Journal of Science 24:360–371.

Webster, H. E., & J. E. Benedict. 1884. The Annelida Chaetopoda from Provincetown and Wellfleet, Massachusetts.—Report of the United States Commissioner of Fisheries 1881. pp. 699–747.

———. 1887. The Annelida Chaetopoda from Eastport, Maine.—Report of the United States Commissioner of Fisheries 1885, pp. 707–755.

Westheide, W. 1974. Interstitielle Fauna von Galapagos. XI. Pisionidae, Hesionidae, Pilargidae, Syllidae (Polychaeta).—Mikrofauna des Meeresbodens 44:195–338.

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Luriculus minos (Platyhelminthes: Rhabdocoela: Luridae) from the Canary Islands

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Abstract.—Previously known from Crete (Eastern Mediterranean), the statocyst-bearing turbellarian *Luriculus minos* (Sterrer, 1992) was found in subtidal fine sand off the island of Gran Canaria (eastern Atlantic). Of six species of Luridae known, this is the first to be reported from outside its type locality. Significant biometric differences in the sclerotized structures of the reproductive system between the Cretan and Canarian populations suggest that contemporary means of dispersal are sufficient for island colonization, but insufficient to prevent this species from diverging into distinct populations.

Marcus (1950) described the marine microturbellarian *Lurus evelinae* which combined the general organization of Dalyellioida-Provorticidae with the possession of a statocyst, a unique feature that prompted Sterrer & Rieger (1990) to erect the family Luridae. Five additional species have been described to date (Sterrer & Rieger 1990, Sterrer 1992, Faubel et al. 1994), and the ultrastructure of spermiogenesis (Rohde & Watson 1993a), of sensory receptors (Rohde & Watson 1993b), and of the statocyst (Rohde et al. 1993) has been documented. Because *L. evelinae* was described by Marcus as having paired testes as well as separate germaria and vitellaria, Faubel et al. (1994) proposed the genus *Luriculus* for those species that have germovitellaria and a single testis. The family Luridae thus comprises the species *Lurus evelinae* Marcus, 1950, from the Atlantic coast of Brazil; *Luriculus castor* (Sterrer & Rieger, 1990) from the Atlantic coast of the United States; *Luriculus tyndareus* (Sterrer & Rieger, 1990) from Fiji; *Luriculus minos* (Sterrer, 1992) from Crete; and *Luriculus australiensis* Faubel et al., 1994, from New South Wales. *Lurus pollux* Sterrer & Rieger, 1990, also from the Atlantic coast of the United States, remains a *species inquirenda* since neither its vitellaria nor its testes are known. No species of Luridae has ever been reported outside its type locality.

During a brief collecting trip to Gran Canaria in February 1996 I found specimens that clearly belonged to *Luriculus minos* (Sterrer, 1992) but differed consistently in details of the male copulatory organ. Samples were collected by snorkeling over the shallow bottom and scooping sand into a bucket. Specimen extraction, documentation and analysis follow Sterrer (1971). This study is based on observation of live animals in squeeze preparation.

Luriculus minos (Sterrer, 1992)
(Figs. 1, 2; Table 1)

Localities.—Gran Canaria, Las Palmas, Playa de Las Canteras, fine sand with sparse seagrass (*Cymodocea nodosa*) at 2-3 m depth, collected 16 Feb 1996; 5 specimens. Arinaga, harbor basin, fine sand between and in *Cymodocea nodosa* at 4-5 m depth, collected 21 Feb 1996; 9 specimens.

Description.—Mature specimens (Fig. 1A) are 245–420 μm long (vs. 275–500 μm in Crete). The statocyst (Figs. 1B, 2C) contained 3 statoliths in 3 specimens and 4 statoliths in one, which gives a mean statolith

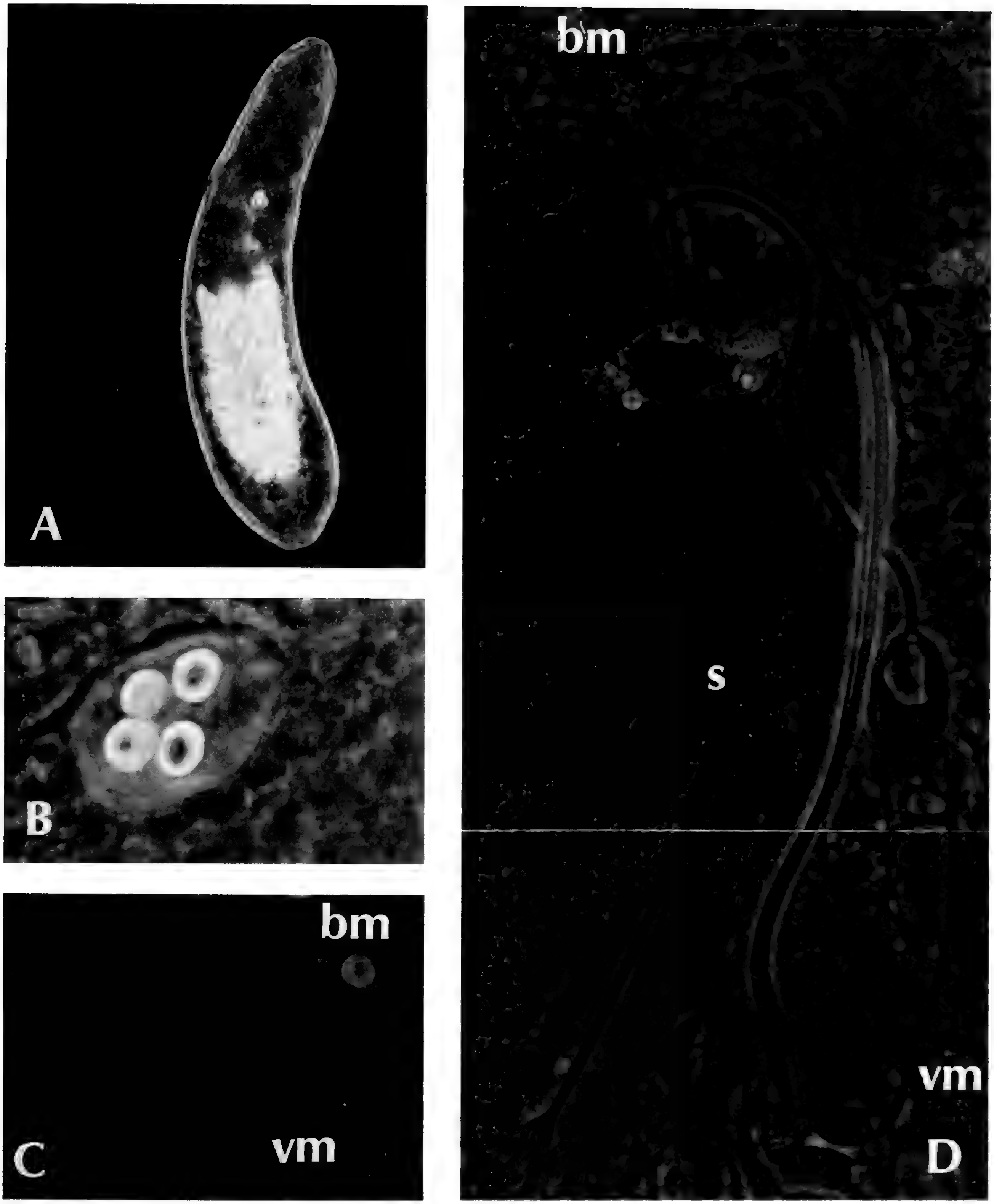

Fig. 1. *Luriculus minos.* A, Habitus of free-swimming adult; B, Statocyst; C, Bursa mouthpiece; D, Sclerotized parts of reproductive system. Phase contrast micrographs of living specimens from Gran Canaria. Abbreviations: bm bursa mouthpiece, pf perforation of vagina mouthpiece, s male copulatory stylet, vm vagina mouthpiece.

number of 3.25 for the sample (3.22 in Crete).

The complex sclerotized structures of the reproductive system, which consist of a male stylet, a vagina mouthpiece, and a bursa mouthpiece (Fig. 1D), are nearly identical between Cretan and Canarian specimens except for two consistent differences (Table

Table 1. Biometric comparison of vagina mouthpiece of individual specimens from the Canaries and Crete.

Specimens from			
Canaries	1	x (µm)*	y (µm)*
	2	13	65
	3	13	62
		13	60
Mean		13.00	62.33
Crete		x′ (µm)**	y′ (µm)**
	1	22	52
	2	21	52
	3	19	50
	4	20	51
Mean		20.50	51.25

* See Fig. 2A.
** See Fig. 2B.

1). The distal, funnel-shaped portion of the vagina mouthpiece (Fig. 2A; y) is 60–65 µm (mean 62.33 µm) long in Canarian specimens but only 50–52 µm (mean 51.25 µm) in those from Crete (Fig. 2B; y′). The "lateral perforation" is 13.0 µm long in Canarian specimens (Fig. 2A; x) vs. 19–22 µm (mean 20.5 µm) in Cretan specimens (Fig. 2B; x′). The distal width is the same in both populations. An additional yet less consistent difference is that the distal end of the male stylet, a prominent papilla made up of concentric rings, reemerges from the vagina mouthpiece not straight, as in most Cretan specimens, but always bent at a 90° angle. The proximal end of the vagina mouthpiece flares into a shallow saucer into which the bursa mouthpiece also opens. Shaped like a roll of unequal-sized coins, the bursa mouthpiece is considerably more robust in Canarian than in Cretan specimens (Figs. 1C, 2D–F).

Discussion.—Global distribution and speciation of marine interstitial sand fauna continue to pose the paradox of a high degree of taxonomic uniformity, including ap-

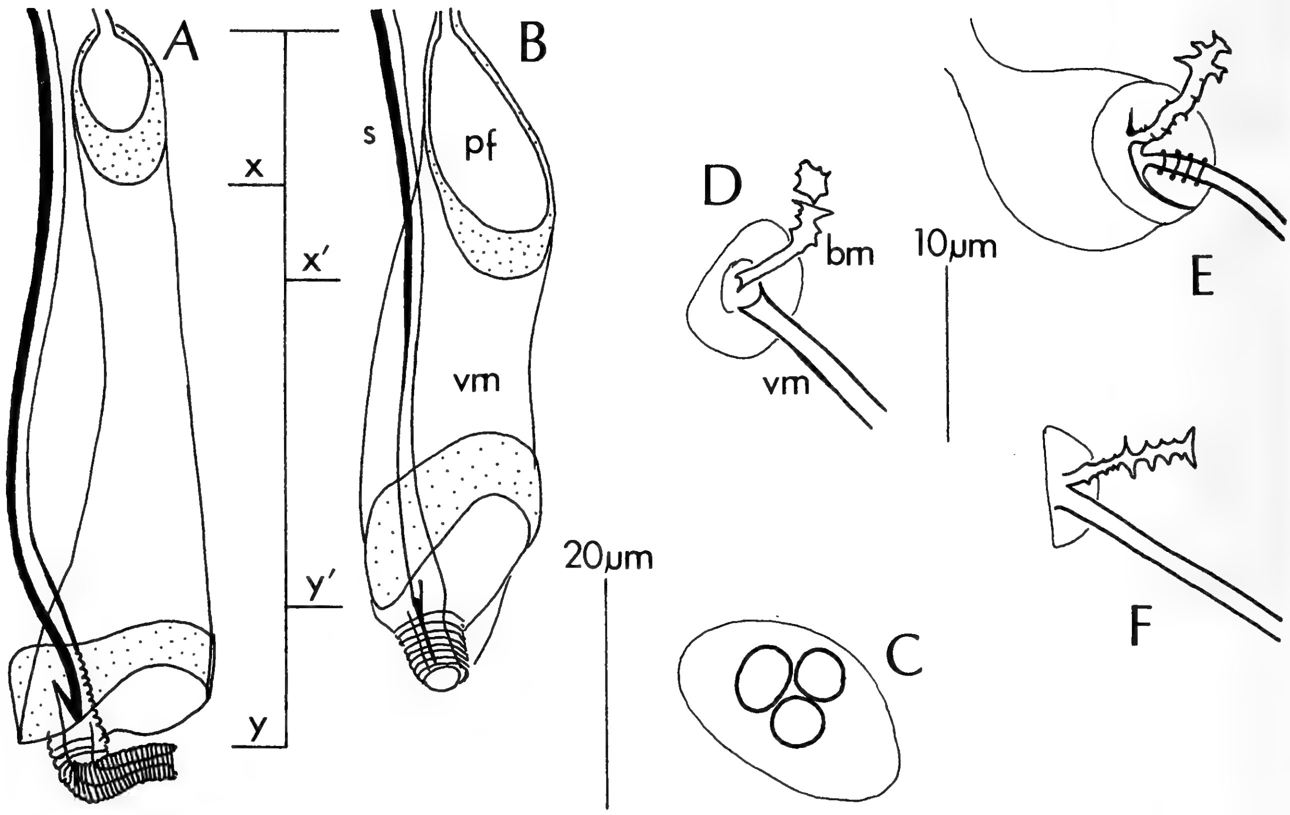

Fig. 2. *Luriculus minos*. A, distal portion of vagina mouthpiece of a specimen from Gran Canaria; B, the same of a specimen from Crete; C, statocyst; D–F, proximal end of vagina mouthpiece (vm) and bursa mouthpiece (bm) of 3 specimens from Gran Canaria. The scales apply to A–C and D–F, respectively. Abbreviations: bm bursa mouthpiece, pf perforation of vagina mouthpiece, vm vagina mouthpiece; x, y and x′, y′ indicate distances measured (see Table 1).

parent cosmopolitan species, combined with the absence of a ready dispersal mechanism. Some authors consider contemporary means of dispersal—such as passive water-column transport, rafting on drifting objects, or clinging to "marine snow"—as sufficient to explain all existing patterns (Giere 1993), whereas others invoke plate tectonics, coupled with very slow speciation rates, as the primary vector for global distribution (Sterrer 1973). Differences between populations of *Luriculus minos* at Crete and the Canary Islands suggest that contemporary means of dispersal must have been sufficient for this species to colonize islands such as Crete and the Canaries, but not powerful enough to prevent its fragmentation into significantly different populations.

Acknowledgments

I am grateful to Dr. Angel Luque Escalona and Lic. Javier Pérez Fernández of the Universidad de Las Palmas for providing lab facilities and helping with sample collection.

Literature Cited

Faubel, A., K. Rohde, & N. A. Watson. 1994. Sandy beach meiofauna of Eastern Australia (Southern Queensland and New South Wales). II. *Luriculus australiensis*, gen. et sp. nov. (Luridae: Dalyelliida: Platyhelminthes).—Invertebrate Taxonomy 8:1009–1015.

Giere, O. 1993. Meiobenthology. Springer-Verlag, Berlin, 328 pp.

Marcus, E. 1950. Turbellaria Brasileiros (8).—Boletins da Faculdade de filosofia, ciências e letras, Universidade de São Paulo (Zoologia) 15:5–191.

Rohde, K., & N. A. Watson. 1993a. Ultrastructure of spermiogenesis and sperm of an undescribed species of Luridae (Platyhelminthes: Rhabdocoela).—Australian Journal of Zoology 41:13–19.

———. 1993b. Ultrastructure of sensory receptors of an undescribed species of Luridae (Platyhelminthes: Rhabdocoela).—Australian Journal of Zoology 41:53–65.

———, & A. Faubel. 1993. Ultrastructure of the statocyst in an undescribed species of Luridae (Platyhelminthes: Rhabdocoela: Luridae).—Australian Journal of Zoology 41:215–224.

Sterrer, W. 1971. On the biology of Gnathostomulida.—Vie et Milieu, Suppl. 22:493–508.

———. 1973. Plate tectonics as a mechanism for dispersal and speciation in interstitial sand fauna.—Netherlands Journal of Sea Research 7: 200–222.

———. 1992. *Lurus minos*, the first species of Luridae (Turbellaria: Rhabdocoela) from the Old World.—Proceedings Biological Society Washington 105:636–639.

———, & R. M. Rieger. 1990. New species of the statocyst-bearing marine dalyellioid genus *Lurus* Marcus (Luridae nov. fam., Turbellaria-Rhabdocoela).—Cahiers de Biologie Marine 31:485–500.

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Selection of a type species for *Farfantepenaeus* Burukovsky (Crustacea: Decapoda: Penaeidae)

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Abstract.—*Penaeus brasiliensis* Latreille, 1817, is selected as the type species of the subgenus *Farfantepenaeus* Burukovsky, of the genus *Penaeus.*

The complex penaeid shrimp genus *Penaeus* Fabricius, 1798, has over time, been divided into a number of subgenera, including the nominate subgenus *Penaeus, Melicertus* Rafinesque-Schmaltz, 1814, *Litopenaeus* Pérez Farfante, 1969, *Fenneropenaeus* Pérez Farfante, 1969, and *Farfantepenaeus* Burukovsky, 1972.

In a paper on the systematics and distribution of species of *Penaeus,* Burukovsky (1972) proposed the new subgenus *Farfantepenaeus,* included in it the species *P. duorarum, P. brasiliensis, P. aztecus, P. californiensis, P. brevirostris,* and *P. paulensis,* but did not designate a type species. According to Article 13b of the International Code of Zoological Nomenclature (1985), any genus-group name published after 1930 must be accompanied by the fixation of a type species, to make the name available. This brief note is published to correct this situation.

Family Penaeidae
Genus *Penaeus* Fabricius, 1798
Farfantepenaeus, new subgenus

Penaeus (Farfantepenaeus) Burukovsky, 1972:10, 13, 17.—Pérez Farfante, 1988:9.

Type species: By present designation, *Penaeus brasiliensis* Latreille, 1817:156. Type locality: Brazil ["côtes du Brésil"].

Literature Cited

Burukovsky, R. N. 1972. Nekotorye voprosy sistematiki i rasprostraneniya krevetok roda *Penaeus.* Rybokhozyaistvennye issledovaniya v Atlanticheskom okeane. [Some problems of the systematics and distribution of shrimps of the genus *Penaeus*].—Trudy AtlantNIRO, Kaliningrad 42:3–21.

Fabricius, J. C. 1798. Supplementum Entomologiae Systematicae. Hafniae, 572 pp.

Latreille, P. A. 1817. Pénée. *In* Nouveau dictionnaire d'histoire naturelle applique aux arts, principalement l'agriculture et l'economie rurale . . . Volume 25:152–156, Paris. Deterville.

Pérez Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus.*—Fisheries Bulletin, U.S. 67(3):461–591.

———. 1988. Illustrated key to penaeoid shrimps of commerce in the Americas.—NOAA Technical Report NMFS 64:1–32.

Rafinesque-Schmaltz, C. S. 1814. Précis des découvertes et travaux somiologiques de M. r. C. S. Rafinesque-Schmaltz entre 1800 et 1814 ou choix raisonné de ses principales découvertes en zoologie et en botanique, pour servir s'introduction à ses ouvrages futurs. Palermo, Royale Typographie Militaire, 55 pp.

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110(1):155–156. 1997.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 30 September 1996 in Vol. 53, Part 3 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.

Case No.	
2978	*Plumularia* Lamarck, 1816 (Cnidaria, Hydrozoa): proposed conservation by the designation of *Sertularia setacea* Linnaeus, 1758 as the type species.
2935	*Lirobarleeia* Ponder, 1983 (Mollusca, Gastropoda): proposed designation of *Alvania nigrescens* Bartsch & Rehder, 1939 as the type species.
2977	*Arca pectunculoides* Scacchi, 1834 and *A. philippiana* Nyst, 1848 (currently *Bathyarca pectunculoides* and *B. philippiana*; Mollusca, Bivalvia): proposed conservation of the specific names.
2992	*Parapronoe crustulum* Claus, 1879 (Crustacea, Amphipoda): proposed conservation of the specific name.
3003	*Meristella* Hall, 1859 (Brachiopoda): proposed designation of *Atrypa laevis* Vanuxem, 1842 as the type species.
2960	*Hemidactylus garnotii* Duméril & Bibron, 1836 (Reptilia, Squamata): proposed conservation of the specific name.
2969	*Bombycilla cedrorum* Vieillot, [1808] and *Troglodytes aedon* Vieillot, [1809] (Aves, Passeriformes): proposed conservation of the specific names.

The 124th Annual Meeting of the Biological Society of Washington will be held on Thursday, 8 May, 1997, at 11:00 in the Waldo Schmitt Room, National Museum of Natural History, Washington, D. C.

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 September 1996 in Vol. 53, Part 3 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Opinion No.

1843. *Stictostroma* Parks, 1936 (Porifera, Stromatoporoidea): conserved, and *Stictostroma gorriense* Stearn, 1995 designated as the type species.
1844. *Aplysia juliana* Quoy & Gaimard, 1832 (Mollusca, Gastropoda): specific name conserved.
1845. *Tropidoptera* Ancey, 1889 (Mollusca, Gastropoda): *Endodonta wesleyi* Sykes, 1896 designated as the type species.
1846. *Eophacops* Delo, 1935 and *Acernaspis* Campbell, 1967 (Trilobita): conserved.
1847. *Diplocentrus mexicanus* Peters, 1861 (Arachnida, Scorpiones): rediscovered holotype confirmed as the name-bearing type.
1848. *Cubaris murina* Brandt, 1833 (Crustacea, Isopoda): generic and specific names conserved.
1849. *Livoneca* Leach, 1818 (Crustacea, Isopoda): the original spelling confirmed as correct, and the spelling *Lironeca* rejected.
1850. *Nepa rustica* Fabricius, 1781 and *Zaitha stollii* Amyot & Serville, 1843 (currently *Diplonychus rusticus* and *Belostoma stollii*; Insecta, Heteroptera): specific names conserved.
1851. XANTHOLININI Erichson, 1839 and QUEDIINI Kraatz, [1857] (Insecta, Coleoptera): given precedence over some senior synonyms; *Quedius* Stephens, 1829: *Staphylinus levicollis* Brullé, 1832 designated as the type species.
1852. *Melissodes desponsa* Smith, 1854 and *M. agilis* Cresson, 1878 (Insecta, Hymenoptera): specific names conserved.
1853. *Xerammobates* Popov, 1951 (Insecta, Hymenoptera): *Ammobates oxianus* Popov, 1951 designated as the type species.
1854. *Rhabdomeson* Young & Young, 1874 (Bryozoa): *Rhabdomeson progracile* Wyse Jackson & Bancroft, 1995 designated as the type species.
1855. *Agonus* Bloch & Schneider, 1801 (Osteichthyes, Scorpaeniformes): conserved; and AGONIDAE Kirby, 1837 (Insecta, Coleoptera): spelling emended to AGONUMIDAE, so removing the homonymy with AGONIDAE Swainson, 1839 (Osteichthyes, Scorpaeniformes).
1856. *Lycognathophis* Boulenger, 1893 (Reptilia, Serpentes): conserved.

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Review of the genus *Schizopathes* (Cnidaria: Antipatharia: Schizopathidae) with a description of a new species from the Indian Ocean

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Abstract.—The genus *Schizopathes* is reviewed and its relationship with other genera in the family is discussed. The genus contains two previously described species, *S. affinis* Brook and *S. crassa* Brook, and one new species described here as *S. amplispina. Schizopathes amplispina* can be differentiated from *S. affinis* and *S. crassa* by its larger spines and more closely spaced pinnules. *Schizopathes amplispina* is known only from the type locality in the western Indian Ocean.

In the course of examining the antipatharian collections in the National Museum of Natural History (USNM) at the Smithsonian Institution, several colonies of a species of *Schizopathes* were located which upon closer study were found to represent a new species. This is the first new species added to the genus since its establishment by Brook in 1889. The type specimens, which were collected by the R/V *Anton Brunn* in the Indian Ocean east of Madagascar, are deposited at the Smithsonian Institution, Washington, DC.

Schizopathidae (Brook, 1889)

Diagnosis.—Antipatharians with polyps transversely elongated and subdivided by "mesogloeal septa" into three sections, each bearing one pair of tentacles (Brook 1889). Middle section of each polyp with sagittal tentacles, mouth, stomodeum (actinopharynx), and six primary and four secondary mesenteries. Lateral sections of each polyp with pair of lateral tentacles and single transverse mesentery containing reproductive cells.

Remarks.—The Schizopathinae was originally established by Brook as one of two subfamilies in the family Antipathidae. Included in the subfamily were the genera *Schizopathes, Bathypathes, Cladopathes,* and *Taxipathes.* The basis for subfamily recognition by Brook was the division of each polyp along the transverse axis into three sections each bearing one pair of tentacles, and which Brook regarded as dimorphic zooids (i.e., two gonozooids and one gastrozooid for each polyp). In *Schizopathes* these divisions of a polyp are associated externally with "peristomal involutions" (constrictions of the coenenchyme between the sagittal and lateral tentacles) and internally with "mesogloeal septa" (also referred to as peristomal partitions by later workers) placed at right angles to the transverse axis of the polyp (Brook 1989). Most later workers have not considered this a case of true dimorphism but rather one of polyp modification and specialization, with the reproductive tissues being isolated in the lateral chambers of the coelenteron (Thompson 1905, van Pesch 1914). There are other antipatharian genera such as *Parantipathes* in which the polyps are elongated along the transverse axis and in which the reproductive organs are located at the distal and proximal ends of the primary transverse mesenteries; however, all the genera originally placed in the subfamily Schizopathinae presumably had "mesogloeal septa" which further isolated the distal and proximal coelenteral chambers of each polyp. It should be noted, however, that Brook did not provide as detailed a description of the internal anatomy of the polyps of *Bathypathes, Cladopathes,* and *Taxipathes* as he did for *Schizopathes.* Although the polyps of these genera are elongated transversely (in some cases to a greater degree than that occurring in *Schizopathes*), the occurrence of internal "mesogloeal septa" was not specifically mentioned by Brook. Brook did report, however, that the polyps of *Bathypathes* and *Taxipathes,* like those of *Schizopathes,* possessed 10 mesenteries, six primary and four secondary; the number, location and arrangement being identical to that occurring in the family Antipathidae. The polyps of *Cladopathes* were described as having six primary mesenteries but no secondaries.

In his revision of the order, Schultze (1896) divided the family Antipathidae into three subfamilies based on the number of mesenteries in the polyps; the Dodekamerota with 12 mesenteries, the Dekamerota with ten mesenteries, and the Hexamerota with six mesenteries. The Dekamerota were further divided into two unnamed tribes, one of which contained *Schizopathes, Bathypathes,* and *Taxipathes.* The genus *Cladopathes* was placed by Schultze (1896) in the new subfamily, the Hexamerota. van Pesch (1914) renamed Schultze's Dekamerota as the Heterotaeniales and established the name Ptuchaephora for the tribe containing *Schizopathes, Bathypathes* and *Taxipathes.* Other workers, however, have taken the opposite approach and elevated the Schizopathinae to the family level (Hickson 1907, Pax 1918). With the recent removal of the Dendrobrachiidae from the Antipatharia (see Opresko & Bayer 1991), family level distinctions within the order need to be reevaluated. Based on the pronounced transverse elongation of the polyps, the recognition of the Schizopathidae as a distinct family seems appropriate; however, further investigation is needed into the importance of the "mesogloeal septa" as a family level character.

Schizopathes Brook, 1889

Schizopathes Brook, 1889:146.—Hickson, 1907:6.—Cooper, 1909:308.—Pax, 1918: 468.

Bathypathes.—van Pesch 1914:27 (part).—Pasternak, 1977:157 (part).—Zhou & Zou, 1992:46 (part).

Type species.—*Schizopathes crassa* Brook, 1989. Brook (1889) does not specifically designate a type species for any of his new genera; however, he makes the statement that the type species of all but one of the genera were examined microscopically (Brook 1889:75). Of the three species that Brook referred to *Schizopathes,* only *S. crassa* was evaluated histologically (Brook 1889:46); therefore, by inference, it can be concluded that *S. crassa* is the type species of the genus.

Diagnosis.—Colony monopodial, unbranched, but pinnulate. Pinnules simple, arranged alternately and bilaterally; decreasing in length towards top of corallum. Basal section of stem not pinnulated, but modified to serve as holdfast in soft sediments; upper part laterally compressed in plane at right angles to plane of pinnules; lower part curved away from polyp side of colony, sometimes spatula-like near base. Spines usually simple (rarely bifid), smooth, and triangular in lateral view. Polyps crowded, arranged in a single row usually on the upper side of the pinnules, and elongated transversely; transverse diameter (from distal side of distal lateral tentacles to proximal side of proximal lateral tentacles) usually greater than 2.5 mm.

Remarks.—Brook originally placed three species in *Schizopathes, S. crassa, S. affinis,* and *S. conferta.* The type material of the first two species consisted of complete colonies with the unique basal holdfast intact.

Schizopathes conferta was described from an incomplete specimen in which the bottom and top parts of the corallum were missing. Although the polyps of *S. conferta* were described by Brook as being very similar to those of the other two species in the genus, the absence of the holdfast, and the very narrow internal angle formed by the lateral rows of pinnules suggest that *S. conferta* may actually be a specimen of the related genus *Bathypathes* in which the corallum is attached permanently to the substrate by a basal plate. Brook stated that he could not determine if *S. conferta* had been attached by a basal plate.

Excluding *S. conferta* from consideration, features that are consistent among species of this genus are: the unique basal holdfast; the regular decrease in the length of the pinnules higher up on the corallum; the simple, triangular, laterally compressed spines; and the transversely elongated polyps. Features which have been used to separate species of the genus include the size of the polyps and spines and the density of the pinnules. In all *Schizopathes* species there is a strong tendency for the pinnule density to increase towards the top the corallum and for the spines and polyps to be largest along the distal parts of the pinnules; however, these characteristics vary considerably from specimen to specimen and even with the same colony.

It should be noted that some earlier workers such as van Pesch (1914) relegated the genus *Schizopathes* to subgeneric status within *Bathypathes,* and Pasternak (1977) even synonomized two of the three species described by Brook (*S. crassa* and *S. affinis*) with *Bathypathes patula* Brook. The latter decision was based on the assumption that the type of holdfast formed by the colony was simply a function of the type of substrate on which the planulae settled. Although there are similarities in terms of pinnulation pattern and size of the polyps and spines, the very distinctive basal holdfast of all the species of *Schizopathes* (that have been described from complete specimens) would argue for their being recognized as a separate genus.

Schizopathes crassa Brook, 1889
Fig. 1

Schizopathes crassa Brook, 1889:147–148, pl. VIII, figs. 1–5.
Bathypathes (Schizopathes) affinis.—van Pesch, 1914:27–29 (part).
?*Schizopathes crassa.*—Hickson, 1907:6 (incomplete colony).

Material examined.—SW Indian Ocean, S of Tasmania, 58°06′S, 144°55′E, 3089–3164 m, USNS *Eltanin* sta. 126, 1 Oct. 1965 (1 specimen, USNM 78796).—Antarctica, NW of Balleny Ids, 64°59′S, 160°36′E, 2836–2864 m, USNM *Eltanin* sta. 1957, 7 Feb. 1967 (1 specimen, USNM 78820).—SE Indian Ocean, 55°01′S, 39°55′E, 2886–3040 m, USNS *Eltanin* sta. 1537, 8 Feb. 1966 (2 specimens, USNM 78810).

Description.—Colony monopodial, unbranched, but pinnulate (Fig. 1B). Pinnules simple, arranged alternately in two lateral rows along the stem, and decreasing in length from base to apex. Maximum length of pinnules about 20 cm on colonies 30 cm tall (total length of stem) and about 30 cm on colonies 55 cm tall. Pinnules in each row usually 10–12 mm apart on lower parts of stem; becoming more closely spaced towards apex of corallum. Interior angle formed by lateral rows of pinnules 180° over most of corallum; <180° for lowermost pair, and greater or less than 180° for several pairs at top of corallum. Distal angle of pinnules 55–60° on lower parts of corallum but ≤45° near apex.

Spines small, triangular and compressed; typically 0.06–0.08 mm tall (from midpoint of base to apex; range, 0.04–0.1 mm); arranged in rows with varying degrees of regularity; 3–5 spines per millimeter. Largest spines usually on polyp side of pinnules; abpolypar spines slightly smaller than polypar spines.

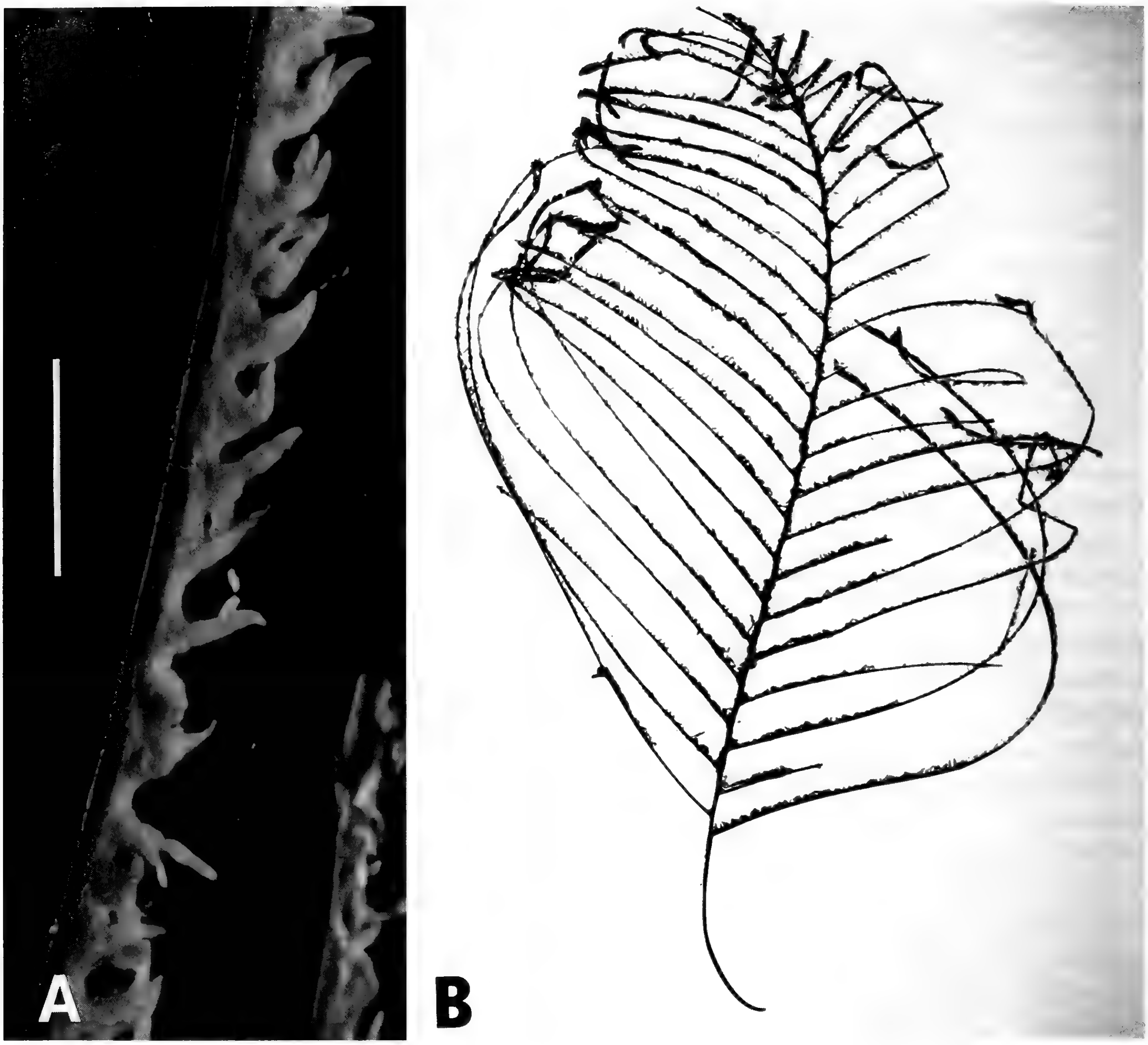

Fig. 1. *Schizopathes crassa* Brook, USNM 78820. A. Pinnule with polyps; scale equals 5 mm. B. Corallum; height 30 cm.

Polyps (Fig. 1A) 4–6 mm in transverse diameter on pinnules; ≤4 mm at basal end of pinnules and on stem. Polyps arranged uniserially, with two per centimeter.

Discussion.—The unpinnulated section of the stem of the type specimen of *S. crassa* was reported by Brook (1889) to be only 3.3 cm long. The unpinnulated stalks of the *Eltanin* specimens range from 6 to 8 cm. The maximum size of the spines in both the type and in the *Eltanin* specimens is about 0.1 mm. According to Brook (1889), the rows of spines on the flattened part of the stalk of the type are confined to the narrow anterior edge; however, in the *Eltanin* specimens they are present on the wider sides as well.

Brook (1889) reported that the "zooids" in the type specimen measured 3 mm across the base of the tentacles, and the illustrations given of the type indicate that the total transverse width of the polyps is 6 mm. Polyps of a similar size (commonly 5 mm, but up to 6 mm in transverse diameter) are present on the pinnules of the specimen from *Eltanin* sta. 126, with smaller polyps (as small as 3 mm or less) occurring at the base of the pinnules and on the stem. In the specimens from *Eltanin* sta. 1957 and 1537, most of the polyps on the pinnules are 4–

4.5 mm and only a few are as large as 5 mm. As in the case with the other Eltanin specimen, smaller polyps (3–3.5 mm) occur at the base of the pinnules and on the stem.

The specimen of *S. crassa* from *Eltanin* sta. 126 (USNM 78796) is 56 cm tall with pinnules up to 31 cm long. It is unique in that the pinnules in each lateral row are spaced up to 16 mm apart on the lowermost part of the corallum and as much as 12 cm apart near the apex of the corallum. In comparison, the pinnules in the type and in the other *Eltanin* specimens are 10–12 cm apart on the lower part of the stem and 7–8 cm apart near the apex of the corallum.

Comparisons.—See description of *Schizopathes affinis* Brook.

Distribution.—The type locality, 35°39′S, 50°47′W, is off Montevideo, Uruguay (*Challenger* sta. 323). All the *Eltanin* specimens were collected in the southern oceans.

Schizopathes affinis Brook, 1889
Fig. 2

Schizopathes affinis Brook, 1889:148–150, pl. IX, figs. 1–6.—Cooper, 1909: 310, pl. 41, fig. 1–2.

Bathypathes (*Schizopathes*) *affinis.*—van Pesch 1914:27 (part).—Zhou & Zou, 1992:46–47.

Material examined.—Western Atlantic, Bahamas, Tongue of the Ocean, 25°16.00′ N, 77°45.3′ W, 2780 m, R/V *Columbus Iselin* sta. 172, 8 Feb. 1974 (2 specimens, USNM 59011).—Western Atlantic, Bahamas, Tongue of the Ocean, 25°16′ N, 77°42.16′ W, 2911 m, R/V *Columbus Iselin* sta. 288, 11 Nov 1974 (1 specimen, USNM 59009).

Description.—Colony monopodial, unbranched, but pinnulate (Fig. 2B). Pinnules simple, up to 20 cm long in colonies 30 cm tall, and arranged alternately in two lateral rows along stem; decreasing in length toward apex of corallum; and inclined upward (distal angle formed with stem ~60° for lowermost pairs, decreasing to 30° or less for those near apex). Lowermost pinnules mostly 8–10 mm apart in each lateral row, decreasing to 5–6 mm apart near top of corallum. Interior angle formed by pinnules in opposing rows generally 180°.

Spines small, triangular and compressed; arranged, with varying degrees of regularity, in axial rows (4–5 rows visible in lateral view); 0.15–0.20 mm apart in each row (about six per millimeter). Spines usually 0.03–0.04 mm tall (from midpoint of base to apex), but occasionally up to 0.08 mm near the distal end of pinnule. Abpolypar spines equal to or slightly smaller than polypar spines.

Polyps (Fig. 2A) uniserially arranged, on front or upper side of pinnules; 3.0–4.5 mm in transverse diameter; about three polyps per centimeter. Polyps slightly reduced in size at base of pinnules and on stem.

Discussion.—Several features of the type specimen of *S. affinis,* including the pronounced triangular shape of the corallum, the relatively long unpinnulated stalk, and the very distinctly curved hook at the end of the holdfast, are also evident in two of the *Columbus Iselin* specimens. The unpinnulated stalk is 12 cm in the type specimen and 10–12 cm in the *Columbus Iselin* specimens from sta 172, but only 7.5 cm in the specimen from *Columbus Iselin* sta. 288. Other features of the type, such as the size of the spines and polyps, were not specifically described by Brook; however, based on the illustrations given, it can be estimated that the spines in the type are not more than 0.06 mm and the polyps not more than 4.5 mm in transverse diameter. In the *Columbus Iselin* material, the spines on the pinnules are mostly 0.03–0.04 mm, although in places they reach 0.08 mm, and the polyps (only present in the specimen from *Columbus Iselin* sta. 288) are 2.4–3.2 mm in transverse diameter.

Brook (1889) states that the spines on the flattened section of the unpinnulated stalk are confined to the wider lateral sides. In the *Columbus Iselin* material, the spines occur on the lateral sides on the upper portion

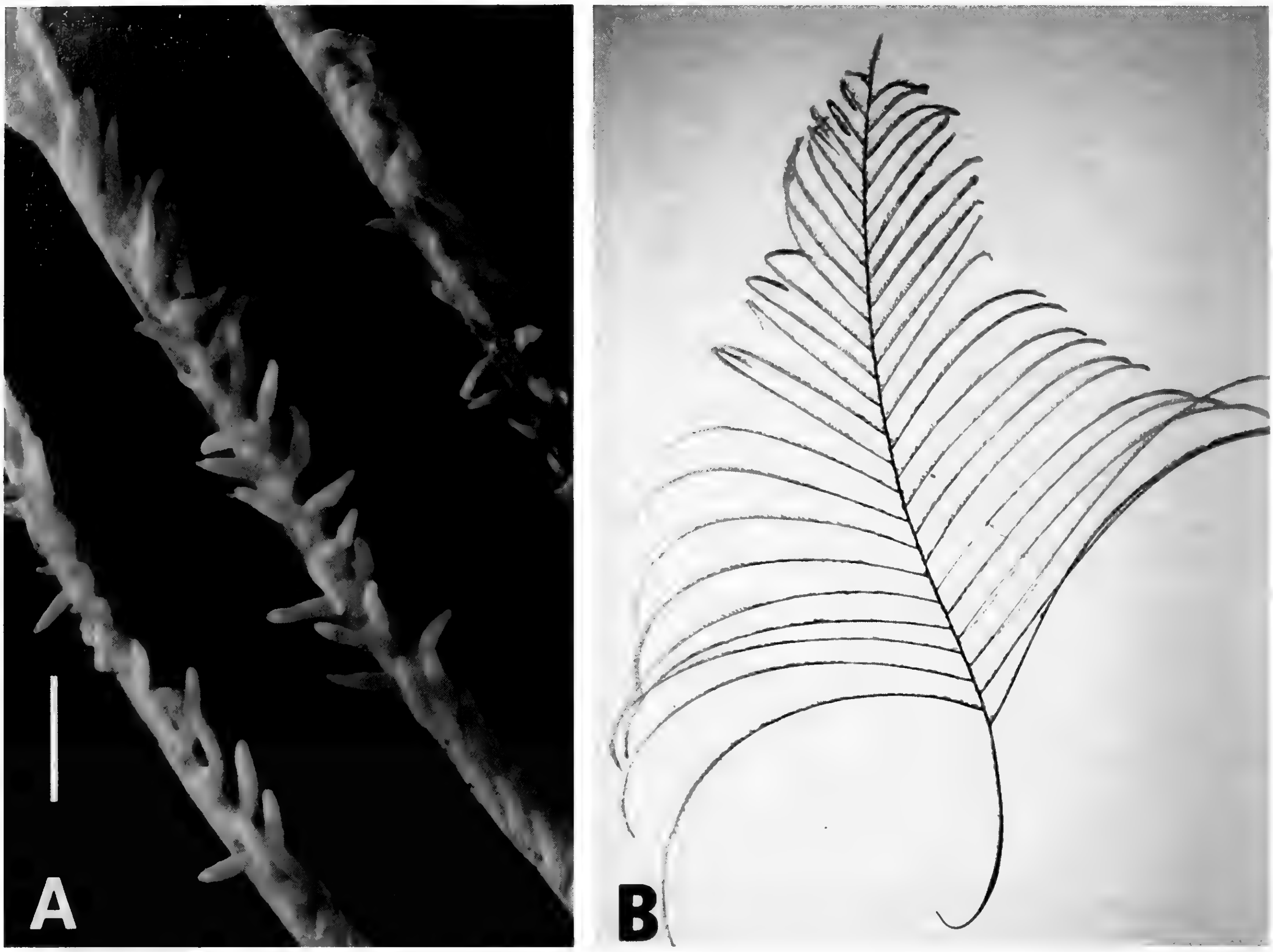

Fig. 2. *Schizopathes affinis* Brook, USNM 59009. A. Pinnule with polyps; scale equals 3 mm. B. Corallum; height 28.5 cm.

of this section of the stalk, but along the narrow front edge further down towards the base.

Comparisons.—According to Brook (1889), *S. affinis* can be differentiated from *S. crassa* by a greater curvature in the hooked base, and by a more pronounced triangular shape caused by a more abrupt decrease in length of the pinnules from the lower to the upper parts of the corallum. The *Columbus Iselin* and *Eltanin* specimens tend to follow this pattern. For colonies of comparable size (about 30 cm), the ratio of the length of the lowermost pinnules to those 10 cm higher up on the axis is less than 0.5 in *S. affinis* and more than 0.5 in *S. crassa.* An analysis of a much larger suite of specimens would be needed to determine if this pattern is consistent for specimens of all sizes. From the limited number of specimens examined, it appears that colonies of *S. crassa* reach a larger maximum size then *S. affinis* (i.e., >50 cm in height).

The major features that can be used to distinguish *S. affinis* from *S. crassa* are the size of the spines and polyps. The pinnular spines in *S. affinis* are typically 0.03–0.04 mm, but occasionally reach 0.08 mm. In contrast, the pinnular spines in *S. crassa* are usually 0.06–0.08 mm and sometimes as large as 0.10 mm.

Brook (1889) reported that the polyps of *S. affinis* were smaller than those in *S. crassa.* Although polyp size was not specifically mentioned in the type description of *affinis,* the type illustrations do indicate a slight difference in polyp size between the two species (maximum of 6 mm in *crassa* and 4.5 mm in *affinis*). In the *Eltanin* specimens of *S. crassa* the polyps on the pinnules are 4–6 mm in transverse diameter, whereas those in the *Columbus Iselin* specimens of *S. af-*

finis are not larger than about 3.2 mm. These data support Brook's conclusions.

Brook (1889) also states that the spines in *S. affinis* are more numerous than those in *S. crassa.* Although estimates made from the type illustrations indicate a spine density of about 3/mm in both species, the *Columbus Iselin* and *Eltanin* specimens indicate a density of about 6/mm for *S. affinis* and 3–5/mm for *S. crassa.*

Distribution.—Cosmopolitan. Four of the type specimens and the colony described by van Pesch (1914) were collected in the western Pacific, off the Banda Islands. The fifth type specimen was obtained west of the Admiralty Islands. The species has also been reported from the Indian Ocean (Cooper 1909) and the South China Sea (Zhou & Zou 1992). The *Columbus Iselin* specimens were collected in the Western Atlantic, near the Bahama Islands.

Schizopathes amplispina, new species

Figs. 3–4

Material examined.—Indian Ocean, east of Madagascar, 21°18′S, 36°18′E, 1510–1600 m, R/V *Anton Brunn* sta. 399C, 10 Oct. 1964 (3 specimens; holotype USNM 96966, paratypes USNM 96967).

Diagnosis.—Corallum monopodial, unbranched, but pinnulate (Fig. 3). Pinnules simple, arranged alternately and bilaterally; spaced 6–8 mm apart in each row on lower section of stem, decreasing to 2–5 mm apart near apex. Spines on basal half of pinnules small, triangular and compressed; 0.04–0.10 mm from midpoint of base to apex (Fig. 4D); becoming larger (0.12–0.18 mm) and less symmetrical on upper parts of pinnules (Figs. 4A–B). Polyps transversely elongated; 3.0–3.5 mm from distal side of distal lateral tentacles to proximal side of proximal lateral tentacles; arranged uniserially, with about three polyps per centimeter.

Description.—Holotype about 42 cm tall; unpinnulated stalk 8 cm; tip of stem and basal end of stalk missing. Stem compressed laterally in plane at right angles to plane of pinnules; most strongly compressed along midsection of unpinnulated stalk (axis about 1 mm wide across anterior edge, but 3.5 mm along sides). Unpinnulated stalk sigmoidal; upper portion curved slightly away from polyp side of corallum, midsection curved strongly anteriorly, lower section curved strongly posteriorly. Basal end of holdfast pointing away from abpolypar side of corallum; flattened, spatula-like near tip, with ridge extending down center of one side.

Lowermost pinnules 24 cm long; pinnules 10 cm higher on corallum about 19 cm long; those 10 cm higher about 16 cm; and smallest pinnules near apex 2–3 cm long. Pinnules spaced 6–8 mm apart on lower parts of corallum, decreasing to 2–3 mm apart near apex; inclined upward (distal angle formed with stem 55–60° for lowermost pairs, decreasing to about 30° at apex). Largest pinnules about 1.0 mm in diameter at base and 0.5–0.6 mm in diameter near midpoint. Rows of pinnules nearly opposite (interior angle about 180°) over most of corrallum; lowermost pair forming acute interior angle; uppermost pairs anterolateral or posterolateral in position.

Polypar spines on basal half of pinnules (axis diameter 0.5–1.0 mm) triangular and symmetrical (Fig. 4D); 0.04–0.10 mm tall (from midpoint of base to apex); abpolypar spines 0.04–0.07 mm. Polypar spines on distal parts of pinnules (axis diameter 0.3–0.4 mm) large, less symmetrical, sometimes pointing proximally (Figs. 4A–B); 0.12–0.18 mm tall (from midpoint of base to apex); abpolypar spines 0.10–0.12 mm. Bifid and double spines present on distal parts of pinnules, but usually absent on lower sections. Spines arranged in axial rows of varying regularity; 2–4 rows visible in lateral view on basal section of pinnules; 4–5 rows visible along distal section. Spines in each row mostly 0.25–0.35 mm apart (range 0.2–0.4 mm); with 4–5 spines per millimeter in each row. Rows of spines on unpinnulated stalk confined to wider sides

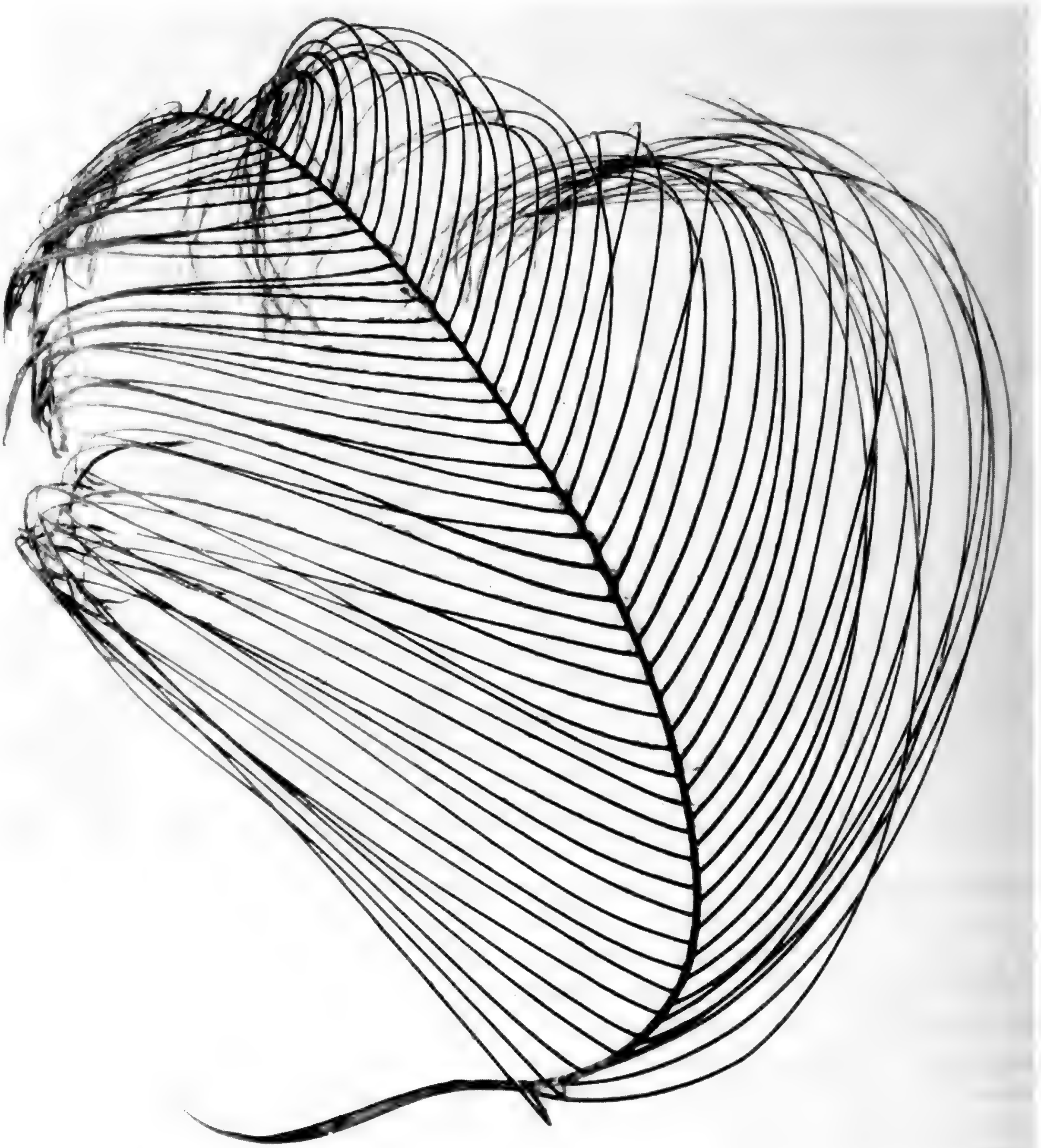

Fig. 3. *Schizopathes amplispina,* holotype USNM 96966; height 42 cm.

(2–3 rows on each side) above, but with rows converging near anterior edge further down. Spines absent on lowermost 2 cm of stalk.

Polyps transversely elongated; 3–3.5 mm from distal side of distal lateral tentacles to proximal side of proximal lateral tentacles; arranged uniserially, usually on the distal or anterior side of the pinnules, with about three polyps per centimeter.

Discussion.—The two paratypes are about the same size as the holotype and are very similar in several other respects. The unpinnulated section of the stem is 8–9 cm long, the lowermost largest pinnules are 24–26 cm long, those 10 cm higher are 18–20 cm and those 10 cm higher are 14–16 cm. The pinnules are as crowded together in the paratypes as they are in the holotype, the distance between adjacent pinnules in each lateral row never being more than 8 mm, even for the lowermost pairs. In all three of the type specimens the stem and the lower sections of the larger pinnules are

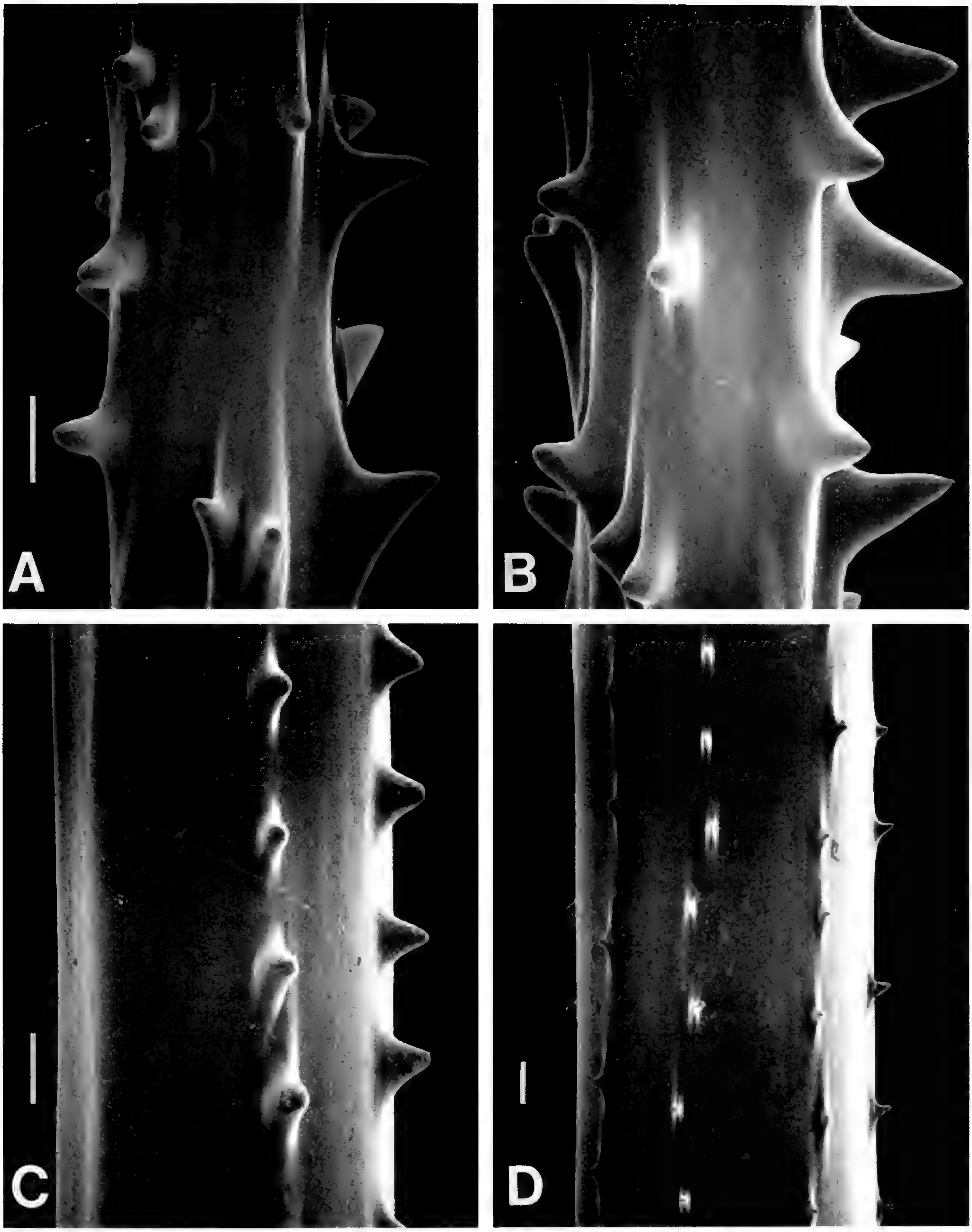

Fig. 4. *Schizopathes amplispina,* holotype USNM 96966. A. Distal section of pinnule; scale equals 0.1 mm. B. Distal section of pinnule; scale as in A. C. Midsection of pinnule; scale equals 0.1 mm. D. Basal section of pinnule; scale equals 0.1 mm.

compressed laterally such that their widest (anterior to posterior) axis is at right angles to the plane containing the pinnules.

As in the holotype the largest spines in both paratypes occur along the distal half of the pinnules and on the side of the pinnules corresponding to the polyp side of the corallum. On the basal sections of the larger pinnules, where the axis is compressed laterally, the rows of spines are not always evenly distributed around the circumference of the axis, and in some places the appearance is given that spines are missing from one side (Fig. 4C). Near the basal end of holdfast, the stem is compressed laterally in the same direction as the upper part of the stem in one specimen, but flattened at right angles to the upper part in the other two specimens. In the latter case, there is a small keel (defined by the central axial canal) extending down the center of one side. The basal end of the holdfast ends in a rounded point.

In none of the specimens are polyps present on all parts of corallum, and only in the holotype can the polyps be measured with any degree of reliability. In the holotype the polyps at the distal ends of the pinnules measure 3–3.5 mm in transverse diameter; they are about the same size or slightly smaller in the middle of the pinnules.

Comparisons.—This species can be differentiated from *S. crassa* and *S. affinis* by its much larger spines (0.08–0.18 mm vs. 0.1 mm or less) and its much more closely spaced pinnules (7–8 mm apart in *S. amplispina* vs. 8–16 mm apart in the other species). Furthermore, both the pinnules and the stem are much more strongly compressed in *S. amplispina* than in the other two species. In the size of its polyps (maximum of 3.5 mm transverse diameter near the tips of the pinnules), *S. amplispina* resembles *S. affinis* (polyps 3–4.5 mm) more than *S. crassa* (polyps 4–6 mm).

Etymology.—Latin *amplius,* larger, and *spina,* spine; in reference to the large spines on the distal sections of the pinnules.

Distribution.—Known only from the type locality.

Acknowledgments

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Literature Cited

Brook, G. 1889. Report on the Antipatharia.—Reports of the Scientific Results of the Voyage of the *Challenger,* Zoology 32:5–222.

Cooper, C. F. 1909. Antipatharia. Reports of the Percy Sladen Trust Expedition to the Indian Ocean.—Transactions of the Linnean Society of London. (Zool. Ser. 2) 12:301–323.

Hickson, S. M. 1907. The Alcyonaria, Antipatharia and Madreporaria, collected by the "Huxley" from the north side of the Bay of Biscay, August, 1906.—Journal of the Marine Biological Association 8:6–14.

Kinoshita, K. 1910. On a new antipatharian *Hexapathes heterosticha* n. gen. and n. sp.—Annotationes Zoologicae Japonenses 7:231–234.

Opresko, D. M., & F. M. Bayer. 1991. Rediscovery of the enigmatic coelenterate *Dendrobrachia,* (Octocorallia: Gorgonacea) with descriptions of two new species.—Transactions of the Royal Society of South Australia 115:1–19.

Pasternak, F. A. 1977. Antipatharia.—*Galathea* Report 14:157–164.

Pax, F. 1918. Die Antipatharien.—Zoologische Jahrbucher 41:419–478.

Schultze, L. S. 1896. Beitrag zur Systematik der Antipatharien.—Abhandlungen der Senckenbergischen naturforschenden Gesellschaft 23:1–40.

Thompson, J. 1905. Report on the Antipatharians, Scotia Collection.—Proceedings of the Royal Physical Society of Edinburgh 16:76–79.

van Pesch, A. J. 1914. The Antipatharia of the Siboga Expedition.—*Siboga* Expeditie Monographie 17:1–258.

Zhou, J., & R. Zou. 1992. Studies on the antipatharians from Zhongsha Islands waters.—Tropical Oceanology 11:45–52. (in Chinese)

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Cnidae of Scleractinia

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Abstract.—Corals and corallimorpharians are considered cnidarians with simple cnidae. This work shows that such a statement is relative, and depends upon the accuracy of the observation. The cnidae of tentacles and mesenterial filaments of 60 species belonging to 17 families of Scleractinia and three families of Corallimorpharia were studied using Normarski optics. The diversity of the cnidae (morphological patterns and their varieties) is described and illustrated, and their distributions are given: In addition, a new type of cnida from the mesenterial filaments of Agariciidae is recorded. Synonym lists of the names used by other authors for the cnidae of Scleractinia and Corallimorpharia are also included, and aspects of their terminology are discussed. Diversity in the cnidae of Scleractinia confirms the potential of soft tissues as an important source of characters that should be explored in taxonomic studies. When used with other characters, the descriptions of cnidae will contribute to the improvement of studies on coral taxonomy and systematics.

The knowledge of the cnidae in terms of their diversity, size and distribution, has been considered as a useful taxonomic character for many groups of Cnidaria (see Pires & Pitombo 1992). The nematocysts represent categories that are usually constant (Gravier–Bonnet 1987, Pires 1988) and their structural complexity provides many features for comparison (Tilbury & Cameron 1989). The systematics of the Scleractinia, the largest order of the subclass Hexacorallia (=Zoantharia) (Wells 1956), with approximately 225 recent genera and 1500 species (Cairns 1990), is not fully satisfactory (Chevalier & Beauvais 1987), being based primarily on skeletal morphology (Wells 1956).

One of the reasons for the neglect of coral cnidae studies is the lack preservation of their tissue. It is not routine in most scientific collections to preserve scleractinian coral tissues, especially in formalin, because the skeleton is the primary or only taxonomic source of characters. Problems with nematocyst nomenclature, some of which have been recently discussed by England (1991), have also made it difficult to understand and compare studies that have included data on cnidae.

The goal of this paper is to describe the diversity of cnidae occurring in tentacles and mesenterial filaments of Scleractinia and to propose a detailed terminology to classify subtypes of coral cnidae. This study is based on a large array of taxa and on features that can be observed through light microscopy, which is easily accessible to most researchers. To help in the understanding and interpretating other papers, synonym lists of terms used for cnidae by other researchers are included. The cnidae of the Corallimorpharia were also studied here due to their great similarities with the Scleractinia, as has been previously pointed out (Schmidt 1974, den Hartog 1980).

The cnidae are structures unique to the

Cnidaria and it seems clear that they must have a distinct place in phylogenetic speculations (Vervoort 1987). This paper contributes to explore some characteristics of coral cnidae, with the aim of providing new perspectives for systematics studies.

Methods and Materials

The cnidae of tentacles and mesenterial filaments of Scleractinia were studied because these structures were found to have the most diversified cnidae (Pires, pers. obs.) Most observations were made on material fixed in 4% formalin and stored in 70% alcohol or 4% formalin. Some species from Brazil were maintained alive for examinating discharged cnidae. Decalcification of the skeleton was obtained using a solution of 10% formic acid and 5% formalin. Measurements were made with an eyepiece micrometer and illustrations were done using camera lucida. Preparations were examined with interference contrast, using a magnification of 1250 ×. The synonyms of the cnidae are cited in the original publication language. For the evaluation of the diversity of the cnidae, the species listed below were examined. The taxa are listed in the same order used by Wells (1956) for Scleractinia (except Fungiacyathidae), and den Hartog (1980) for Corallimorpharia. The families are indicated in parentheses:

Scleractinia.—Suborder Astrocoeniina: *Stephanocoenia michelinii* (Astrocoeniidae); *Madracis decactis* (Pocilloporidae);

Suborder Fungiina: *Agaricia agaricites, A. fragilis, Pavona* sp., *P. gigantea, Leptoseris cucullata* (Agariciidae); *Siderastrea stellata* (Siderastreidae); *Cycloseris marginata* (?), *Lithophyllum mokai, Fungia (Cycloseris) sinensis, Fungia (Verrillofungia) repanda, Fungia (Verrillofungia) concinna, Fungia (Fungia) fungites, Herpolitha limax, Polyphyllia talpina, Halomitra pileus, Zoopilus echinatus* (Fungiidae); *Leptopenus antarcticus* (Micrabaciidae); *Goniopora tenuidens, Porites astreoides* (Poritidae); *Fungiacyathus* sp. (Fungiacyathidae);

Suborder Faviina: *Favia gravida, F. leptophylla, Favites abdita, Platygyra daedalea, Colpophyllia natans, Cladocora debilis, C. arbuscula, Montastrea cavernosa* (Faviidae); *Astrangia rathbuni, Phyllangia americana* (Rhizangiidae); *Oculina patagonica, Madrepora* sp. (Oculinidae); *Meandrina braziliensis* (Meandrinidae); *Mussismilia hartti, M. braziliensis, M. hispida, Scolymia wellsi, Lobophyllia hemprichii, Lobophyllia* sp. (Mussidae); *Pectinia paeonia* (Pectiniidae);

Suborder Caryophylliina: *Caryophyllia ambrosia caribbeana, C. cornuformis, Deltocyathus italicus, D. calcar, D. eccentricus, Dasmosmilia lymani, D. variegata, Rhizosmilia maculata, Physogyra lichtensteini* (Caryophylliidae); *Flabellum* sp., *Javania cailleti* (Flabellidae);

Suborder Dendrophylliina: *Balanophyllia europaea, Balanophyllia* sp., *Dendrophyllia* sp., (Dendrophylliidae).

Corallimorpharia.—Corynactis californica (Corallimorphidae), *Ricordea florida* (Ricordeidae), *Discosoma carlgreni* (Discosomatidae).

The studied material is deposited in the Collection of Cnidaria of the Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ) (Appendix), except *Pavona gigantea* (USNM 81542), *Pectinia paeonia* (USNM 90471) and *Madrepora* sp. from the National Museum of Natural History, Smithsonian Institution, Washington D. C.

Results

The cnidae of tentacles and mesenterial filaments of the studied material can be grouped into five basic morphological patterns: spirocysts, holotrichs, b-rhabdoids, p-rhabdoids D (sensu Schmidt 1974) and agaricysts. Four of these cnidae were already well described in the literature (Weill 1934, Mariscal 1974, 1984; Schmidt 1974) and a new type is described (agaricysts).

Table 1.—Diversity of cnidae and their varieties from tentacles and filaments of Scleractinia and Corallimorpharia.

- Spirocysts
  - Holotrichs
    - holotrich I [with one or two size classes]
    - holotrich I (*Discosoma* var.) [close to holotrich I]
    - holotrich II
  - B-rhabdoids
    - b-rhabdoid (1)
    - b-rhabdoid (*Discosoma* var.) [close to b-rhabdoid (1)]
    - b-rhabdoid (*Favites* var.) [close to b-rhabdoid (1)]
    - b-rhabdoid (2)
    - b-rhabdoid (Dendrophylliina var.) [close to b-rhabdoid (2)]
    - b-rhabdoid (3)
    - b-rhabdoid (*Physogyra* var.) [close to b-rhabdoid (3)]
  - P-rhabdoids D
    - p-rhabdoid D(1)
    - p-rhabdoid D(2) [with one or two size classes]
    - p-rhabdoid D(3)
    - p-rhabdoid D(4)
    - p-rhabdoid D(5)
    - p-rhabdoid D(6)
- Agaricysts

However, subvarieties of previously described types (namely holotrichs, b-rhabdoids, and p-rhabdoids D) are herein introduced and characterized. Table 1 shows the types of cnidae here observed and their subvarieties. Table 2 shows the range of measurements of the cnidae observed. Tables 3–5 show main differences between subvarieties of holotrichs, b-rhabdoids, and p-rhabdoids D. Their distribution in different taxa of Scleractinia and Corallimorpharia is tabulated elsewhere (Pires & Castro, 1997).

Spirocysts
(Figs. 1A, 3A)

Description.—Capsule elongate and thin-walled, with a long tubule of uniform diameter, coiled in numerous spirals. Tubule without spines.

Remarks.—The spirocysts are especially abundant in tentacles, although they may be seen in the other structures of the polyps of both Scleractinia and Corallimorpharia.

Holotrichs

Description.—Capsule of varying shape and size (Table 2), from ellipsoid to very elongated cylinder. Tubule without differentiated parts - without the funnel-shaped "V" notch; long and helicoidal inside the capsule. Discharged tubule bears spines along almost all its length, arranged in distinct coils, and at right angles to the tubule surface.

Remarks.—Two morphological varieties of holotrichs were recognized in Corallimorpharia and Scleractinia.

holotrich I (Figs. 1B, 2, 3B, 3C, Table 3)
- tangled cnidae (cnidae glomiferae) sensu Gosse 1860
- nematocyst type III sensu Matthai 1914
- nematocyst type IIIb and IIIc sensu Matthai 1928
- macrocniden sensu Seifert 1928
- haplonème isorhize holotriche sensu Weill 1934
- nematocyst B sensu Abe 1938
- holotrich sensu Carlgren 1940
- macrobasic p-mastigophore sensu Cutress 1955
- isorhize haploneme holotriche sensu Schmidt 1969
- haploneme holotriche I sensu Schmidt 1972
- haplonem holotrich I sensu Schmidt 1974
- haploneme holotrichous isorhiza sensu Mariscal 1974
- penicilli E sensu den Hartog 1980
- holotrichous isorhiza sensu Song 1988
- holotrich sensu England 1991
- holotrich I sensu Pires & Pitombo 1992

Description.—Capsule of varying shape and size (Table 2), from ellipsoid to very elongate cylinder; of rich contrast, with a very distinct tubule, usually arranged in many regular coils. Tubule isodiametric in dis-

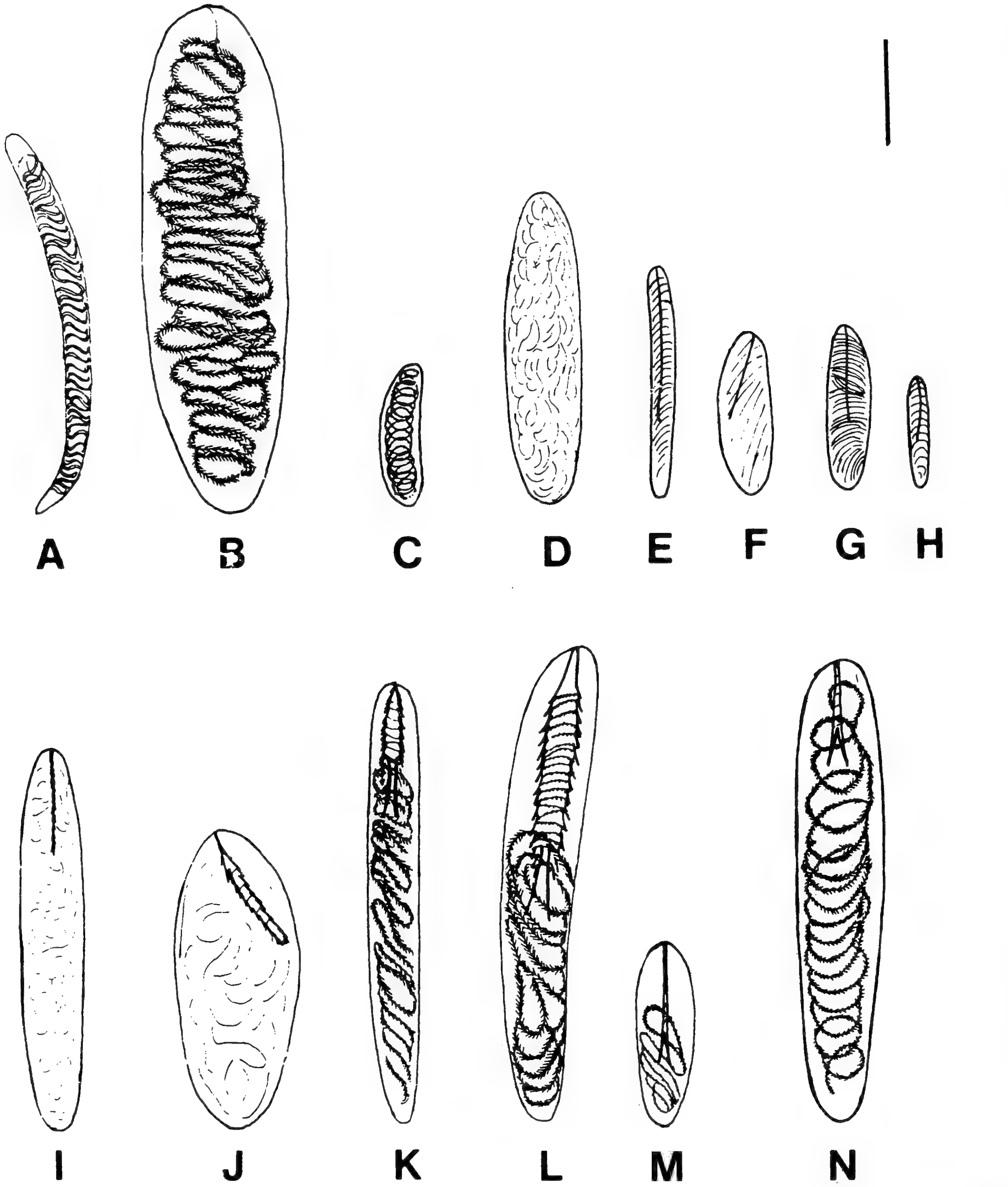

Fig. 1. Cnidae of tentacles of Scleractinia and Corallimorpharia, scale = 10 μm. A, spirocyst of *Leptopenus antarcticus*; B, holotrich I of *Phyllangia americana*; C, holotrich I var. of *Discosoma carlgreni*; D, holotrich II of *Discosoma carlgreni*; E, b-rhabdoid (1) of *Fungia* (*Verrillofungia*) *concinna*; F, b-rhabdoid (1) of *Discosoma carlgreni*; G, b-rhabdoid (1) var. of *Favites abdita*; H, b-rhabdoid (2) of *Discosoma carlgreni*; I, b-rhabdoid (3) of *Stephanocoenia michelinii*; J, b-rhabdoid (3) var. of *Physogyra lichtensteini*; K, p-rhabdoid D(1) of *Montastrea cavernosa*; L, p-rhabdoid D(2) of *Fungia* (*Verrillofungia*) *concinna*; M, p-rhabdoid D(3) of *Siderastrea stellata*; N, p-rhabdoid D(6) of *Halomitra pileus*.

charged state, with spines of equal size present along whole length, except a small naked basal portion that often is present; latter portion easily seen in undischarged capsules (Figs. 1B, 2, 3B, 3C). Tubule of holotrich I of some Corallimorpharia presents an abruptly tapered and spineless distal tip.

Remarks.—Holotrichs I are sparingly pres-

Table 2.—Morphometrics of cnidae (except spirocysts) from tentacles and mesenterial filaments of Scleractinia and Corallimorpharia. All measurements are in μm. mcl = minimum capsule length; MCL = maximum capsule length; mcw = minimum capsule width; MCW = maximum capsule width; C = number of capsules measured; S = number of species in which the cnida was observed.

Cnidae	mcl	MCL	mcw	MCW	C	S	Fig
Tentacles							
holotrich I (1 size)	26.3	82.4	3.8	18.4	312	15	1B
holotrich I (2 sizes—small)	33.8	69.0	11.3	30.0	55	4	2
holotrich I (2 sizes—large)	51.3	145.0	21.3	60.0	73	4	2
holotrich I (*Discosoma* var.)	12.5	21.0	3.1	6.0	4	1	1C
holotrich II	21.9	42.0	5.0	12.0	20	1	1D
b-rhabdoid (1)	16.3	56.8	1.3	6.3	1074	44	1E
b-rhabdoid (*Discosoma* var.)	15.0	26.0	5.0	7.0	6	1	1F
b-rhabdoid (*Favites* var.)	11.9	18.8	2.5	4.4	23	1	1G
b-rhabdoid (2)	7.5	11.3	1.3	2.5	10	1	1H
b-rhabdoid (3)	13.1	63.2	2.5	8.1	618	25	1I
b-rhabdoid (*Physogyra* var.)	24.4	35.6	9.4	12.5	37	1	1J
p-rhabdoid D(1)	24.0	88.1	4.0	8.1	1144	32	1K
p-rhabdoid D(2)	20.0	67.5	3.8	13.1	641	21	1L
p-rhabdoid D(3)	10.6	25.0	3.1	7.0	139	6	1M
p-rhabdoid D(6)	18.1	49.4	4.4	8.1	53	4	1N
Filaments							
holotrich I (1 size)	17.6	101.9	4.8	29.6	709	22	3B
holotrich I (2 sizes—small)	17.5	60.0	4.8	20.0	457	22	3C
holotrich I (2 sizes—large)	40.6	186.3	8.0	72.0	596	22	3C
holotrich II	8.1	29.4	2.0	12.5	497	14	3D
b-rhabdoid (1)	15.0	31.0	2.0	5.0	42	2	3E
b-rhabdoid (*Favites* var.)	13.8	29.4	3.1	5.0	22	1	3F
b-rhabdoid (2)	5.6	28.8	1.3	4.8	1038	49	3G
b-rhabdoid (Dendrophylliina var.)	11.3	16.3	3.1	4.4	38	1	3H
p-rhabdoid D(2) (1 size)	16.0	59.4	3.8	15.6	957	25	4A
p-rhabdoid D(2) (2 sizes—small)	16.9	77.6	4.0	11.9	666	25	4B
p-rhabdoid D(2) (2 sizes—large)	34.4	136.0	5.0	18.1	736	25	4B
p-rhabdoid D(3)	8.1	32.0	2.5	7.5	843	41	4C
p-rhabdoid D(4)	51.3	112.5	9.4	15.6	155	6	4D
p-rhabdoid D(5)	73.1	96.9	17.5	28.1	24	1	4E
Agaricyst	25.0	63.8	5.6	12.5	104	4	7

ent in the tentacles of corals. They occur in Micrabaciidae, Poritidae, Fungiacyathidae, Rhizangiidae, Oculinidae, in some Caryophylliidae (Caryophylliinae), Flabellidae and Dendrophylliidae, and are common in the tentacles of corallimorpharians. They occur in two size classes in the tentacles of Micrabaciidae, Flabellidae and Discosomatidae (Fig. 2). These size classes are present in both kinds of tentacles of Discosomatidae (marginal and discal), which uniquely presented also another distinct morphological variety of holotrich I. The latter shows poor contrast and is rather small (=holotrich I *Discosoma* var., Table 1, 2; Fig. 1C).

The occurrence of two distinct size classes of holotrich I is very common in the mesenterial filaments of some Faviina, Caryophylliina and Dendrophylliina (Fig. 3C). They also occur in two size classes in the mesenterial filaments of Corallimorpharia of the families Corallimorphidae and Discosomatidae. The anterior end of smaller ones is usually slightly tapered.

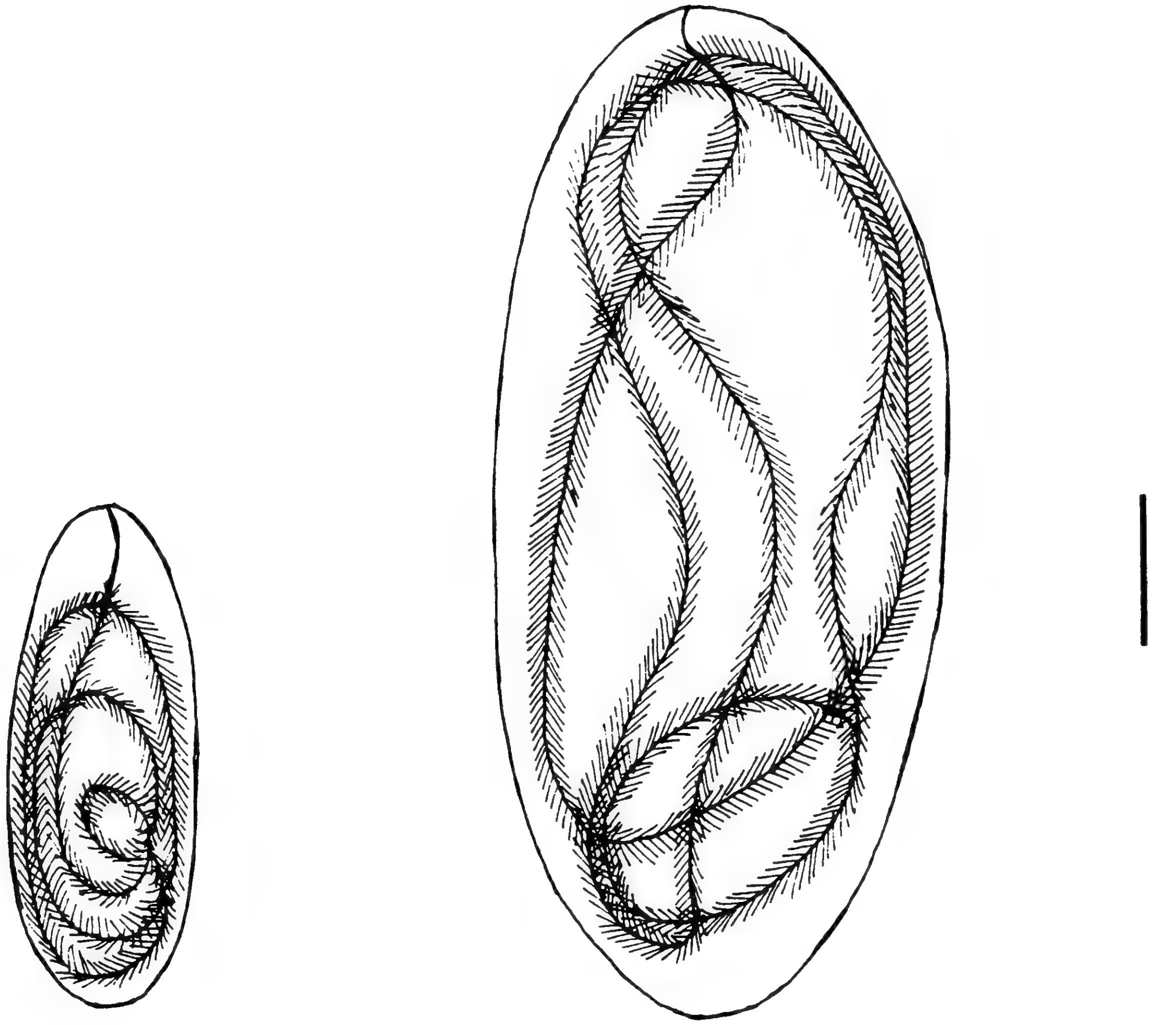

Fig. 2. Two size classes of holotrichs I from discal tentacles of *Discosoma carlgreni,* scale = 10 μm.

holotrich II (Figs. 1D, 3D, Table 3)
- haplonème anizorhize homotriche sensu Weill 1934
- haploneme holotrich II sensu Schmidt 1972 (part)
- homotrich sensu den Hartog 1980
- homotrich sensu England 1991

Description.—Capsule cylindrical, little refractive, of varying size (Table 2); content is composed of a long tubule, irregularly coiled in small turns, filling whole undischarged capsule. Basal portion of tubule slightly enlarged and tapering toward distal end. Spines smaller than those of holotrichs I and shorter as the width of tubule decreases. Sometimes the slightly enlarged proximal part of tubule, which bears longer spines, is visible in undischarged capsule. When discharged, this portion is smaller than length of capsule.

Table 3.—Main differences between holotrichs I and holotrichs II.

	Contrast of the capsule	Capsule sizes	Discharged tubule	Undischarged tubule	Spines along discharged tubule	Spines in undischarged state
I	high	may occur in two distinct size classes	isodiametric	regular coils, not filling the whole capsule	equal in size	clearly visible
II	low	only one size class	basal portion slightly enlarged	irregular coils, filling the whole capsule	shorter as the tubule width decreases	undistinct

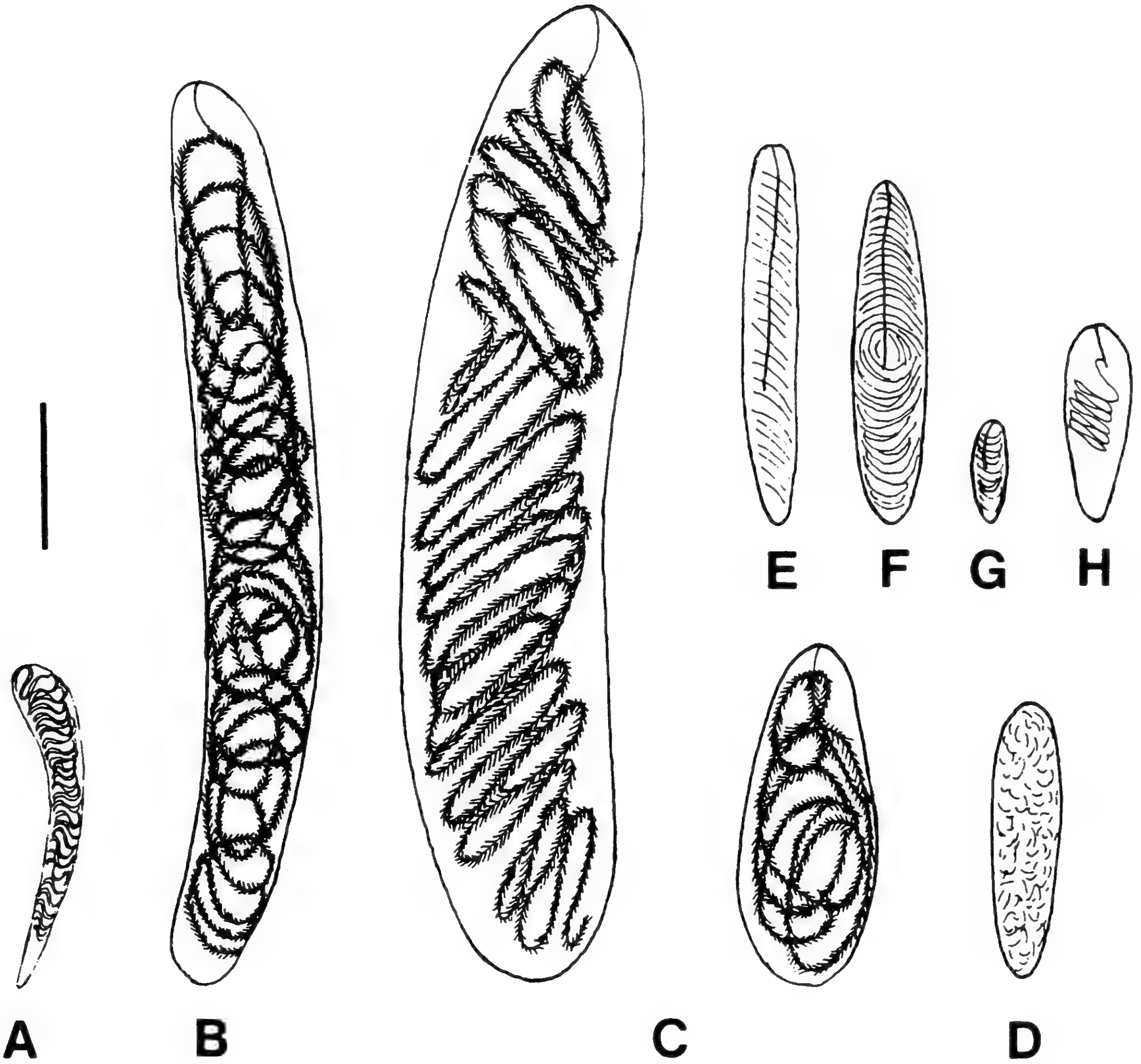

Fig. 3. Cnidae of mesenterial filaments of Scleractinia, scale = 10 μm. A, spirocyst of *Colpophyllia natans*; B, holotrich I (1 size class) of *Cycloseris marginata* (?); C, holotrich I (2 size classes) of *Phyllangia americana*; D, holotrich II of *Porites astreoides*; E, b-rhabdoid (1) of *Balanophyllia* sp.; F, b-rhabdoid (1) var. of *Favites abdita*; G, b-rhabdoid (2) of *Zoopilus echinatus*; H, b-rhabdoid Dendrophylliina var.

Remarks.—This cnida is very common in the mesenterial filaments of Poritidae, Faviidae, and Mussidae. It also occurs in the marginal tentacles of Discosomatidae.

B-rhabdoids

Description.—Capsule of varying shape and size (Table 2). Tubule with no differentiated parts - without funnel-shaped "V" notch. Spines of proximal part of tubule slightly longer than those of distal portion. In the undischarged capsules, proximal part is visible as a rod. Tubule tapers very gradually; distal portion bears tiny spines.

Remarks.—Three morphological varieties of b-rhabdoids were here recognized (b-rhabdoids (1), (2) and (3)).

b-rhabdoid (1) (Figs. 1E, 3E, Table 4)
- spirulae sensu Stephenson 1928
- basitriche sensu Weill 1934
- heteroneme b-rhabdoide sensu Schmidt 1969, 1972
- heteronem b-rhabdoid sensu Schmidt 1974
- basitrich sensu England 1991

Description.—Capsule cylindrical and elongated, sometimes slightly curved. Basal portion of tubule slightly enlarged, and can be seen in undischarged state as a thin axial

Table 4.—Main differences of b-rhabdoids subvarieties.

	Capsule contrast	Capsule shape	Size of enlarged basal portion of undischarged tubule	Arrangement of distal portion of undischarged tubule
(1)	high	elongated cylinder, sometimes slightly curved	almost equal to capsule length	few distinct regular coils
(2)	high	oval	approximately ½ of capsule length	few distinct regular coils
(3)	low	cylindrical	approximately 1/5 of capsule length	many small irregular coils, filling the whole interior of the capsule

rod, almost of same size of capsule length. Width of tubule diminishes toward distal end. Tubule arranged in few distinct regular coils, somewhat horizontally arranged inside capsule. When discharged, basal portion bearing larger spines is a little longer than entire length of capsule.

Remarks.—B-rhabdoid (1) is very common in the tentacles of most scleractinian families. They may also be present in the mesenterial filaments of Dendrophylliidae. A similar morphological variety of b-rhabdoid (1) was observed in the tentacles (Fig. G) and mesenterial filaments (Fig. 3F) of *Favites abdita.* That variety is more ellipsoid in shape, the tubule being longer and arranged in many coils. The coils fill all the interior of the capsule. The marginal and discal tentacles of *Discosoma carlgreni* contain another variety of b-rhabdoid, similar of b-rhabdoid (1). It is more translucent, the tubule is arranged in fewer coils, and usually the axial rod is oblique inside the capsule (Fig. 1F).

b-rhabdoid (2) (Figs. 1H, 3G, Table 4)
- mastigophore microbasique sensu Weill 1934
- microbasic b-mastigophore sensu Carlgren 1940
- b-rhabdoide sensu Schmidt 1969
- b-rhabdoid sensu Schmidt 1972, 1974
- spirulae 2 sensu den Hartog 1980
- microbasic b-mastigophore sensu England 1991

Description.—Capsule oval, very small (Table 2), and of strong contrast. Basal part of tubule clearly distinguished in undischarged state, this rigid part approximately ½ of capsule length. Thinner part of tubule bears tiny spines; these latter arranged in few conspicuous turns. Thinner part of tubule often coiled down to rigid basal part.

Remarks.—B-rhabdoids (2) occur in the mesenterial filaments of all examined Scleractinia, and in some Corallimorpharia (Corallimorphidae), and exceptionally in the discal tentacles of Discosomatidae (Fig. 1H). A variety of b-rhabdoid (2) of larger capsule and shorter tubule occurs in the mesenterial filaments of Dendrophylliidae (Fig. 3H, Table 2).

b-rhabdoid (3) (Fig. 1I, Table 4)
- basitrichs sensu Weill 1934
- microbasic b-mastigophore sensu Carlgren 1940
- b-rhabdoide sensu Schmidt 1969, 1972
- b-rhabdoid sensu Schmidt 1974
- spirulae 1 sensu den Hartog 1980
- microbasic b-mastigophore sensu England 1991

Description.—Capsule of varying shape, but usually cylindrical, and slightly refractive. Proximal part of tubule bears spines somewhat longer than those from distal part. This region can be distinguished in undischarged capsule as a rod; approximately 1/5 of the length of the capsule; thicker than rods of b-rhabdoids (1) and (2). Distal part of tubule long; irregularly arranged; fills whole interior of undischarged capsule. Basal portion of tubule, approximately ⅓ of capsule length, in discharged state, with spines somewhat longer than those from thinner part of tubule.

Remarks.—This variety can be confused with holotrich II, especially in the undischarged state. Sometimes it is difficult to distinguish the slightly larger tubule basal portion, a characteristic of b-rhabdoids. Den Hartog (1980) considered them homologous, since he observed transitional stages between both types.

This variety occurs in the tentacles of Scleractinia (Astrocoeniidae, Pocilloporidae, Agariciidae, Fungiidae, Faviidae Montastreinae, Rhizangiidae, Oculinidae, few Caryophylliina, Dendrophylliidae) and Corallimorpharia (Ricordeidae and Corallimorphidae).

A morphological variety was observed in the tentacles of *Physogyra lichtensteini*. The proximal part of its tubule is exceptionally thick and very distinct (Fig. 1J)

P-rhabdoids D
- chambered cnidae (cnidae cameratae) sensu Gosse 1860
- type II sensu Matthai 1914, 1928
- hétéronème mastigophore microbasique sensu Weill 1934
- nematocyst A sensu Abe 1938
- microbasic p-mastigophore sensu Carlgren 1940
- p-rhabdoid D sensu Schmidt 1974
- penicilli D sensu den Hartog 1980
- microbasic p-mastigophore D sensu England 1991

Description.—Capsule of varying contrast, size and shape, from oval to very elongate cylinder. Tubule with two clearly differentiated parts: larger basal shaft and tapered distal tubule. These two regions delimited by sudden change in diameter of tubule and in length of spines; seen as funnel-shaped "V" notch in undischarged capsules. Shaft often isodiametric; usually oriented straight inside capsule. In few cases it presents discrete coil in its base or, more rarely, shaft entirely coiled. This disposition of tubule varies inside capsule. Both regions, shaft and tubule, usually coarsely spined. When discharged, spines arranged at perpendicular to shaft surface; distinctly longer than shaft diameter. Tubule long; bearing spines rather smaller than those of shaft.

Remarks.—This cnida is exclusive to and very common in Scleractinia and Corallimorpharia. Six morphological varieties of p-rhabdoids D were here recognized (p-rhabdoids D(1), D(2), D(3), D(4), D(5) and D(6)).

p-rhabdoid D(1) (Fig. 1K, Table 5)
- nematocyst IIb sensu Matthai 1928
- penicilli D1 sensu den Hartog 1980
- microbasic p-mastigophores type III sensu Thomason & Brown 1986

Description.—Capsule elongate; cylindrical; slightly curved; of rich contrast. Shaft short (approximately ⅓ of capsule length) in undischarged state. A protruding tip commonly projects at anterior end of capsule. Spines of tubule clearly distinguished even in undischarged state.

Remarks.—This variety has a restricted distribution, occurring in the tentacles of most Scleractinia and commonly in the tentacles of Corallimorpharia, but not Discosomatidae.

p-rhabdoid D(2) (Figs. 1L, 4A, 4B, Table 5)
- nematocyst IId sensu Matthai 1928
- penicilli D3 sensu den Hartog 1980
- microbasic p-mastigophores type II sensu Thomason & Brown 1986

Description.—Capsule often cylindrical; of rich contrast. Spines of shaft arranged in obvious turns—approximately ½ of capsule length. Tubule long, irregularly arranged inside capsule.

Remarks.—This variety occurs in the

Table 5.—Main differences of p-rhabdoids D subvarieties.

	Capsule contrast	Capsule shape	Length of undischarged shaft	Diameter of undischarged shaft	Spines in undischarged tubule
D(1)	high	elongated cylinder, slightly curved	approximately ⅓ of capsule length	isodiametric	clearly distinguishable
D(2)	high	cylindrical	approximately ½ of capsule length	isodiametric	clearly distinguishable
D(3)	low, almost transparent	cylindrical to oval	approximately ½ of capsule length	isodiametric	almost indistinct
D(4)	high	cylindrical	approximately equal to capsule length	isodiametric	clearly distinguishable
D(5)	low	cylindrical	approximately equal to capsule length	anisodiametric with three distinct parts	clearly distinguishable
D(6)	low	cylindrical	approximately 1⁄5 of capsule length	isodiametric	slightly distinguishable

mesenterial filaments of all Scleractinia and Corallimorpharia. In the mesenterial filaments of Astrocoeniidae and Pocilloporidae it is characteristically thick and club-shaped. It occurs in two distinct size classes in the mesenterial filaments of most Faviina (Fig. 4B). Exceptionally, it is also present in the tentacles of some Fungiidae (Fig. 1L).

p-rhabdoid D(3) (Figs. 1M, 4C, Table 5)
– penicilli D2 [?] sensu den Hartog 1980

Description.—Capsule thin-walled; little refractive; almost transparent; often ovoid in shape. Shaft thin; approximately ½ of capsule length. Tubule short; occupying small portion of capsule. Spines of shaft and tubule almost indistinct in undischarged state.

Remarks.—This variety is very common in the mesenterial filaments of most Scleractinia and Corallimorpharia. It also occurs in the tentacles of Siderastreidae and Agariciidae.

p-rhabdoid D(4) (Fig. 4D, Table 5)

Description.—Capsule cylindrical; of rich contrast. Shaft long, in undischarged state filling almost whole capsule length; its basal portion slightly to coarsely coiled. Tubule long; irregularly coiled. Spines clearly distinguished in both shaft and tubule.

Remarks.—This variety occurs in mesenterial filaments of some Fungiina and Caryophylliina. When present, it substitutes the larger class of D(2), which is common in the mesenterial filaments of some Faviina (Fig. 4B). Only undischarged capsules were observed. The length of the shaft of this variety is similar to those belonging to the "macrobasic state" of Weill (1934). The inclusion of this variety in p-rhabdoid D is tentative, pending the examination of discharged capsules.

p-rhabdoid D(5) (Fig. 4E, Table 5)
– type IV sensu Abe 1938

Description.—Capsule very refractive in undischarged state. Shaft anisodiametric with three distinct parts: 1) short coiled basal portion, very thin and apparently naked, clearly distinguished in undischarged state; 2) middle part with abrupt enlargement, coiled, coarsely armed with long spines, and diminishes toward distal part, both in width of shaft and length of spines, comprises the longest and thickest part of shaft; and 3) distal part, gradually thicker, with very deep "funnel-shaped "V" notch. Tubule relatively short; irregularly coiled; with tiny spines.

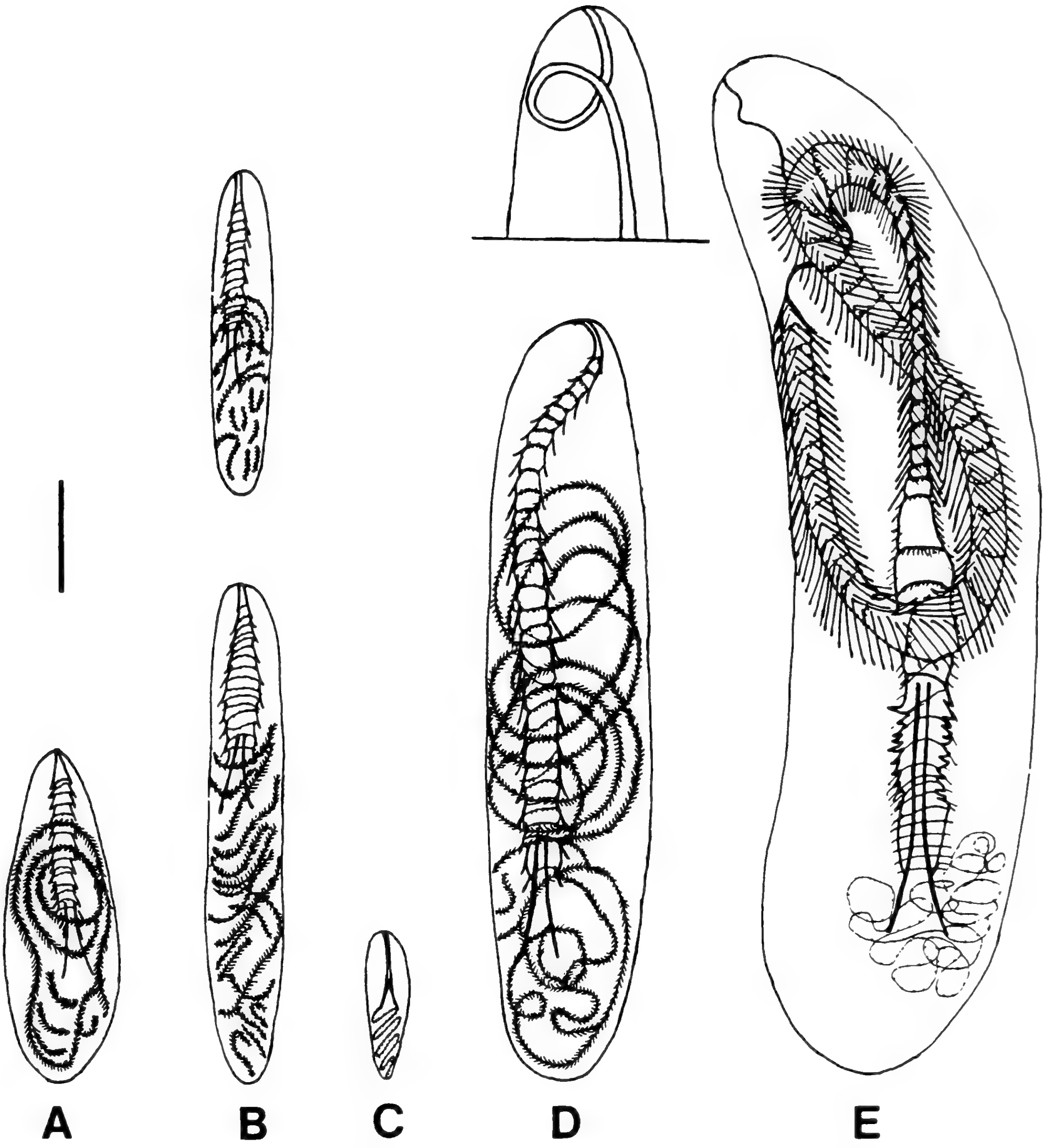

Fig. 4. Cnidae of mesenterial filaments of Scleractinia, scale = 10 μm. A, p-rhabdoid D(2) (1 size class) of *Madracis decactis*; B, p-rhabdoid D(2) (2 size classes) of *Favia leptophylla*; C, p-rhabdoid D(3) of *Cladocora debilis*; D, p-rhabdoid D(4) of *Polyphyllia talpina*; E, p-rhabdoid D(5) of *Goniopora tenuidens.*

Remarks.—This peculiar and very characteristic variety was found only in the mesenterial filaments of *Goniopora tenuidens.* Only undischarged capsules were examined. It clearly belongs to the "macrobasic state" of Weill (1934). The inclusion of this variety in p-rhabdoid D is tentative, pending the examination of discharged capsules.

p-rhabdoid D(6) (Fig. 1N, Table 5)

Description.—Capsule cylindrical; little refractive. Shaft thin; approximately $\frac{1}{5}$ the capsule length. Spines of shaft and of tubule poorly distinguished in undischarged state. Tubule irregularly coiled; almost fills entire capsule.

Remarks.—Only undischarged capsules were examined. This variety can be confused with p-rhabdoids D(3); however, besides its larger capsule, it presents a proportionally shorter shaft, and the tubule is

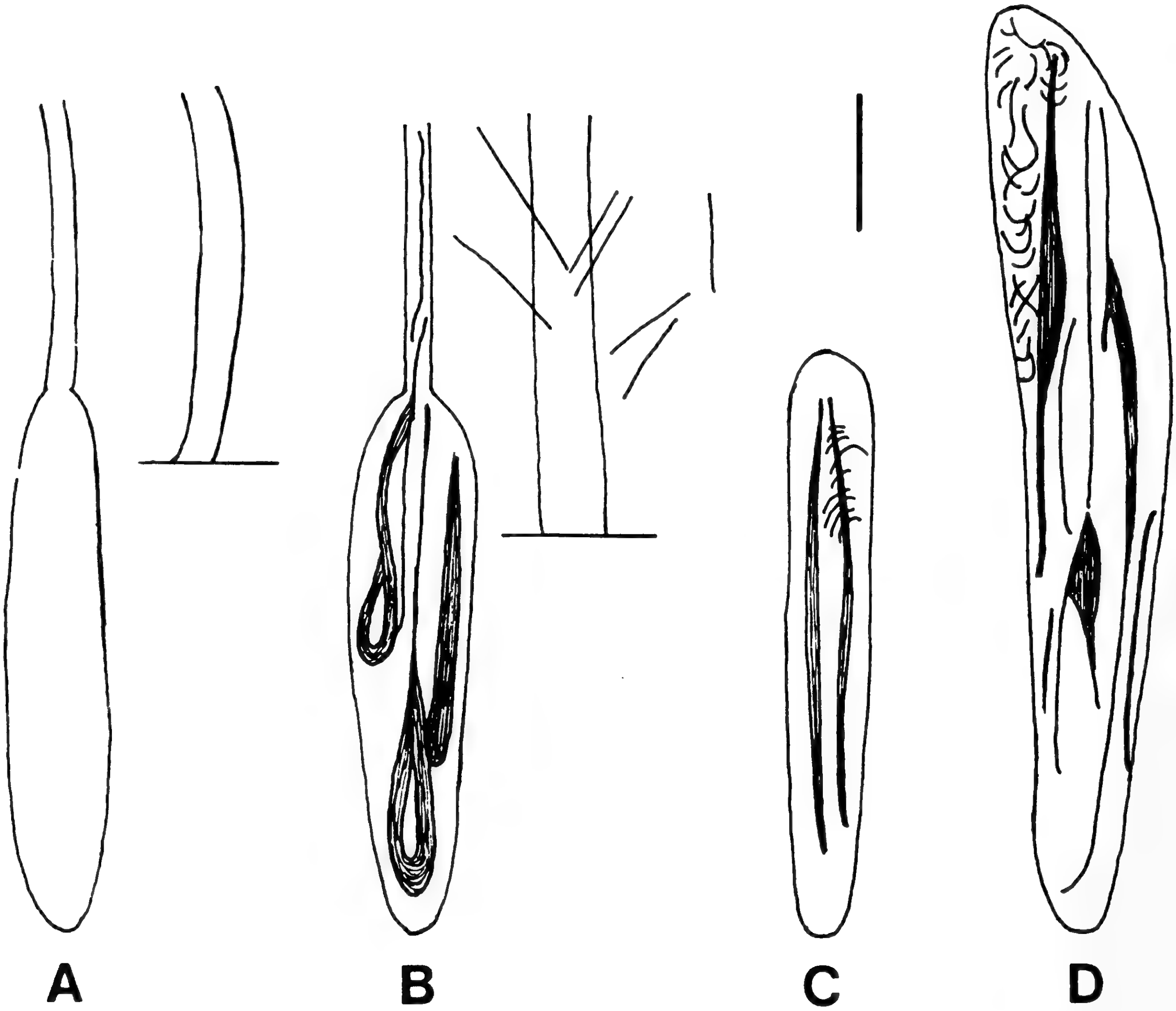

Fig. 5. Agaricysts from the mesenterial filaments, scale = 10 μm. A, discharged capsule and spineless tubule of *Agaricia agaricites*; B, discharging capsule and tubule with few attached and detached spines of *Agaricia agaricites*; C, undischarged capsule of *Pavona* sp.; D, undischarged capsule of *Leptoseris cucullata*.

somewhat longer than in p-rhabdoids D(3). It was only observed in the tentacles of species of *Fungia* and *Halomitra*.

Agaricysts
(Figs. 5, 6)

Description.—Capsule elongated; thick-walled; usually has a somewhat crushed appearance. Capsular content only slightly refractive. Tubule occupies almost whole length of capsule; arranged in two or three parallel bands (Fig. 5); running along longer axis of capsule. Apparently some spines are found around some of these bands (Figs. 5C, 5D). Discharged tubule long; anisodiametric (Fig. 5A). Proximal part of tubule approximately 2.4 mm in width, 4.0 mm in median region, and 1.6 mm close to tapering tip. Discharged tubule may seem to be spineless; however, spines can be observed on tubule surface without a distinct arrangement. Few unattached spines close to discharged tubule also present (Fig. 5B). Spines long; seem to loose contact with tubule when it discharges. Discharged tubule forms almost right angle with longer axis of capsule (Fig. 6).

Remarks.—This is a previously undescribed cnida, which was observed only in the mesenterial filaments of members of Agariciidae. Mariscal et al. (1977) classified the coelenterate cnidae in two major groups; helicoptychonemes and heteroptychonemes. The first group presents the un-

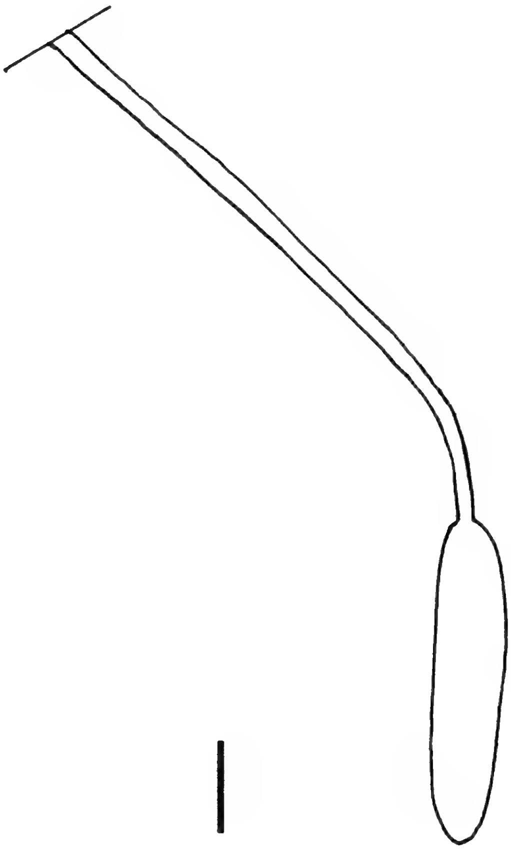

Fig. 6. Agaricyst from the mesenterial filaments of *Agaricia agaricites*, scale = 10 μm. Discharged tubule forming almost a right angle with the longer axis of the capsule.

discharged thread helically folded to form multiple pleats in length and three pleats in circumference and includes the nematocysts and spirocysts. The second one have the undischarged thread not helically folded, with a variable number of pleats in circumference but none in length, and includes the ptychocysts. The agaricysts are similar to the heteroptychonemes described by Mariscal et al. (1977). Both present the uneverted tubule not helically arranged inside the capsule. When discharged, both tubules are anisodiametric, with longitudinal ridges along their length. Commonly, both tubules evert at an angle of about 60 to 90 degrees with the plane of the capsule.

Discussion

A detailed study of the cnidae can provide characters for a better understanding of the different groups of Cnidaria. This holds true even among taxa in which cnidae have been previously considered of less taxonomic value. Even spirocysts, which show less structural variation, can be used as a source for comparative studies.

Weill's major work (1934) was a turning point in the study of nematocysts. However, its broad scope did not allow him to detail the cnidae of all cnidarian groups. In Scleractinia, for example, he superficially examined only eight species. He overlooked many cnidae, and he did not examine their distribution within the polyp. As the knowledge of the morphological structure of the cnidae of some groups accumulated, it became clear that some of Weill's categories included a wide variety of morphological types. The "rhabdoïdes" of Weill (1934), for example, represent a group of different types of nematocysts with few characteristics in common, and a most diverse structure. Schmidt (1974) divided the "rhabdoïdes" of Weill (1934) into four basic types: p-rhabdoids A, B, C and D. He subdivided these in some subcategories, and created a new terminology. Although his terminology is poorly known, his typology was accepted by some workers (den Hartog 1980, Östman 1983, England 1991, Pires & Pitombo 1992, Schlenz & Belém 1992). England (1991), pointed out the difficulties in using and adopting a codified alphanumeric system, without the descriptive elements of Weill's classification. Nevertheless, Schmidt's system is the one that most closely represents the diversity of the Anthozoa cnidae, and therefore is partially adopted in this paper.

According to Schmidt (1972, 1974) Scleractinia presents only one type of p-rhabdoid belonging to his category D. When discharged, the shaft of this type is rarely longer, frequently equal or shorter, than the length of the capsule (Schmidt 1972), corresponding to the microbasic state of Weill. However, the p-rhabdoids D(4) and D(5) cited in this paper, even when examined only undischarged, belong to the macrobasics of Weill, in contradiction to Schmidt's definition of his type D.

Moreover, p-rhabdoids D present the same basic structure as p-rhabdoids A. Both of them have the length of the shaft and capsule ratio as described above. I believe the p-rhabdoids A and D belong to the same unit, as suggested by den Hartog (1980).

Problems in fitting cnidae into a previous system of classification led different authors to propose their own system (see synonymies here). However, some of these authors, and others who used these systems, did not always clearly define and illustrate the types they were working with. As a result, the usefulness of some papers on cnidae was partly lost. Misunderstandings related to the use of different terminologies must be avoided by using more precise descriptions and illustrations, based on large arrays of material.

Corals and corallimorpharians present the four basic morphological patterns of cnidae found in Hexacorallia, with the most diversified cnidae: spirocysts, holotrichs, b- and p-rhabdoids. Agaricysts were observed only in Agariciidae. In agaricysts, the arrangement of the undischarged tubule within the capsule and the appearance of the tubule following discharge look very similar to that of the heteroptychonemes described by Mariscal et al. (1977). The study of its ultrastructure in eletronic microscopy would be very helpful for describing it more precisely.

The evidence of the diversity occurring in the cnidae of Scleractinia presented in this paper support the important role of soft tissues as a source of useful taxonomic characters. The inclusion of morphological descriptions of cnidae in further studies will contribute to improving studies on coral taxonomy and systematics.

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Literature Cited

Abe, N. 1938. Feeding behaviour and the nematocysts of *Fungia* and 15 other species of corals.—Palao Tropical Biological Station Studies 3:469–521.

Cairns, S. D. 1990. Antarctic Scleractinia. Pp.1–78 *in* J. W. Wägele & J. Sieg, eds., Synopses of the Antarctic Benthos. Vol. 1. Koeltz Scientific Books, Koenigstein.

Carlgren, O. 1940. A contribution to the knowledge of the structure and distribution of the cnidae in the Anthozoa.—Lunds Universitets Arsskrift. N. F. Avd. 2, Bd 36, Nr 3:1–62.

Chevalier, J. P., & L. Beauvais. 1987. Pp. 679–764 *in* P. P. Grassé, ed., Systématique. Traité de Zoologie. Anatomie, systématique, biologie. Tome III. Cnidaires, Anthozoaires, Masson, Paris, 859 pp.

Cutress, C. E. 1955. An interpretation of the structure and distribution of cnidae in Anthozoa.—Systematic Zoology 4(5):120–137.

England, K. W. 1991. Nematocysts of sea anemones (Actiniaria, Ceriantharia and Corallimorpharia: Cnidaria): nomenclature.—Hydrobiologia 216/217:691–697.

Gosse, P. H. 1860. Actinologia Britannica: a history of British sea-anemones and corals. Van Voorst, London, 362 pp.

Gravier-Bonnet, N. 1987. Pp. 43–45 *in* J. Bouillon, F. Boero, F. Cicogna, & P. F. S. Cornelius, eds., Nematocysts as taxonomic discriminations in the thecate hydroids. Modern Trends in the Systematics, Ecology and Evolution of Hydroids and Hydromedusae, Oxford University Press, New York, 328 pp.

Hartog, J. C. Den. 1980. Caribbean Shallow Water Corallimorpharia.—Zoologische Verhandelingen 176:1–83.

Mariscal, R. N. 1974. Nematocysts. Pp. 129–178 *in* L. Muscatine & H. M. Lenhoff, eds., Coelenterate Biology: Reviews and New Perspectives. Academic Press, New York.

———. 1984. Cnidaria: cnidae. Pp. 57–68 *in* J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards, eds., Biology of integument. Vol. 1. Invertebrates. Springer-Verlag, Berlin.

———, E. J. Conklin, & C. H. Bigger. 1977. The ptychocyst, a major new category of cnida used in tube construction by a cerianthid anemone.—Biological Bulletin 152:392–405.

Matthai, G. 1914. A revision of the recent colonial astraeidae possessing distinct corallites. Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905 under the leadership of Mr. J. Stanley Gardiner, Vol. VI.—The Transactions of the Linnean Society of London (Zoology) 2nd series, 17:1–140.

———. 1928. A monograph of the recent meandroid Astraeidae.—Catalogue of the Madreporarian corals in the British Museum (Natural History) 7:1–288

Östman, C. 1987. Pp. 67–82 *in* J Bouillon, F. Boero, F. Cicogna, & P. F. S. Cornelius, eds., New techniques and old problems in hydrozoan systematics. Modern Trends in the Systematics, Ecology and Evolution of Hydroids and Hydromedusae, Oxford University Press, New York, 328 pp.

Pires, D. O. 1988. *Tricnidactis errans* n. gen, n. sp. (Cnidaria, Actiniaria, Haliplanellidae), from Guanabara Bay, Rio de Janeiro, Brazil.—Revista Brasileira de Biologia 48(3):507–516.

———, & C. B. Castro. 1997. Scleractinia and Corallimorpharia: an analysis of cnidae affinity.—Proceedings of the 8th International Coral Reef Symposium, In press.

———, & F. B. Pitombo. 1992. Cnidae of the Brazilian Mussidae (Cnidaria: Scleractinia) an their value in taxonomy.—Bulletin of Marine Science 51(2):231–244.

Schlenz, E., & M. J. C. Belém. 1992. *Phyllactis correae* n. sp. (Cnidaria, Actiniaria, Actiniidae) from Atol das Rocas, Brazil, with notes on *Phyllactis flosculifera* (Lesueur, 1817).—Boletim de Zoologia, Universidade de São Paulo 12: 91–117.

Schmidt, H. 1969. Die nesselkapseln der Aktinien und ihre differential diagnostische bedeutung.—Helgoländer wissenschaftliche Meeresuntersuchungen 19(2):284–317.

———. 1972. Die nesselkapseln der Anthozoen und ihre bedeutung für die phylogenetische systematik.—Helgoländer wissenschaftliche Meeresuntersuchungen 23:422–458.

———. 1974. On evolution in the Anthozoa. Pp. 533–560 *in* Proceedings of the Second International Coral Reef Symposium, Vol. 1, Brisbane.

Seifert, R. 1928. Die Nesselkapseln der Zoantharien und ihre differentialdiagnostiche Beceutung.—Zoologische Jahrbücher Band 55 Heft 5/6:419–500.

Song, J. I. 1988. A systematic study on the Korean Anthozoa 11. Cnidae of Scleractinia.—The Korean Journal of Systematic Zoology Special Issue 2:25–36.

Stephenson, T. A. 1928. British Sea Anemones. Vol. I (Series 113 for 1927), Pp. xii + 148. Ray Society London.

Thomason, J., & B. E. Brown. 1986. The cnidom: an index of aggressive proficiency in scleractinian corals.—Coral Reefs 5(2):93–101.

Tilbury, R., & A. M. Cameron. 1989. Cnidom of *Goniopora* species in 5th International Conference on Coelenterate Biology. Programme and abstracts. P. 95. July 10-14, 1989, University of Southampton, Southampton.

Vervoort, W. 1987. Pp. 83–103 *in* J. Bouillon, F. Boero, F. Cicogna, & P. F. S. Cornelius, eds., Evaluation of taxonomic characters in the Hydroida, particularly in the Thecata (=Leptomedusae). Modern Trends in the Systematics, Ecology and Evolution of Hydroids and Hydromedusae, Oxford University Press, New York, 328 pp.

Weill, R. 1934. Contribution à l'étude des cnidaires et de leurs nématocystes. I, II.—Travaus de la Station zoologique de Wimereux 10 & 11:1–701.

Wells, J. W. 1956. Scleractinia. Pp. 328–477 *in* R. C. Moore, ed., Treatise on Invertebrate Paleontology, part F. Geological Society of America and Kansas University Press, Lawrence, 498 pp.

Appendix

Collection data of studied material from the Museu Nacional, Universidade Federal do Rio de Janeiro

(MNRJ). Donations of some specimens were obtained from the Instituto Oceanográfico, Universidade de São Paulo (IO/USP), through Dr. A. M. S. Vanin; from the Nationaal Natuurhistorisch Museum (Rijksmuseum van Natuurlijke Historie) (RMNH), through Dr. J. C. den Hartog; from the National Museum of Natural History, Smithsonian Institution (USNM), through Dr. S. D. Cairns; from the Bodega Marine Laboratory (BML) through Dr. C. Hand and from the Academia de Ciências de Cuba (ACC), through Dr. A. Herrera.

Agaricia agaricites (Linnaeus, 1758). MNRJ 02686. Brazil, Bahia, Nova Viçosa, Coroa Vermelha Reef, coll. D. O. Pires 26 Jan 1991, det. D. O. Pires 3 Nov 1994.

Agaricia agaricites (Linnaeus, 1758). MNRJ 02051. Brazil, Bahia, Prado, Coroa de Cumuruxatiba Reef, coll. C. B. Castro Jan 1992, det. D. O. Pires Jan 1992.

Agaricia agaricites (Linnaeus, 1758). MNRJ 02052. Brazil, Bahia, Prado, Coroa de Cumuruxatiba Reef, coll. C. B. Castro Jan 1992, det. D. O. Pires Jan 1992.

Agaricia agaricites (Linnaeus, 1758). MNRJ 02684. Brazil, Bahia, Abrolhos, SE Pedra Lixa, 16 m, coll. D. O. Pires 25 Jan 1991, det. D. O. Pires 3 Nov 1994.

Agaricia agaricites (Linnaeus, 1758). MNRJ 02685. Brazil, Bahia, Abrolhos, SE Pedra Lixa, 16 m, coll. D. O. Pires 25 Jan 1991, det. D. O. Pires 3 Nov 1994.

Agaricia fragilis Dana, 1848. MNRJ 02681. Brazil, Bahia, Prado, Aprofundados de Cumuruxatiba Reefs, coll. P. S. Young 30 Jan 1991, det. D. O. Pires 1 Nov 1994.

Astrangia rathbuni Vaughan, 1906. MNRJ 02600. Brazil, Rio de Janeiro, Angra dos Reis, Queimada Pequena Island, coll. Coelenterology/MNRJ 6 Dec 1992, det. D. O. Pires 31 Aug 1994.

Astrangia rathbuni Vaughan, 1906. MNRJ 01093. Brazil, Santa Catarina, Porto Belo, Quatro Ilhas Beach, coll. D. O. Pires 25 Jan 1986, det. D. O. Pires.

Astrangia rathbuni Vaughan, 1906. MNRJ 02615. Brazil, Rio de Janeiro, Guanabara Bay, near "lage do Cação", coll. P. S. Young 19 Jun 1991, det. D. O. Pires 8 Sep 1994.

Balanophyllia europaea (Risso, 1826). MNRJ 00090. Spain, Mediterranean, Cala Reona, Cabo Depalos, 1–2 m, coll. H. Zibrowius, 9 Apr 1981, det. H. Zibrowius. Obs.: donation RMNH.

Balanophyllia sp. MNRJ 02377. Brazil, Bahia, Prado, Aprofundados de Cumuruxatiba Reefs. 17°00′S, 039°05′W, 18 m, coll. C. B. Castro 30 Jan 1991, det. S. D. Cairns. Obs.: donation USNM (USNM 90329).

Caryophyllia ambrosia caribbeana Cairns, 1979. MNRJ 02376. Brazil, São Paulo, off Couves Island. 24°35.05′S, 044°12′W, 600 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. P. S. Young & D. O. Pires 2 Mar 1994. Obs.: donation IO/USP.

Caryophyllia cornuformis Pourtalès 1868. MNRJ 02442. Brazil, São Paulo, off Couves Island. 24°35.05′S, 044°12′W, 600 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. S. D. Cairns May 1991. Obs.: donation IO/USP.

Cladocora arbuscula (Lesueur, 1821) MNRJ 02550. USA, off Florida, Gulf of Mexico. 25°45.53′N, 082°31.37′W coll. Continental Shelf Ass. MMS/BLM 9 May 1983, det. S. D. Cairns. Obs.: donation USNM (USMN 71945).

Cladocora debilis Milne Edwards & Maime, 1849. MNRJ 02407. Brazil, São Paulo, off Couves Island. 24°23.03′S, 044°18′W, 240 m, coll. R/V *Prof. W. Besnard* 8 Dec 1988, det. P. S. Young & D. O. Pires 7 Mar 1994. Obs.: donation IO/USP.

Corynactis californica Carlgren, 1936. MNRJ 02130. USA, California, Bodega Harbor, coll. C. Hand, det. C. Hand. Obs.: donation BML.

Corynactis sp. MNRJ 01453. Brazil, Rio de Janeiro, Rio de Janeiro, Cagarras Islands, 20.5 m, coll. C. C. Ratto 19 Nov 1988.

(?) *Cycloseris marginata* (Boschma, 1923). MNRJ 02118. Indonesia, SW Sulawesi, coll. B. W. Hoeksema, 2 May 1985. Obs.: donation RMNH.

Dasmosmilia lymani (Pourtalès, 1871). MNRJ 02372. Brazil, São Paulo, off Couves Islands. 24°25′S, 044°16.05′W, 320 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. P. S. Young & D. O. Pires 2 Mar 1994. Obs.: donation IO/USP.

Dasmosmilia variegata (Pourtalès, 1871). MNRJ 02373. Brazil, São Paulo, off Couves Islands. 24°25′S, 044°16.05′W, 320 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. P. S. Young & D. O. Pires 2 Mar 1994. Obs.: donation IO/USP.

Deltocyathus calcar Pourtalès, 1874. MNRJ 02378. Brazil, São Paulo, off São Sebastião Island. 24°42.05′S, 044°30′W, 320 m, coll. R/V *Prof. W. Besnard* 6 Dec 1988, det. P. S. Young & D. O. Pires 3 Mar 1994. Obs.: donation IO/USP.

Deltocyathus calcar Pourtalès, 1874. MNRJ 02380. Brazil, São Paulo, off Vitória Island. 24°31′S, 044°28′W, 240 m, coll. R/V *Prof. W. Besnard* 8 Dec 1988, det. P. S. Young & D. O. Pires 3 Mar 1994. Obs.: donation IO/USP.

Deltocyathus eccentricus Cairns, 1979. MNRJ 02409. Brazil, São Paulo, off Vitória Island. 24°41.01′S, 044°18.05′W, 510 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. S. D. Cairns May 1994. Obs.: donation IO/USP.

Deltocyathus eccentricus Cairns, 1979. MNRJ 02411. Brazil, São Paulo, off Couves Island. 24°35.05′S, 044°12′W, 600 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. S. D. Cairns May 1994. Obs.: donation IO/USP.

Deltocyathus italicus (Michellotti, 1838). MNRJ 02412. Brazil, São Paulo, off Vitória Island.

24°41.01′S, 044°18.05′W, 510 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. S. D. Cairns May 1994. Obs.: donation IO/USP.

Deltocyathus italicus (Michellotti, 1838). MNRJ 02413. Brazil, São Paulo, off Couves Island. 24°35.05′S, 044°12′W, 600 m, coll. R/V *Prof. W. Besnard* 7 Dec 1988, det. S. D. Cairns May 1994. Obs.: donation IO/USP.

Dendrophyllia sp. MNRJ 02352. Cabo Verde, S coast of São Tiago, SE Porto. 14°55′N, 023°30′W, 15 m, coll. 5 Jun 1982. Obs.: CANCAP VI 1982, Sta. 6 DO1 "Tydan", donation RMNH.

Discosoma carlgreni (Watzl, 1922). MNRJ 00331. Brazil, Espírito Santo, Guarapari, Três Ilhas Archipelago, coll. S. Rosso et al. 17 Jul 1981, det. E. Schlenz & M. J. C. Belém 15 Oct 1981.

Discosoma carlgreni (Watzl, 1922). MNRJ 02259. Brazil, Bahia, Abrolhos Archipelago, coll. F. B. Pitombo 23 Nov 1993, det. S. M. Pinto 8 Dec 1993.

Favia leptophylla Verrill, 1868. MNRJ 02280. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. D. O. Pires et al. 24 Jan 1991, det. D. O. Pires 29 Dec 1993.

Favia leptophylla Verrill, 1868. MNRJ 02574. Brazil, Bahia, Abrolhos, SE Pedra Lixa Reef, coll. Coelenterology/MNRJ 25 Jan 1991, det. D. O. Pires 26 Aug 1994.

Favites abdita (Ellis & Solander, 1786). MNRJ 02342. Australia, Queensland, Swain Reefs Complex, Sweetlip Reef, 3–5 m, coll. P. Alderslade 4 Jul 1981, det. F. B. Pitombo 25 Jan 1981 Obs.: donation RMNH.

Flabellum sp. MNRJ 02720. Off Guiana. 07°56′N, 057°12′W, 618 m, coll. "Luymes" Guyana Shelf Expedition 1 Sep 1970. Obs.: donation RMNH.

Fungia (*Cycloseris*) *sinensis* Milne Edwards & Haime, 1851. MNRJ 02116. Indonesia, SW Sulames, coll. B. W. Hoeksena, 2 May 1985, det. B. W. Hoeksema 2 May 1985. Obs.: donation RMNH.

Fungia (*Fungia*) *fungites* (Linnaeus, 1758). MNRJ 02679. Indonesia, S Sulawesi, N side of Samalona, 2–5 m, coll H. Moll 20 Nov 1980. Obs.: donation RMNH.

Fungia (*Verrillofungia*) *repanda* Dana, 1846. MNRJ 02120. Indonesia, S Sulawesi, N side of Samalona, coll. H. Moll, 20 Nov 1980, det. H. Moll, 20 Nov 1980. Obs.: donation RMNH.

Fungia (*Verrillofungia*) *concinna* (Verrill, 1864). MNRJ 02113. Indonesia, reef S. of Pilau Tikus, NW Java, coll. B. W. Hoeksema, 7 May 1983, det. B. W. Hoeksema, 7 May 1983. Obs.: conation RMNH.

Fungiacyathus sp. MNRJ 02391. Brazil, São Paulo, off Vitória Island. 24°31′S, 044°28′W, 250 m, coll. R/V *Prof. W. Besnard* 8 Dec 1988. Obs: donation IO/USP.

Fungiacyathus sp. MNRJ 02393. Brazil, São Paulo, off Ilha de São Sebastião, 320 m, coll. R/V *Prof. W. Besnard* 6 Dec 1988. Obs.: donation IO/USP.

Goniopora tenuidens (Quelch, 1886). MNRJ 02459. Australia, Queensland, Swain Reefs Complex, Sweetlip Reef, 3–5 m, coll. P. Alderslade 4 Jul 1981, det. D. O. Pires May 1994. Obs.: donation RMNH.

Halomitra pileus (Linnaeus, 1758). MNRJ 02119. Indonesia, North of Pulau Tikus, NW Java, coll. B. W. Hoeksema 11 May 1983, det. B. W. Hoeksema 11 May 1983. Obs.: donation RMNH.

Herpolitha limax Esper, 1797. MNRJ 02115. Indonesia, W of Pulau Tikus, NW Java, coll. B. W. Hoeksema 10 May 1985, det. B. W. Hoeksema, 10 May 1985. Obs.: donation RMNH.

Herpolitha limax Esper, 1797. MNRJ 02111. Indonesia, N side of Pulau Pajung, coll. B. W. Hoeksema 12 May 1983, det. B. W. Hoeksema 12 May 1983. Obs.: donation RMNH.

Javania cailleti (Duchassaing & Michelotti, 1864). MNRJ 02383. Brazil, São Paulo, off São Sebastião Island. 24°35.04′S, 044°33.03′W, 184 m, coll. R/V *Prof. W. Besnard* 6 Dec 1988, det. P. S. Young & D. O. Pires 3 Mar 1994. Obs.: donation IO/USP.

Javania cailleti (Duchassaing & Michelotti, 1864). MNRJ 02384. Brazil, São Paulo, off Vitória Island. 24°23.02′S, 044°24.08′W, 180 m, coll. R/V *Prof. W. Besnard* 20 Jul 1987, det. P. S. Young & D. O. Pires 3 Mar 1994. Obs.: donation IO/USP.

Leptopenus antarcticus Cairns, 1989. MNRJ 02554. Antarctica, Ross Sea, approx. 200 Km W of Pennel Bank. 74°55′S, 174°12′W, 2022–2060 m, coll. R/V *Eltanin,* Usarp 7 Feb 1988, det. S. D. Cairns. Obs.: donation USNM (USNM 47482, 2 paratypes).

Leptoseris cucullata (Ellis & Solander, 1786). MNRJ 02561. Venezuela, Curaçao, Isle Bay, 20 m, coll. R. P. M. BAK. Obs.: donation P. S. Young (MNRJ).

Lithophyllum mokai Hoeksema, 1989 MNRJ 02114. Indonesia, SW Sulawesi, coll. B. W. Hoeksema 2 May 1985. Obs.: donation RMNH.

Lobophyllia hemprichii (Ehrenberg 1834). MNRJ 02129. Seychelles, Alphonse Atoll, SE of the lagoon. 07°02′S, 052°44′E, 0–8 m, coll. R/V *Tyro* Seychelles Expedition 4 Jan 1993, det. J. C. den Hartog. Obs.: Netherlands Indian Ocean Expedition, donation RMNH.

Lobophyllia sp. MNRJ 02677. Australia, Queensland, Swain Reefs Complex, Sweetlip Reef, 3–5 m, coll. P. Alderslace 4 Jul 1981. Obs.: donation RMNH.

Madracis decactis (Lyman, 1859). MNRJ 02125. Brazil, Bahia, Parcel das Paredes Reefs, SE Pedra Lixa, coll. Coelenterology/MNRJ 25 Jan 1991, det. D. O. Pires 25 Jan 1991.

Madracis decactis (Lyman, 1859). MNRJ 02070. Brazil, Rio de Janeiro, Angra dos Reis, Queimada Pequena Island, coll. D. O. Pires et al. 6 Dec 1992, det. D. O. Pires 28 Dec 1992.

Madracis decactis (Lyman, 1859). MNRJ 02124. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 10 m, coll. Coelenterology/MNRJ 24 Jan 1991, det. D. O. Pires 24 Jan 1991.

Madracis decactis (Lyman, 1859). MNRJ 02127. Brazil, Bahia, Prado, Aprofundados de Cumuruxatiba Reefs, coll. Coelenterology/MNRJ 30 Jan 1991, det. D. O. Pires 30 Jan 1991.

Madracis decactis (Lyman, 1859). MNRJ 02680. Brazil, Rio de Janeiro, Angra dos Reis, "Ponta do Cantador", coll. F. B. Pitombo Feb 1989, det. D. O. Pires 1 Nov 1994.

Meandrina braziliensis (Milne Edwards & Haime, 1848). MNRJ 02275. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. D. O. Pires et al. 24 Jan 1991, det. D. O. Pires 21 Dec 1993.

Meandrina braziliensis (Milne Edwards & Haime, 1848). MNRJ 02276. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. Coelenterology/MNRJ 24 Jan 1991, det. D. O. Pires 21 Dec 1993.

Meandrina braziliensis (Milne Edwards & Haime, 1848). MNRJ 02277. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. D. O. Pires et al. 24 Jan 1991, det. D. O. Pires 21 Dec 1993.

Meandrina braziliensis (Milne Edwards & Haime, 1848). MNRJ 02278. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, coll. D. O. Pires et al. 24 Jan 1991, det. D. O. Pires 21 Dec 1993.

Montastrea cavernosa (Linnaeus, 1767). MNRJ 01441. Brazil, Bahia, Abrolhos Archipelago, Santa Bárbara Island, 5.2 m, coll. A. C. Marques & F. D. Amaral 7 Mar 1989, det. F. D. Amaral 5 Apr 1989.

Montastrea cavernosa (Linnaeus, 1767). MNRJ 01442, Bahia, Abrolhos Archipelago, Santa Bárbara Island, 4 m, coll. A. C. Marques & F. D. Amaral 7 Mar 1989, det. F. D. Amaral 5 Apr 1989.

Montastrea cavernosa (Linnaeus, 1767). MNRJ 01520. Brazil, Bahia, Abrolhos Archipelago, Santa Bárbara Island, 3 m, coll. F. D. Amaral & S. M. Pinto 5 Aug 1989, det. F. D. Amaral 15 Aug 1989.

Montastrea cavernosa (Linnaeus, 1767). MNRJ 02350. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. Coelenterology/MNRJ 24 Jan 1991, det. D. O. Pires 21 Dec 1993.

Montastrea cavernosa (Linnaeus, 1767). MNRJ 02612. Brazil, Bahia, Abrolhos, SE Pedra Lixa, 16 m, coll. Coelenterology/MNRJ 25 Jan 1994, det. D. O. Pires 08 Sep 1994.

Montastrea cavernosa (Linnaeus, 1767). MNRJ 02676. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. D. O. Pires 24 Jan 1991, det. D. O. Pires 19 Oct 1994.

Mussismilia braziliensis (Verrill, 1868). MNRJ 01704. Brazil, Bahia, Abrolhos Archipelago, Santa Bárbara Island, coll. F. B. Pitombo 3 Apr 1989, det. F. B. Pitombo 18 Apr 1990.

Mussismilia braziliensis (Verrill, 1868). MNRJ 01710. Brazil, Bahia, Abrolhos Archipelago, Santa Bárbara Island, Portinho, coll. F. B. Pitombo 5 Apr 1989, det. F. B. Pitombo 18 Apr 1980.

Mussismilia braziliensis (Verrill, 1868). MNRJ 01717. Brazil, Bahia, Morro de São Paulo, coll. F. B. Pitombo 22 Jan 1989, det. F. B. Pitombo 24 Apr 1980.

Mussismilia hartti (Verrill, 1868). MNRJ 01707. Brazil, Bahia, Abrolhos Archipelago, Santa Bárbara Island, coll. F. B. Pitombo 4 Apr 1989, det. F. B. Pitombo 18 Apr 1990.

Mussismilia hartti (Verrill, 1868). MNRJ 01709. Brazil, Bahia, Abrolhos Archipelago, Siriba Island, coll. F. B. Pitombo 5 Apr 1989, det. F. B. Pitombo 18 Apr 1980.

Mussismilia hartti (Verrill, 1868). MNRJ 01746. Brazil, Bahia, Morro de São Paulo, coll. F. B. Pitombo 14 Mar 1990, det. F. B. Pitombo 26 Jun 1990.

Mussismilia hispida (Verrill, 1902). MNRJ 01711. Brazil, Bahia, Abrolhos Archipelago, Santa Bárbara Island, coll. F. B. Pitombo 5 Apr 1989, det. F. B. Pitombo 18 Apr 1980.

Mussismilia hispida (Verrill, 1902). MNRJ 01718. Brazil, Pernambuco, Porto de Galinhas, coll. F. B. Pitombo 6 Mar 1990, det. F. B. Pitombo 26 Apr 1990.

Mussismilia hispida (Verrill, 1902). MNRJ 01719. Brazil, Rio de Janeiro, Angra dos Reis, Grande Island, coll. F. B. Pitombo 31 Apr 1990, det. F. B. Pitombo.

Oculina patagonica de Angelis, 1908. MNRJ 02351. Spain, Mediterranean, Portman, appr. 20 km E of Cartagena, 1 m, coll. H. Zibrowius 10 Apr 1981, det. H. Zibrowius 31 Jan 1994. Obs.: donation RMNH.

Pavona sp. MNRJ 02576. Indonesia, S. Sulawesi, N side of Samalona, 2–5 m, coll. H. Moll 20 Nov 1980. Obs.: donation RMNH.

Phyllangia americana Milne Edwards & Haime, 1850. MNRJ 02563. Brazil, Rio de Janeiro, Angra dos Reis, Botinas Islands, 2 m, coll. F. B. Pitombo 30 Jul 1991, det. D. O. Pires 26 Aug 1994.

Phyllangia americana Milne Edwards & Haime, 1850. MNRJ 01056. Brazil, Bahia, Morro de São Paulo. 3 m, coll. F. B. Pitombo 4 Mar 1987, det. P. S. Young 24 Apr 1987.

Phyllangia americana Milne Edwards & Haime, 1850. MNRJ 02601. Brazil, Rio de Janeiro, Angra dos Reis, Queimada Pequena Island, coll. Coelenterology/MNRJ 6 Dec 1992, det. D. O. Pires 31 Aug 1994.

Phyllangia americana Milne Edwards & Haime, 1850. MNRJ 02611. Brazil, Bahia, Abrolhos, Nova Vicosa Reef. 18°0047′S, 039°16.57′W, 9 m, coll. C. C. Ratto & C. B. Castro 23 Aug 1994, det. D. O. Pires 8 Sep 1994.

Physogyra lichtensteini Milne Edwards & Haime, 1851. MNRJ 02272. Seychelles, Alphonse Atoll, parte SE of the lagoon, STA SEY 788. 07°02′S, 052°44′E, 8 m, coll. R/V *Tyro* 4 Jan 1993, det. J. C. den Hartog 16 Dec 1993. Obs.: Netherlands Indian Ocean Expedition 1992/93, donation RMNH.

Physogyra lichtensteini Milne Edwards & Haime,

1851. MNRJ 02273. Seychelles, St. Joseph Atoll, NW Rim lagoon, STA SEY 754. 05°24′S, 053°19′E, coll. R/V *Tyro* 26 Dec 1992, det. J. C. den Hartog 16 Dec 1993. Obs.: Netherlands Indian Ocean Expedition 1992/93, donation RMNH.

Platygyra daedalea (Ellis & Solander, 1786). MNRJ 02346. Australia, Queensland, Swain Reefs Complex, Sweetlip Leef, 3–5 m, coll. P. Alderslade 4 Jul 1981, det. F. B. Pitombo 25 Jan 1994 Obs.: donation RMNH.

Polyphyllia talpina (Lamarck, 1801). MNRJ 02112. Indonesia, Spermonde Archipelago, SW Sulawesi, coll B. W. Hoeksema 1985, det. B. W. Hoeksema 1985. Obs.: donation RMNH.

Porites astreoides Lamarck, 1816. MNRJ 02281. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, SE Pedra Lixa, 2–16 m, coll. D. O. Pires et al. 25 Jan 1991, det. D. O. Pires 29 Dec 1993.

Porites astreoides Lamarck, 1816. MNRJ 02354. Brazil, Bahia, Nova Vicosa Reef, coll. C. B. Castro & P. S. Young Aug 1993, det. C. C. Ratto 31 Jan 1994.

Porites astreoides Lamarck, 1816. MNRJ 02713. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. Coelenterology/MNRJ 24 Jan 91, det. D. O. Pires 20 Mar 1995.

Porites astreoides Lamarck, 1816. MNRJ 02714. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. Coelenterology/MNRJ 24 Jan 91, det. D. O. Pires 20 Mar 1995.

Rhisosmilia maculata (Pourtalès, 1874). MNRJ 02390. Brazil, Bahia, Prado, Aprofundados de Cumuruxatiba Reefs, coll. C. B. Castro 30 Jan 1991, det. S. D. Cairns 4 Mar 1994.

Ricordea florida Duchassaing & Michelotti, 1860. MNRJ 02108. Cuba, La Juventud Island, Punta del Este Reef, 10 m, coll. A. Herrera 26 Aug 1992, det. M. J. C. Belém 21 Aug 1992. Obs.: donation ACC.

Scolymia wellsi Laborel, 1967. MNRJ 01198. Brazil, Bahia, Parcel dos Abrolhos Reef, Rosalina Ship wreck., 17 4 m, coll. Coelenterology/MNRJ 8 Oct 1987, det. C. C. Ratto 3 Nov 1987.

Scolymia wellsi Laborel, 1967. MNRJ 01713. Brazil, Bahia, Abrolhos Archipelago, Guarita Island, coll. F. B. Pitombo 6 Apr 1989, det. F. B. Pitombo 23 Apr 1980.

Scolymia wellsi Laborel, 1967. MNRJ 01714. Brazil, Bahia, Abrolhos Archipelago, Guarita Island, coll. F. B. Pitombo 6 Apr 1989, det. F. B. Pitombo 24 Apr 1990.

Siderastrea radians (Pallas, 1766). MNRJ 01555. Mexico, Quintana Roo, Punta Brava, coll. F. D. Amaral 11 Nov 1989, det. F. D. Amaral 7 Dec 1989.

Siderastrea stellata Verrill, 1868. MNRJ 02675. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, 5–10 m, coll. D. O. Pires 24 Jan 1991, det. D. O. Pires 19 Oct 1994.

Siderastrea stellata Verrill, 1868. MNRJ 02271. Brazil, Rio de Janeiro, Cabo Frio, Búzios, coll. F. Pitombo et al. 2 Feb 1993, det. F. B. Pitombo 5 Dec 1993.

Siderastrea stellata Verrill, 1868. MNRJ 02283. Brazil, Bahia, Abrolhos, Parcel das Paredes Reef, SE Pedra Lixa coll. D. O. Pires 25 Jan 1991, det. D. O. Pires 25 Jan 1991.

Stephanocoenia michelinii Milne Edwards et Haime, 1848. MNRJ 02121. Brazil, Bahia, Parcel das Paredes Reef, SE Pedra Lixa, coll. Coelenterology/MNRJ 25 Jan 1991, det. D. O. Pires 25 Jan 1991.

Zoopilus echinatus Dana, 1846. MNRJ 02117. Indonesia, SW Sulawesi, coll. B. W. Hoeksema 2 May 1985. Obs.: donation RMNH.

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Gnathostomulida from the Canary Islands

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Abstract.—Five species of Gnathostomulida are reported from Gran Canaria (northeastern Atlantic). One, *Paragnathiella trifoliceps* new genus, new species, represents a new genus in the family Mesognathariidae, another a new species, *Austrognathia clavigera*; one is known from the northwestern North Atlantic (*Labidognathia longicollis*), and the remaining two are cosmopolitan (*Haplognathia rosea* and *H. ruberrima*).

As part of an ongoing investigation of the taxonomy and biogeography of Gnathostomulida (Sterrer et al. 1986, Sterrer 1991a, 1991b, 1991c, 1991d, 1992, 1997), a phylum of microscopic worms inhabiting marine sand, I collected sediment samples in the Canary Islands (northeastern Atlantic) in February 1996. Of ten samples from eight localities on two islands, only one locality produced Gnathostomulida (Table 1). Samples were collected by hand, snorkeling or SCUBA, and extracted as described earlier (Sterrer 1971, 1991a). The way in which specimens and species are analyzed and described follows Sterrer (1991a). This includes the use of a relative scale of 100 units (*U*) for the body length, various indices for length-width ratios, and the mean ($\bar{X}$), standard deviation (*SD*), maximum (Max), minimum (Min), and number (*n*) of measurements.

Order Filospermoidea Sterrer, 1972

Composition.—Two families, Haplognathiidae Sterrer, 1972, and Pterognathiidae Sterrer, 1972 emend. Sterrer, 1991a.

Family Haplognathiidae Sterrer, 1972.

One genus, *Haplognathia* Sterrer, 1970.

Haplognathia rosea (Sterrer, 1969)
(Figs. 1A, 2A)

Material.—One juvenile from Gran Canaria, Playa de Las Canteras (sample C1).

Description.—The faintly reddish specimen had jaws 20 μm long, with 9 μm long rostral apophyses (apophysis index 0.45). Of the basal plate, only the rostral outline could be recorded, as well as the lack of teeth or thorns.

Discussion.—Sterrer (1997) merged *H. rosacea* Sterrer, 1970 with *H. rosea,* which is now known from the North Sea (Sterrer 1969), the northwestern Atlantic (Sterrer 1997), and the southern Pacific (Sterrer 1991a, 1991c). This species, which is difficult to distinguish from, and possibly hybridizes with *H. ruberrima,* has been redefined as having jaws with rostral apophyses less than half as long as the jaws (index 0.5 or smaller), and a basal plate that lacks thorns. In the northwestern Atlantic, jaw length ranges from 15 to 23 μm, with a mean of 18.89 μm.

Haplognathia ruberrima (Sterrer, 1966)
(Figs. 1B–G, 2B–C, Table 2)

Material.—Nine specimens, of which one adult, from Gran Canaria, Playa de Las Canteras (sample C1).

Description.—The only adult was 2150 μm long and 75 μm wide at U 41.9 (index

Table 1.—Localities and samples.

Island	Locality	Sample	Date	Depth	Substratum	Gnathostomulida spp.
Gran Canaria	Las Palmas, Playa de Las Canteras	C1	16–Feb–96	2–3 m	fine sand with sparse Cymodocea	5
	Puerto de San Nicolas	C2	17–Feb–96	2 m	fine sand with ripples	—
	Playa del Ingles	C3	18–Feb–96	4 m	very fine sand	—
	Playa de las Burras	C4	18–Feb–96	8 m	very fine sand with Cymodocea	—
	Playa Ojo de Garza	C6	18–Feb–96	intertidal	fine sand bar at river mouth	—
	Melenara	C7	18–Feb–96	intertidal	fine sand in and around beach rock	—
	Las Palmas, Playa de Las Canteras	C8	19–Feb–96	2–3 m	fine sand with sparse Cymodocea	—
	Las Palmas, Playa de Las Canteras	C9	20–Feb–96	2–3 m	fine sand with Cymodocea rhizomes	1
	Arinaga	C10	21–Feb–96	4–5 m	fine sand holes in Cymodocea bed	—
Lanzarote	La Papagaya	L1	21–Feb–96	7 m	fine sand with Cymodocea	—

28.67). The smallest intact specimen measured 310 μm by 35 μm, with a rostrum 140 μm by 35 μm; these are the dimensions of a recently hatched juvenile (Sterrer 1997). Most of the specimens were colourless to faintly pink; only one was red. All had a basal plate in the shape of a transverse, ventrally concave buckle (length 6–9 μm, width 8–13 μm; index 0.57), with rows of regularly spaced thorns on the dorsal surface. The jaws are 22–29 μm long ($\bar{X}$ = 25.57 μm), with well delimited rostral apophyses whose length usually equals or exceeds the jaw length. The jaws have one strong tooth, possibly with numerous small, thorn-like bristles surrounding it. A pair of pharyngeal glands, with fine granula and large vacuoles, is typical for this species (Fig. 1G).

Discussion.—The most cosmopolitan species of the entire phylum is now known from the North Sea and Mediterranean (Sterrer 1969), the northwestern Atlantic (Sterrer 1997), and the Pacific islands of Hawaii (Sterrer 1991b) and Fiji (Sterrer 1991a). It has been redefined as having jaws with rostral apophyses at least half as long as the jaws (index 0.5 or greater), and a basal plate that always bears thorns. The Canaries specimens fall in every respect within the limits of this highly variable species.

Order Bursovaginoidea Sterrer, 1972

Composition.—Two suborders, Scleroperalia Sterrer, 1972, and Conophoralia Sterrer, 1972.

Suborder Scleroperalia Sterrer, 1972

Composition.—Eight families, Agnathiellidae Sterrer, 1972; Mesognathariidae Sterrer, 1972; Clausognathiidae Sterrer, 1992; Gnathostomariidae Sterrer, 1972; Rastrognathiidae Kristensen & Nørrevang, 1977; Problognathiidae Sterrer & Farris, 1975; Onychognathiidae Sterrer, 1972; and Gnathostomulidae Sterrer, 1972.

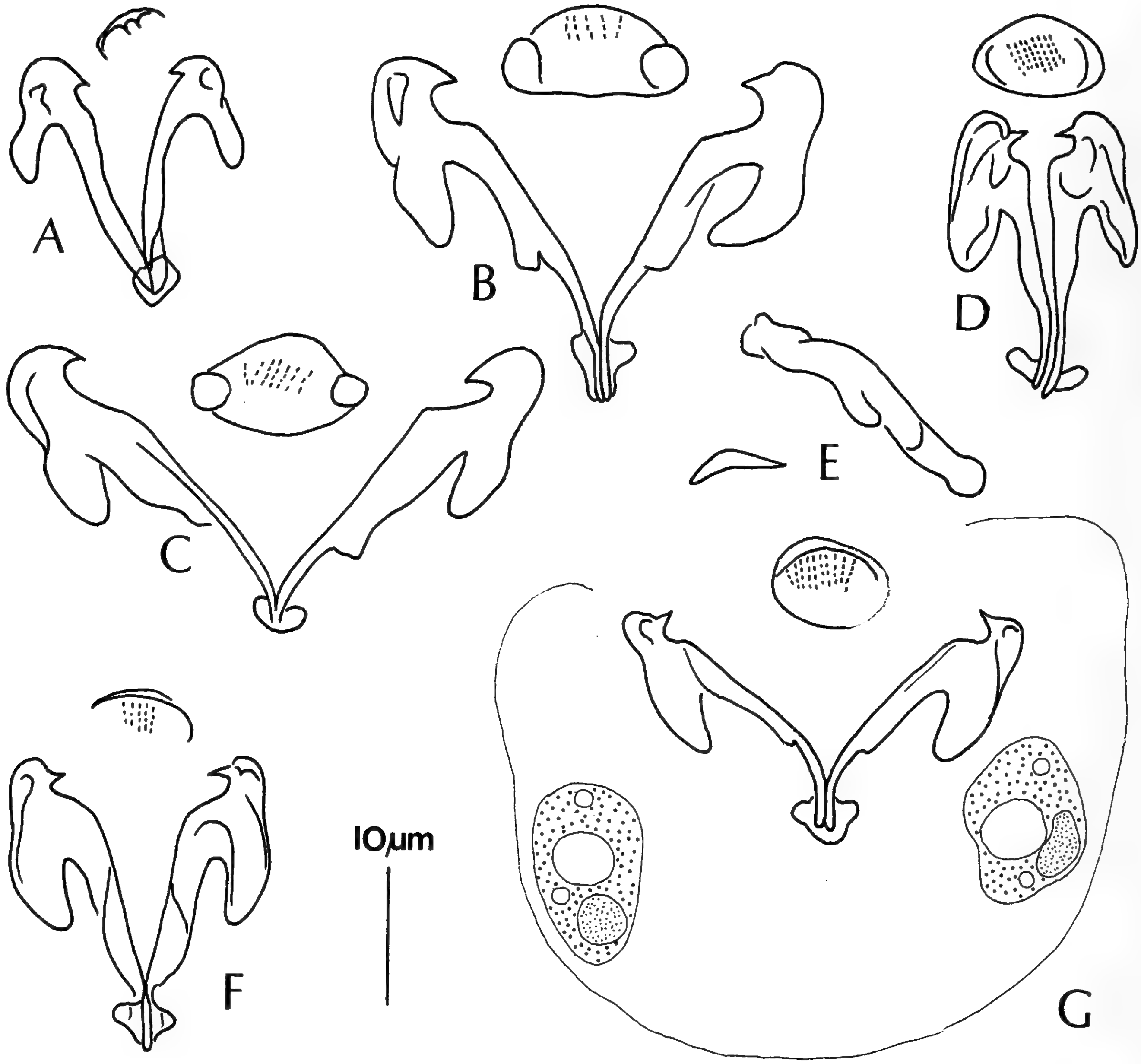

Fig. 1. *Haplognathia rosea* and *H. ruberrima.* A, *H. rosea,* jaws and rostral edge of basal plate; B–G, *H. ruberrima,* basal plate and jaws of several specimens; E shows the same specimen as D but in left lateral view. All to the same scale.

Family Agnathiellidae Sterrer, 1972

Composition.—One genus, *Agnathiella* Sterrer, 1971.

Paragnathiella, new genus

Diagnosis.—Agnathiellidae with jaws but without a basal plate. Type species: *P. trifoliceps,* new species.

Paragnathiella trifoliceps, new species
(Figs. 3A–L, 4A–E, Table 3)

Synonymy.—"Genus IV" and "Genus V" in Sterrer 1972.

Etymology.—From the Greek *par* (beside), to indicate a close relationship with *Agnathiella*; and Latin *trifoli-* (three-leaved) and *-ceps* (-headed), in reference to the clover-shaped rostrum.

Material.—18 specimens, of which 2 adult, from Gran Canaria, Playa de Las Canteras (17 from sample C1; one from sample C9).

Holotype.—USNM 174368, one adult in squeeze preparation.

Type locality.—Gran Canaria, Las Palmas, Playa de Las Canteras, fine sand with sparse sea grass (*Cymodocea nodosa*) at

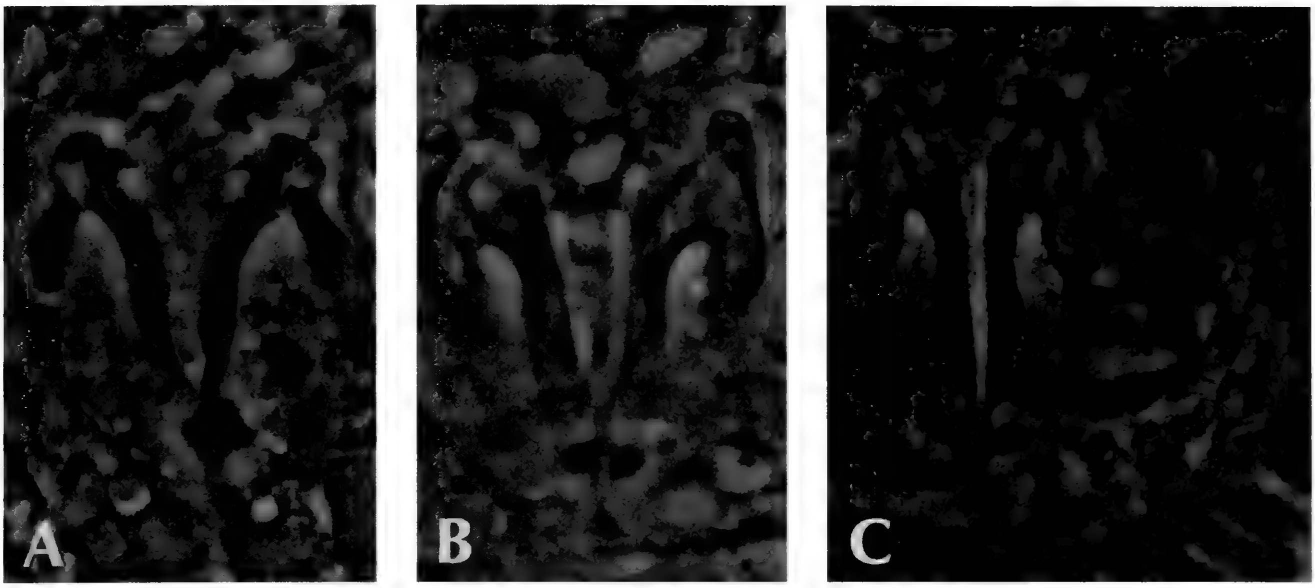

Fig. 2. *Haplognathia rosea* and *H. ruberrima,* phase contrast micrographs. A, *H. rosea,* jaws and rostral edge of basal plate (cf. Fig. 1A); B, *H. ruberrima,* jaws; C, *H. ruberrima,* jaws, and basal plate with thorns (upper right).

2–3 m depth; sample collected 16 Feb 1996.

Diagnosis.—About 1500 μm long *Paragnathiella* (body index 13.42) with clover-shaped rostrum (rostrum index 2.40). Jaws 14–17 μm long bearing 14–20 delicate teeth. Male stylet to 70 μm long.

Description.—Organization and behavior: Colourless and very opaque due to many round, greenish epidermal inclusions. Animals move rather swiftly, often carrying the posterior third of the body curled up, and are able to swim backward. Adults are to 1500 μm long and 120 μm wide at *U* 49.84 (index 13.42); the posterior end tapers into a short tail region. The rostrum of the only adult measured was 120 μm long and 50 μm wide at *U* 8.0 (index 2.40). The rostrum is somewhat clove-shaped, with a 25 μm long frontal lobe separated from lateral lobes by conspicuous ciliary pits. It seems that there is one pair of apicalia (to 16 μm long). Sensory cirri are difficult to analyze since they are poorly defined and usually join the ciliary beat. There is one pair each of frontalia (42 μm), ventralia (30 μm), dorsalia (23 μm), lateralia (40 μm), and postlateralia (35 μm). Sensory bristles originate well apart from each other, and do not coincide in dorsal view.

Digestive tract: The transversely oval mouth extends from *U* 7.3 to *U* 8.0. A basal plate is lacking. The prefrontal epidermis is thickened, and contains many round inclu-

Table 2.—*Haplognathia ruberrima.* Measurements and statistics.

	$\bar{X}$	*SD*	Max	Min	*n*
Body length of adults	2150.00		2150	2150	1
Body width of adults	75.00		75	75	1
Body index of adults	28.67		28.67	28.67	1
Rostrum index of adults	4.33		4.33	4.33	1
Jaw length	25.57	3.15	29	22	7
Apophysis index	0.52	0.03	0.56	0.48	7
Basal plate length	6.33	0.52	7	6	6
Basal plate width	11.50	2.35	13	8	6
Basal plate index	0.57	0.12	0.75	0.46	6

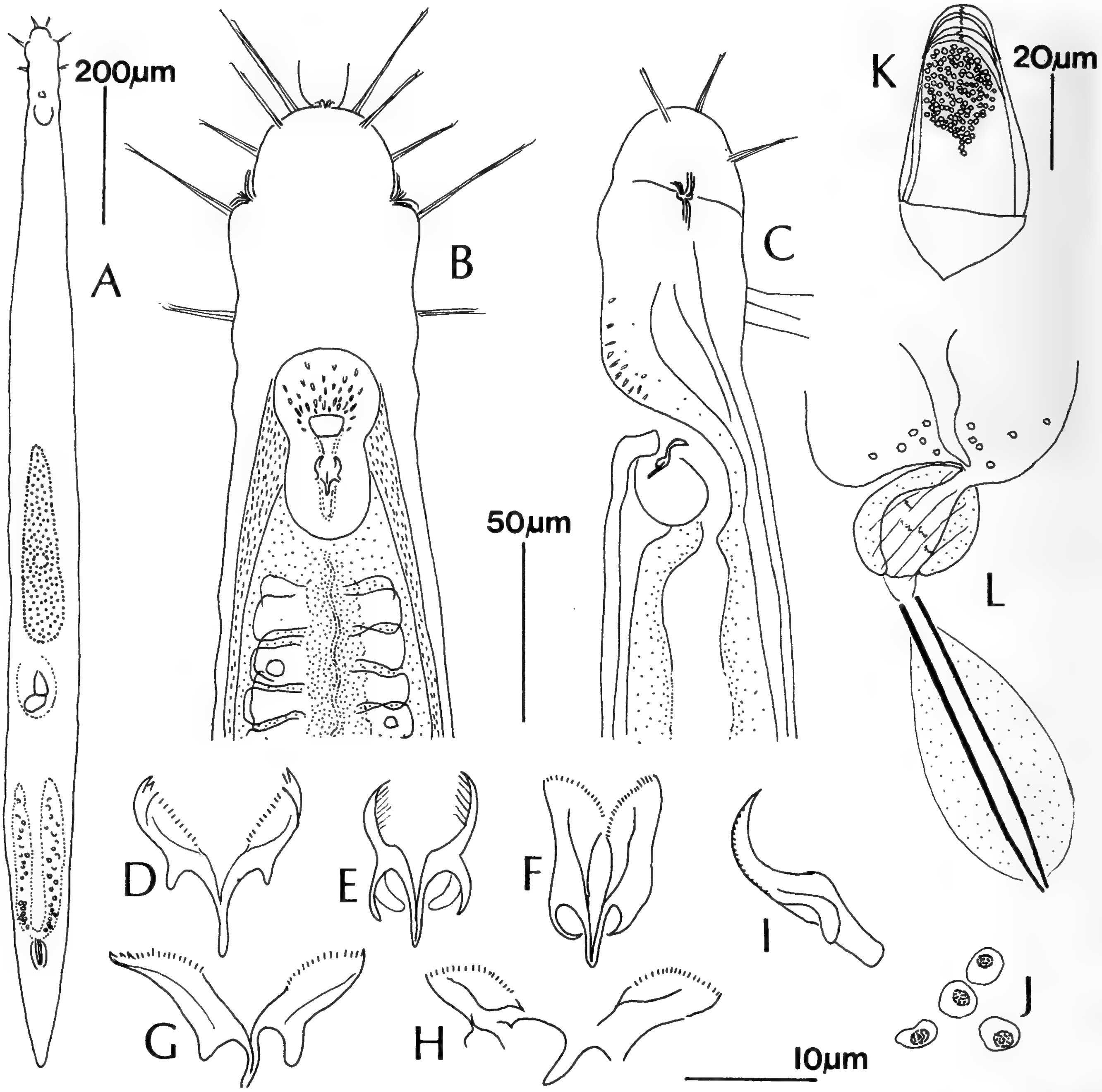

Fig. 3. *Paragnathiella trifoliceps.* A, habitus of adult; B, rostrum of adult, ventral view; C, rostrum of adult, left lateral view; D–I, jaws of several specimens; F–H, strongly squeezed, I, left lateral view; J, bursa; K, male copulatory organ; L, sperm. Scales apply to A, B–C, D–J, and K–L, respectively.

sions. The jaws are 14–17 µm long ($\bar{X}$ = 15.31 µm), delicate, forceps-shaped and lamellar. In resting position the jaws point dorsorostrally at a 50° angle from the horizontal (Fig. 3i). The symphysis is narrow, and there is a pair of rostral apophyses that converge ventro-medio-caudally. Under low squeezing the jaws appear to have only one strongly curved terminal tooth. Stronger squeezing reveals that what appears as a terminal tooth is only the dorsal endpoint of a delicate, caudo-ventrally descending lamella set with 14–20 ($\bar{X}$ = 18.00) teeth, of which all except the 2 or 3 dorsal-most are very short. The pharynx bulb is 12–17 µm ($\bar{X}$ = 14.40 µm) long behind the symphysis. The gut cells appear strongly vacuolized. There is a "lateral system" of unknown function, i.e., tissue strands between gut and epidermis which originate on either side of the pharynx and continue into the tail region.

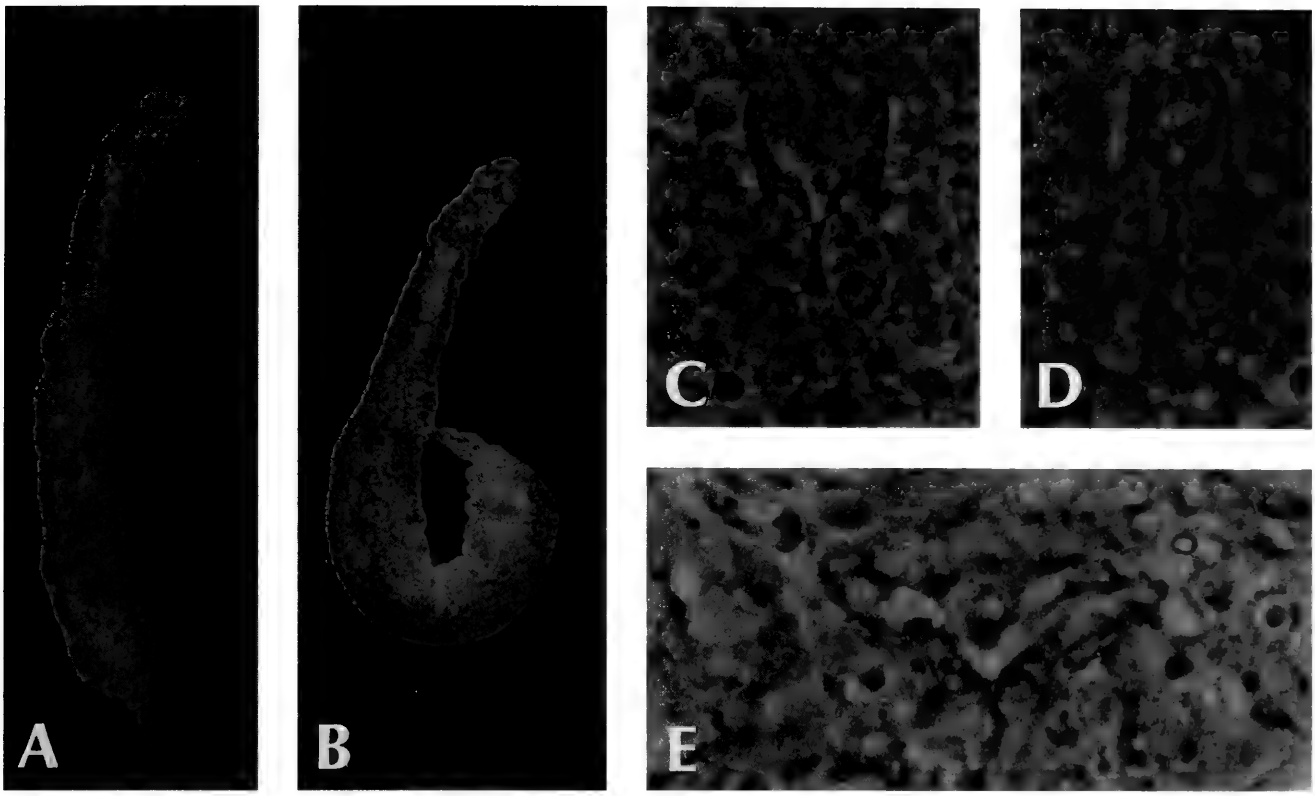

Fig. 4. *Paragnathiella trifoliceps,* phase contrast micrographs. A–B, habitus of free-swimming specimen; C–E, jaws of three specimens, E strongly squeezed to show teeth (cf. Fig. 3H).

Male system: The paired, tubular testes are 200 μm long, extending from *U* 73.3 to *U* 86.7. They empty into a muscular, ovoid vesicula seminalis 28 μm long and 22 μm wide, which in turn connects with the penis (Fig. 3L). Located between *U* 87.35 and *U* 91.48, the male stylet, made up of concentrically arranged rods, is 69–70 μm long and 5 μm wide. Sperm is irregularly round to oval, 2–3 μm in diameter, with no discernible filaments (Fig. 3J).

Female system: The only adult measured had an egg 280 μm long which extended from *U* 40.0 to *J* 58.7. The bursa system lies immediately posteriorly, extending from *U* 60.38 to *U* 64.71. It consists of an anterior bell-shaped bursa, 34–60 μm long ($\bar{X}$ = 44.00 μm) and 27–28 μm wide ($\bar{X}$ = 27.75 μm), and an unstructured, globular prebursa about 50 μm in diameter. The bursa is made up of stacked, layered cells as is usual for the suborder Scleroperalia, but cristae are lacking, and a bursa mouthpiece, although probably present, is not obvious (Fig. 3K). The bursa is usually tightly packed with sperm. A vagina was not observed.

Discussion.—This species has been known to me since 1966 when I found one specimen at Banyuls-sur-Mer (southern France). Another specimen encountered in Rovinj (Adriatic) in 1967 suggested at first that I was dealing with two separate species or even genera, to which I referred as "Genus IV" and "Genus V" (Sterrer 1972). Further material from Tunis in 1971, Rovinj and Crete in 1991, and now Gran Canaria, have convinced me that we are dealing with a single species. The possession of a cuticular bursa and stylet assigns it to Bursovaginoidea-Scleroperalia, and the lack of a basal plate, lamellar forceps structure of jaws, and loose arrangement of the sensorium place it at the lower end of the suborder. The jaws most resemble those of lower Scleroperalia, i.e., *Clausognathia* Sterrer, *Gnathostomaria* Ax, *Mesognatharia* Sterrer, *Labidognathia* Riedl, and *Tenuignathia* Sterrer. With the two latter genera, *Paragnathiella* also shares the possession of an

Table 3.—*Paragnathiella trifoliceps*. Measurements and statistics.

	$\bar{X}$	*SD*	Max	Min	*n*
Body length of adults	1460.00	56.57	1500	1420	2
Body width of adults	110.00	14.14	120	100	2
Body index of adults	13.42	2.24	15.00	11.83	2
Rostrum index of adults	2.40		2.40	2.40	1
Jaw length	15.31	0.85	17	14	13
Penis stylet length	69.50	0.71	70	69	2
Sperm length	3.00	0.00	3	3	8
Sperm width	2.38	0.52	3	2	8
Sperm index	1.31	0.26	1.50	1.00	8

unpaired apical ciliary pit; with *Clausognathia, Tenuignathia, Rastrognathia* Kristensen & Nørrevang and *Agnathiella* Sterrer, it shares the lack of a basal plate. In terms of its habitus, the clover-shape of the rostrum, and the unique possession of an extra pair of sensory cirri (postlateralia), the new genus is nearly identical with the jawless *Agnathiella.* Since the loss of basal plate and/or jaws may have occurred several times independently in lower Scleroperalia, I propose that the new genus be united with *Agnathiella* in the family Agnathiellidae.

Family Mesognathariidae Sterrer, 1972

Composition.—The 3 genera *Mesognatharia* Sterrer, 1966, *Labidognathia* Riedl, 1970, and *Tenuignathia* Sterrer, 1976.

Labidognathia longicollis Riedl, 1970
(Figs. 5A–E, 6A–B, Table 4)

Material.—Nine specimens, of which 3 are adults, from Gran Canaria, Playa de Las Canteras (sample C1).

Description.—Colorless. One adult measured 700 μm by 65 μm at *U* 42.9 (index 10.77). The basal plate is shield-shaped, 14–18 μm long and 10–13 μm wide (index 1.31), with a rostral concavity and an oval knob at the caudal end. In most specimens the rostral concavity clearly showed 8–12 longitudinal striations, whereas each of the lateral wings was set with 9–12 shorter teeth. Jaws are lamellar, 20–23 μm long ($\bar{X}$ = 21.00 μm), and provided with a somewhat coarser dorsal row of 13–15 teeth, and a finer ventral row of 10–15 teeth. Both rows are composed in such a way that a robust tooth always alternates with two delicate teeth (Fig. 5F). The male stylet was 35–48 μm long ($\bar{X}$ = 43.00 μm).

Discussion.—This is the first record of the species outside the northwest Atlantic, where it has been reported from North Carolina (Riedl 1970), and from Florida, Belize, Puerto Rico and Panama (Sterrer in press). The Canaries specimens differ from their western Atlantic counterparts in the longer male stylet (35–48 μm vs. 23–35 μm), but especially in the dentition of the basal plate. Riedl (1970) described "a row of short ridges or projections, perhaps 6 to 8 in number," on the central part of the rostral contour, and Sterrer (1997) recorded specimens from Puerto Rico with nine teeth on each of the lateral lobes. Yet nowhere have I seen specimens in which both the central ridges (or striations) and the lateral teeth were so consistently conspicuous.

Suborder Conophoralia Sterrer, 1972

Composition.—One family, Austrognathiidae Sterrer, 1971.

Family Austrognathiidae Sterrer, 1971

Composition.—Three genera, *Austrognathia* Sterrer, 1965 emend. Sterrer, 1991a; *Austrognatharia* Sterrer, 1971 emend. Sterrer, 1991a; and *Triplignathia* Sterrer, 1991d.

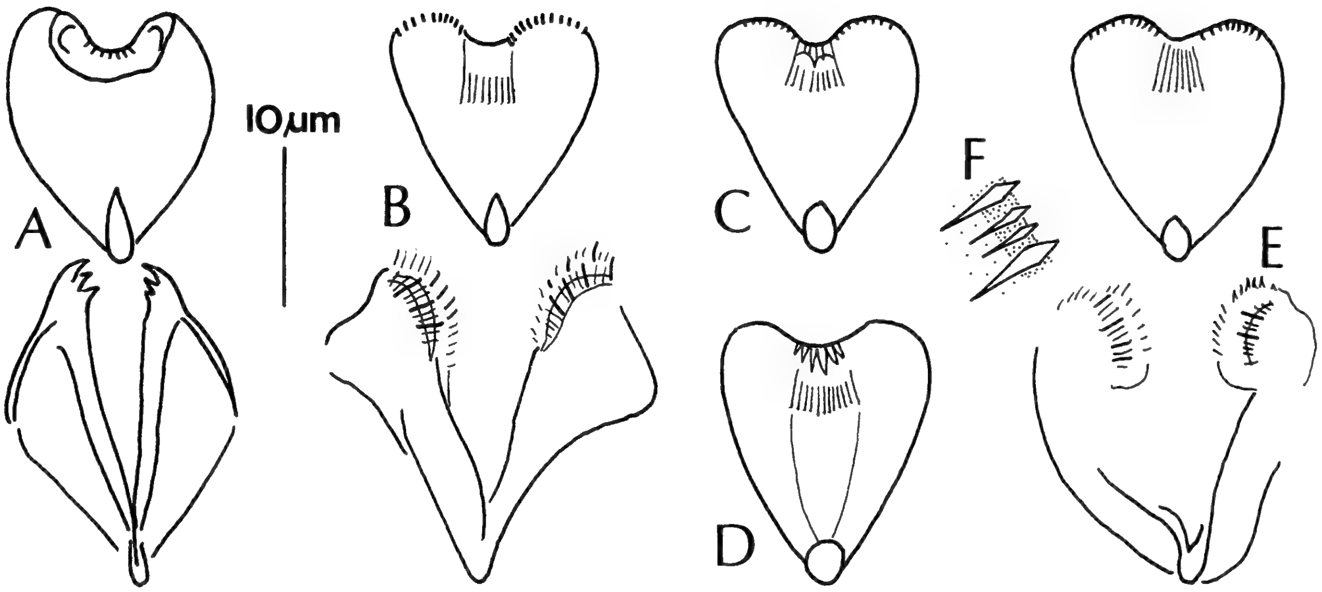

Fig. 5. *Labidognathia longicollis.* A–E, jaws and basal plates of several specimens, strongly squeezed; F, detail of jaw teeth in dorsal row. A–E to the same scale; F not to scale.

Austrognathia clavigera, new species
(Figs. 7A–O, 8A–C, Table 5)

Etymology.—From the Latin *clavus* (nail), and *gerere* (to carry), in reference to the sperm (conuli) which give the appearance of nails or thumbtacks.

Material.—Twenty-eight more specimens, of which 7 adults, from sample C1.

Holotype.—USNM 174367, one adult in squeeze preparation.

Type locality.—Gran Canaria Las Palmas, Playa de Las Canteras, fine sand with sparse sea grass (*Cymodocea nodosa*) at 2–3m depth; sample collected 16 Feb 1996.

Diagnosis.—Stout *Austrognathia* (body index 7.63) with squarish rostrum (rostrum index 0.81) and many bundles of spindle-shaped epidermal rhabdoids. Basal plate 6.30 µm long, 20.09 µm wide (index 0.32), with inconspicuous median and flat lateral lobes. Jaws 20.24 µm long, with 4.78 teeth in dorsal and 8.14 teeth in ventral row; pos-

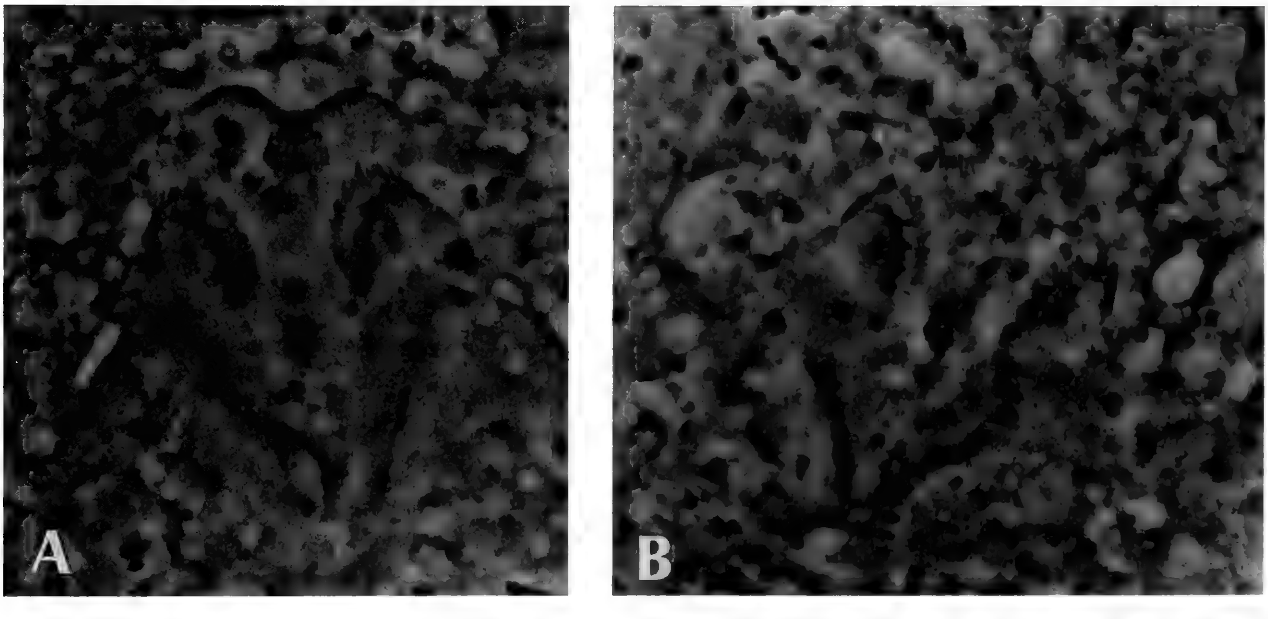

Fig. 6. *Labidognathia longicollis,* phase contrast micrographs. A–B, basal plate and jaws of two specimens, strongly squeezed.

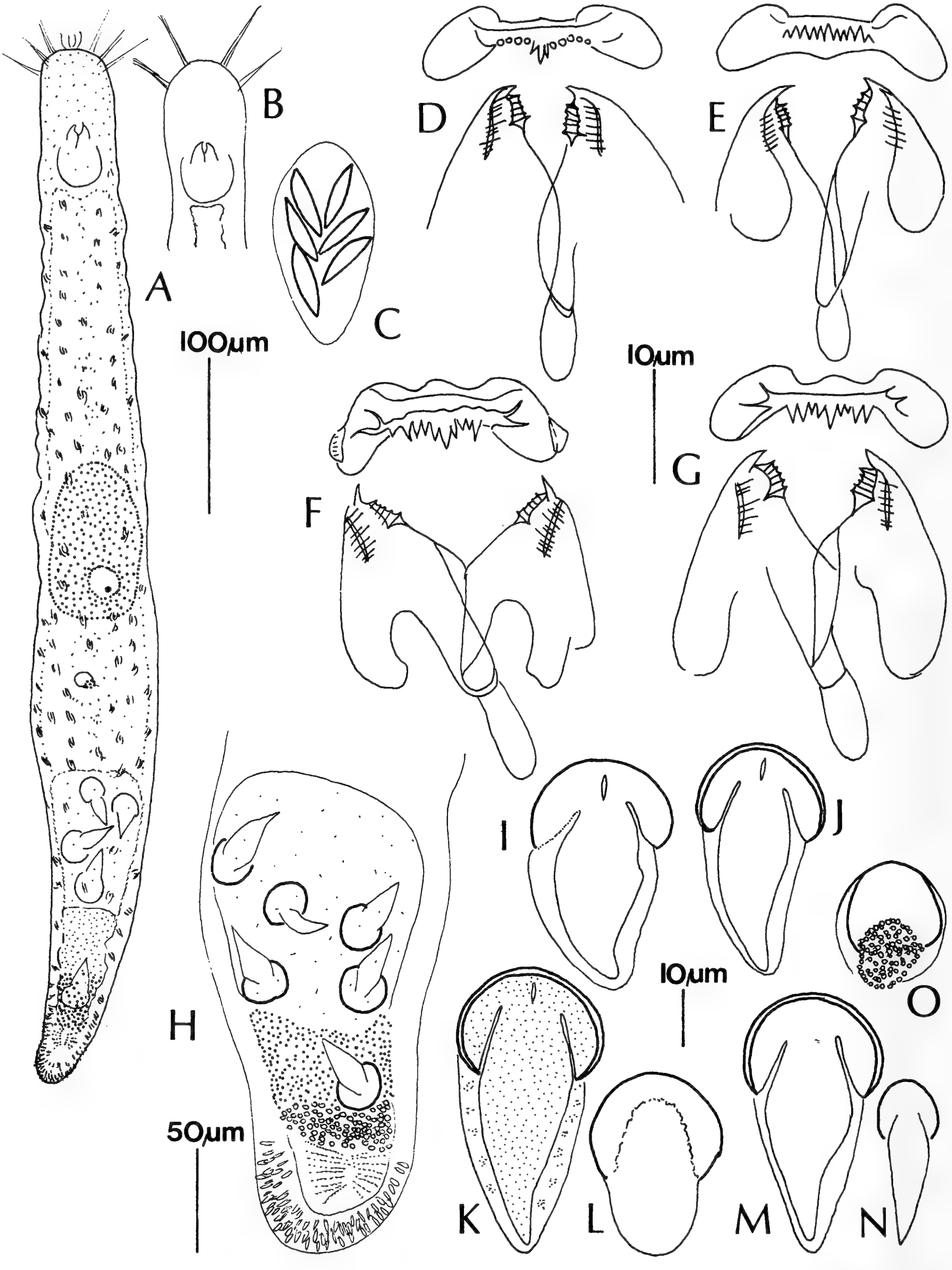

Fig. 7. *Austrognathia clavigera.* A, habitus of adult; B, rostrum of another specimen; C, rhabdoid bundle; D–G, basal plate and jaws of four specimens, strongly squeezed; H, posterior part of body showing male reproductive system; I–M, mature conuli; N, immature conulus; O, bursa conulus. Conuli in K and L, M and N, and J and O, respectively, are from the same specimen. Scales apply to A–B, C–G, H, and I–O, respectively.

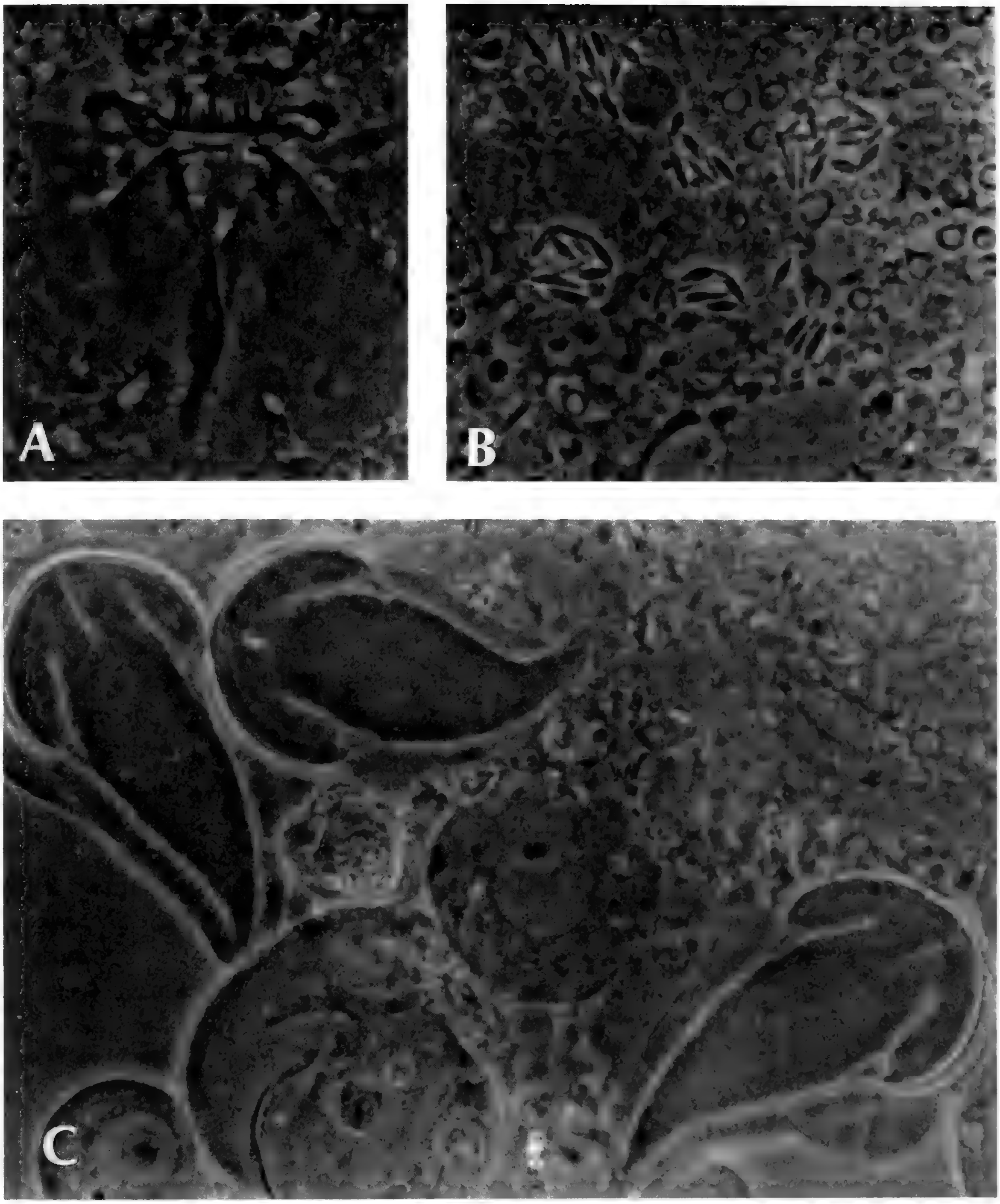

Fig. 8. *Austrognathia clavigera,* phase contrast micrographs. A, basal plate and jaws, strongly squeezed, so that the anterior edge of the basal plate is facing posteriorly; B, rhabdoid bundles; C, terminal conuli.

terior-most dorsal tooth usually rooted. Conuli to 52 μm long and 24 μm wide (index 1.96), without cingulum; hat much wider than cone and circumscribing 250°.

Description.—Organization and behavior: Colorless, and rather opaque from large numbers of epidermal rhabdite bundles. Animals glide slowly, but prefer to attach themselves to detritus particles to which they may cling with tenacity. Adults are 420–900 μm long and 80–90 μm wide at *U* 47.26 (index 7.63). The rostrum is 45–50 μm long and 50–70 μm wide at *U* 6.57; it is typically rather square, with nearly parallel lateral contours. The sensorium—difficult to ascertain since the cirri join the ciliary beat almost continuously—consists of two pairs of single apicalia (to 20 μm long), and the compound frontalia (48 μm), ventralia (50 μm), dorsalia (38 μm), and later-

Table 4.—*Labidognathia longicollis.* Measurements and statistics.

	$\bar{X}$	*SD*	Max	Min	*n*
Body length of adults	700.00		700	700	1
Body width of adults	65.00		65	65	1
Body index of adults	10.77		10.77	10.77	1
Rostrum index of adults	1.88		1.88	1.88	1
Jaw length	21.00	1.15	23	20	7
Basal plate length	15.43	1.40	18	14	7
Basal plate width	11.86	1.07	13	10	7
Basal plate index	1.31	0.11	1.45	1.17	7
Penis stylet length	43.00	7.00	48	35	3

alia (40 μm). Occipitalia and a pair of ciliary pits are probably present. Throughout the body, but especially in the tail region, the epidermis contains ovoid bundles of spindle-shaped rhabdoids (Fig. 7C) 6 μm long and 2 μm wide which presumably serve an adhesive function.

Digestive tract: The basal plate measures 5–8 μm in length and 18–22 μm in width (index 0.32). Its rostro-lateral lobes are fairly low, and a median lobe is inconspicuous or lacking. Caudally the basal plate is set with 8–13 ($\bar{X}$ = 10.18) rather uniform teeth. Jaws are 18–22 μm long ($\bar{X}$ = 20.24), and have a 7 μm long pear-shaped cauda. In addition to a strong terminal tooth there are two rows of teeth: a longer ventral row of 5–12 ($\bar{X}$ = 8.14) long teeth, and a shorter dorsal row of 4–7 ($\bar{X}$ = 4.78) short teeth. In the ventral row, a stronger tooth usually alternates with two weaker teeth. In the dorsal row, the caudal-most tooth is always rooted.

Male system: The single testis is 50–120 μm long, extending dorso-caudally from *U* 71.73 to *U* 83.98. The penis, from *U* 84.62 to 94.58, has three regions characterized by medium, coarse, and fine granula, respectively, with the finely-granular part surrounding the male pore (Fig. 7H). The testis contains up to 11 conuli which come in at least two size classes. Of a total of 46 conuli encountered in 7 specimens, 41 were what I call "terminal" conuli (Fig. 7I–M): to 52 μm long and 24 μm wide (index 1.98), with a towering hat that describes up to 250° of a circle, and whose width significantly exceeds that of the cone. A cingulum is lacking. Only five conuli, seen in three specimens in addition to terminal conuli, were smaller and more slender (30 μm by 10 μm), and endowed with a less prominent hat (Fig. 7N).

Female system: Located between *U* 39.75 and *U* 54.38, a mature egg may be 85–110 μm long. A bursa conulus, 22 μm

Table 5.—*Austrognathia clavigera.* Measurements and statistics.

	$\bar{X}$	*SD*	Max	Min	*n*
Body length of adults	645.00	155.15	900	420	6
Body width of adults	85.00	5.48	90	80	6
Body index of adults	7.63	2.06	11.25	5.25	6
Rostrum index of adults	0.81	0.08	0.90	0.71	4
Jaw length	20.24	1.05	22	18	25
Basal plate length	6.30	0.70	8	5	23
Basal plate width	20.09	1.38	22	18	23
Basal plate index	0.32	0.05	0.40	0.25	23
Sperm length	43.63	3.56	52	38	16
Sperm width	22.31	1.01	24	21	16
Sperm index	1.96	0.14	2.26	1.67	16

by 17 μm, was seen in one specimen (Fig. 7O).

Discussion.—The genus *Austrognathia* Sterrer, 1965 currently comprises 8 valid species: *A. hymanae* Kirsteuer, 1970; *A. microconulifera* Farris, 1977; *A. nannulifera* Sterrer, 1991a; *A. novaezelandiae* Sterrer, 1991a; *A. riedli* Sterrer, 1965; *A. christianae* Farris, 1977; *A. singatokae* Sterrer, 1991a; and *A. macroconifera* Sterrer, 1991c. A comparison with *A. clavigera* sets the first four species apart as having conuli with a maximum length of only 9–20 μm. Of the remaining species, *A. macroconifera* and *A. singatokae* have conuli quite different from those of *A. clavigera.* The conuli of *A. christianae* and *A. riedli* are similar to those of *A. clavigera* except that in the former two species the hat circumscribes no more than 180°, and does not significantly exceed the width of the cone. According to a recently proposed typology of austrognathian mouth parts, the new species belongs in the "novaezelandiae" group characterized by "a basal plate with a flattened or absent central lobe and rounded lateral lobes ... and jaws in which the dorsal row has 3 or more teeth of which the caudalmost is usually rooted" (Sterrer 1991d). In aspects such as the shape of rostrum and conuli, as well as the possession of many adhesive papillae, *A. clavigera* most closely resembles the species reported by Riedl (1966) from the Red Sea and provisionally named *A. riedli* forma *maris-rubri* of which, however, neither the structure nor the dimensions of jaws and basal plate are known.

Acknowledgments

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Literature Cited

Riedl, R. 1966. Faunistische Studien am Roten Meer im Winter 1961/62, III. Die Aufsammlungen in Suez und Al-Ghardaqa, nebst einigen Bemerkungen über Gnathostomulida.—Zoologische Jahrbücher, Systematik 93:139–157.

———. 1970. On *Labidognathia longicollis,* nov. gen., nov. spec., from the West Atlantic Coas (Gnathostomulida).—Internationale Revue der gesamten Hydrobologie 55:227–244.

Sterrer, W. 1969. Beiträge zur Kenntnis der Gnathostomulida. I. Anatomie und Morphologie des Genus *Pterognathia* Sterrer.—Arkiv för Zoologi 22:1–125.

———. 1971. On the biology of Gnathostomulida.—Vie et Milieu, Suppl. 22:493–508.

———. 1972. Systematics and evolution within the Gnathostomulida.—Systematic Zoology 21: 151–173.

———. 1991a. Gnathostomulida from Fiji, Tonga and New Zealand.—Zoologica Scripta 20:107–128.

———. 1991b. Gnathostomulida from Hawaii.—Zoologica Scripta 20:129–136.

———. 1991c. Gnathostomulida from Tahiti.—Zoologica Scripta 20:137–146.

———. 1991d. *Triplignathia adriatica,* new genus and species, and a typology of mouth parts in Austrognathiidae (Gnathostomulida). Proceedings of the Biological Society of Washington 104:640–646.

———. 1992. Clausognathiidae, a new family of Gnathostomulida from Belize.—Proceedings of the Biological Society of Washington 105:136–142.

———. 1997. Gnathostomulida from the subtropical northwest Atlantic.—Studies on the fauna of Curaçao (in press).

———, M. Mainitz, & R. M. Rieger. 1986. Gnathostomulida: enigmatic as ever.—Pp. 181–199 *in* S. Conway Morris, J. D. George, R. Gibson, & H. M. Platt, eds., The origins and relationships of lower invertebrates.—The Systematics Association Special Volume No. 28:1–397.

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A new species of *Stenoninereis* (Polychaeta: Nereididae) from the Gulf of Mexico

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Abstract.—The genus *Stenoninereis* is newly recorded from Mexican waters. The only formerly known species of the genus, *Stenoninereis martini* Wesenberg-Lung, 1958, is recorded from Laguna de Terminos, State of Campeche, Mexico, where it was found associated with mangrove roots. *Stenoninereis tecolutlensis* n. sp. was collected in Tecolutla, State of Veracruz, under oyster shells attached to mangrove roots in an estuarine zone. Both specimens are described and illustrated, and a key is provided in order to distinguish between them.

The genus *Stenoninereis* was established in 1958 by Wesenberg-Lund for those species with dorsal cirri formed by elongate basal cirrophores and subulate distal cirrostyles. Up until now, only the type species (*S. martini* and synonym *Nicon lackeyi* Hartman, 1958) was known, from localities in the Great Caribbean region, western Gulf of Mexico, Cuba and North Carolina (Wesenberg-Lund 1958, Pettibone 1971, Williams et al. 1976, Hartmann-Schröder 1977, Gardiner & Wilson 1979).

The material analyzed for this study was collected in Laguna de Terminos, State of Campeche from sediment associated with mangrove roots, and in Estero de Larios, Tecolutla, State of Veracruz under oyster shells attached to mangrove roots. The specimens were fixed with formalin, preserved in 70% alcohol and stained with a methyl blue solution to highlight some important features. The type material is deposited in the Smithsonian Institution (USNM, Washington, D.C., U.S.A.) as well as in the polychaete collections of the Instituto de Ciencias del Mar y Limnologia (CPICML-UNAM) and Facultad de Ciencias Biologicas, Universidad Autónoma de Nuevo León (UANL), both in Mexico. A diagnosis of *S. martini* is given, in order to complement the original description and to compare it to the new species herein described.

Stenoninereis Wesenberg-Lund, 1958

Type species.—*Stenoninereis martini* Wesenberg-Lund, 1958.

Diagnosis.—Prostomium small, rounded and distally notched, with paired frontal antennae, biarticulate palps and two pairs of eyes, anterior pair crescent-shaped, and posterior pair rounded. Four pairs of tentacular cirri. Pharynx with paired jaws without paragnaths or papillae. First two pairs of parapodia subbiramous. Dorsal cirri with long basal cirrophores and short cirrostyles. Biramous parapodia with notopodia bilobed, with lower acicular lobes and upper ligules reduced in posterior parapodia; neuropodia with bluntly conical acicular lobes in anterior region, becoming more elongate in middle setigers, and shorter, more pointed in posterior region. Ventral cirri cirriform. Notosetae homogomph and sesquigomph spinigers. Neurosetae heterogomph spinigers, sesquigomph and heterogomph falcigers with thin blades. Pygidium with a pair of expanded lobes and a pair of anal cirri.

Stenoninereis martini Wesenberg-Lund, 1958
Fig. 1

Stenoninereis martini Wesenberg-Lund, 1958: 9, figs. 2–4; Pettibone, 1971: 39, figs. 23, 24; Williams, et al., 1976: 83; Hartmann-Schröder, 1977; Gardiner & Wilson, 1979: 165 fig. 2a–h.

Nicon lackeyi Hartman, 1958: 263, figs. 1–5.

Material examined.—México, San Julián, Laguna de Terminos, Campeche, 1/Mar/1984 (18 specimens) (CPICML-UNAM POH-39-39).

Description.—Best preserved specimen complete (33 setigers), olive-green, with small pigmented dots, on the most dorsal part of the body, 6 mm long and 1 mm wide including parapodia. Prostomium pentagonal, slightly notched frontally. Two pairs of eyes: anterior pair crescent shaped, posterior pair small and rounded. Frontal antennae cirriform and not longer than distal margin of palps. Palps globular, biarticulate with elongate conical palpostyles. Peristomium slender, with four pairs of tentacular cirri, anterior dorsal pair reaching up to setiger 6. Pharynx with one pair of jaws armed with 9 teeth.

First two parapodia subbiramous; notopodia reduced to small notoacicula. Following parapodia biramous; anterior ones (Fig. 1A) with long dorsal cirri consisting of elongate basal cirrophore and short piriform cirrostyle, which becomes longer towards the body end (Fig. 1B, C). Notopodia trilobate, superior lobe short and digitiform, inferior lobe subulate, with small presetal lobe at base of upper lobe. Superior notopodial lobes reducing in size in posterior setigers (Fig. 1C). Neuropodia with bluntly conical acicular lobe in anterior region (Fig. 1A), becoming more elongate in middle setigers (Fig. 1B) and shorter, more pointed in posterior region (Fig. 1C).

Supracicular notosetae are sesquigomph spinigers, infra-acicular notosetae are homogomph spinigers; both with slender appendix, serrated on the inner edge. Supracicular neurosetae are heterogomph and sesquigomph spinigers; infracicular ones are sesquigomph spinigers: one heterogomph spiniger with a short blade strongly serrated on at least three quarters of its length on its inner margin (Fig. 1D); heterogomph falcigers with long blade, spinulose, distally hooked. Blades of the most ventral heterogomph falcigers are one fourth of the length of the superior ones.

Pygidium subterminal, with pair of lateral flattened, wide lobes, and pair of long anal cirri. Anal opening ventral.

Distribution.—*Stenoninereis martini* has been reported from the Greater Caribbean region (type locality: San Martin Island; and Sarasota, Florida), western Gulf of Mexico (Texas), Cuba, North Carolina, and herein from Laguna de Terminos, Campeche, Mexico, where it was collected in soft bottoms associated with mangrove roots.

Stenoninereis tecolutlensis, new species
Fig. 2

Material examined.—Mexico, Estero de Larios, Tecolutla, Veracruz, 19/Nov/1994 (Holotype: USNM-174870, and 2 paratypes: UANL-3980 and CPICML-UNAM POH-39-002).

Description.—Holotype complete, green-yellowish, 15 mm long and 2 mm wide with 49 setigers. Palps and eyes contour-pigmented; peristomium and following three setigers with transverse dark stripe, less conspicuous on following segments.

Prostomium rounded, deeply incised frontally, with a pair of small, cirriform frontal antennae, longer than palps. Two pairs of eyes: anterior pair crescent-shaped, posterior pair rounded. Biarticulate palps

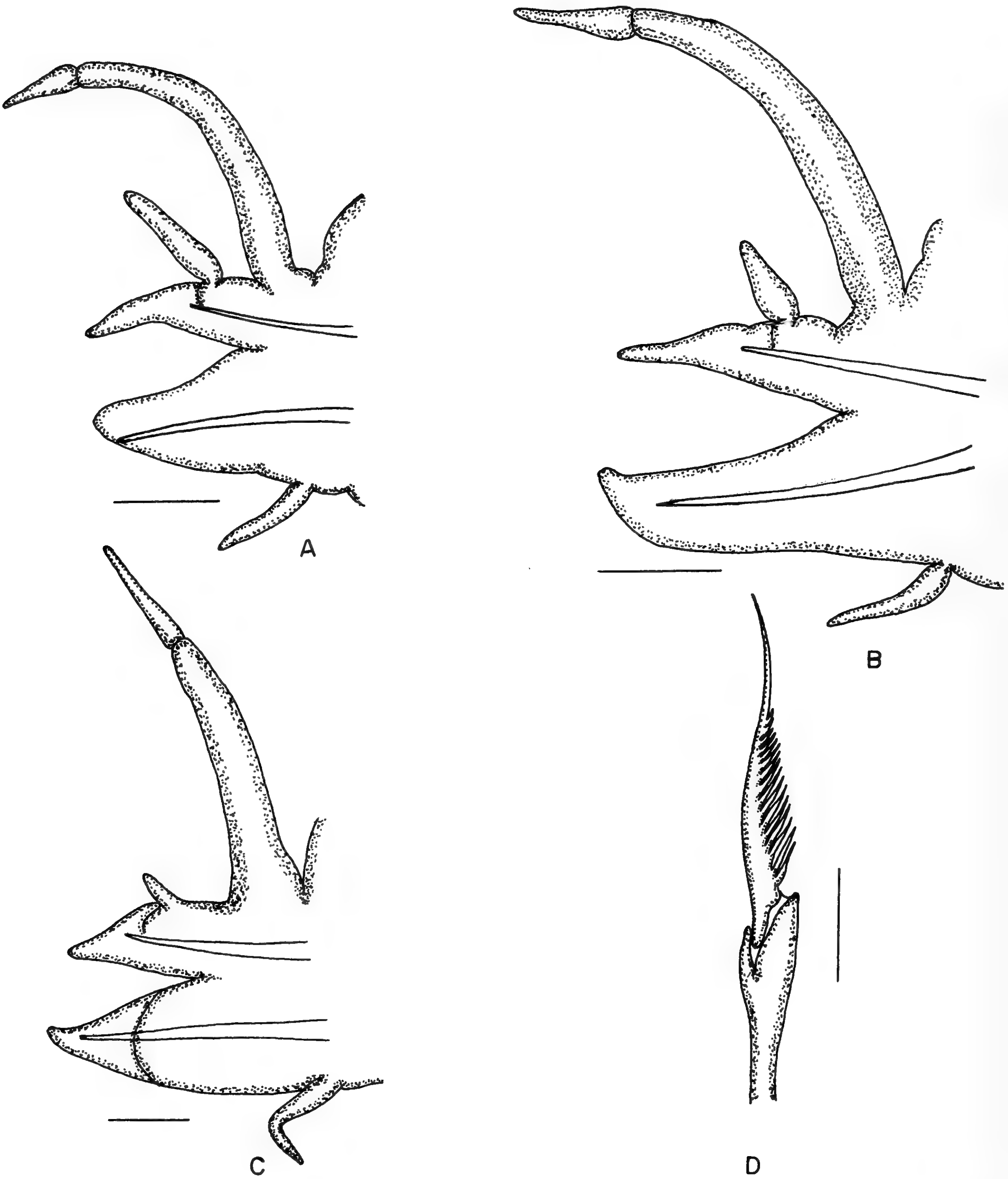

Fig. 1. *Stenoninereis martini.* A. 6th parapodium; B. 18th parapodium; C. 28th parapodium; D. heterogomph spiniger from parapodium of middle segments. (A, B, C anterior view, setae omitted). Scale: A–C = 60 μm; D = 8 μm.

with globular palpophores and conical palpostyles. Peristomium narrow, with four pairs of tentacular cirri, posterodorsal pair longest reaching setiger 12; anterodorsal pair laterally expanded (Fig. 2A). Pharynx with a pair of jaws armed with five minute teeth.

First two parapodia uniramous, the following biramous. In anterior and middle parapodia (Fig. 2 B–C) two long and slender lobes form notopodium, superior one being shorter. Posterior parapodia bearing only an acicular lobe (Fig. 2D). Cirrophores of the dorsal cirri in anterior and middle

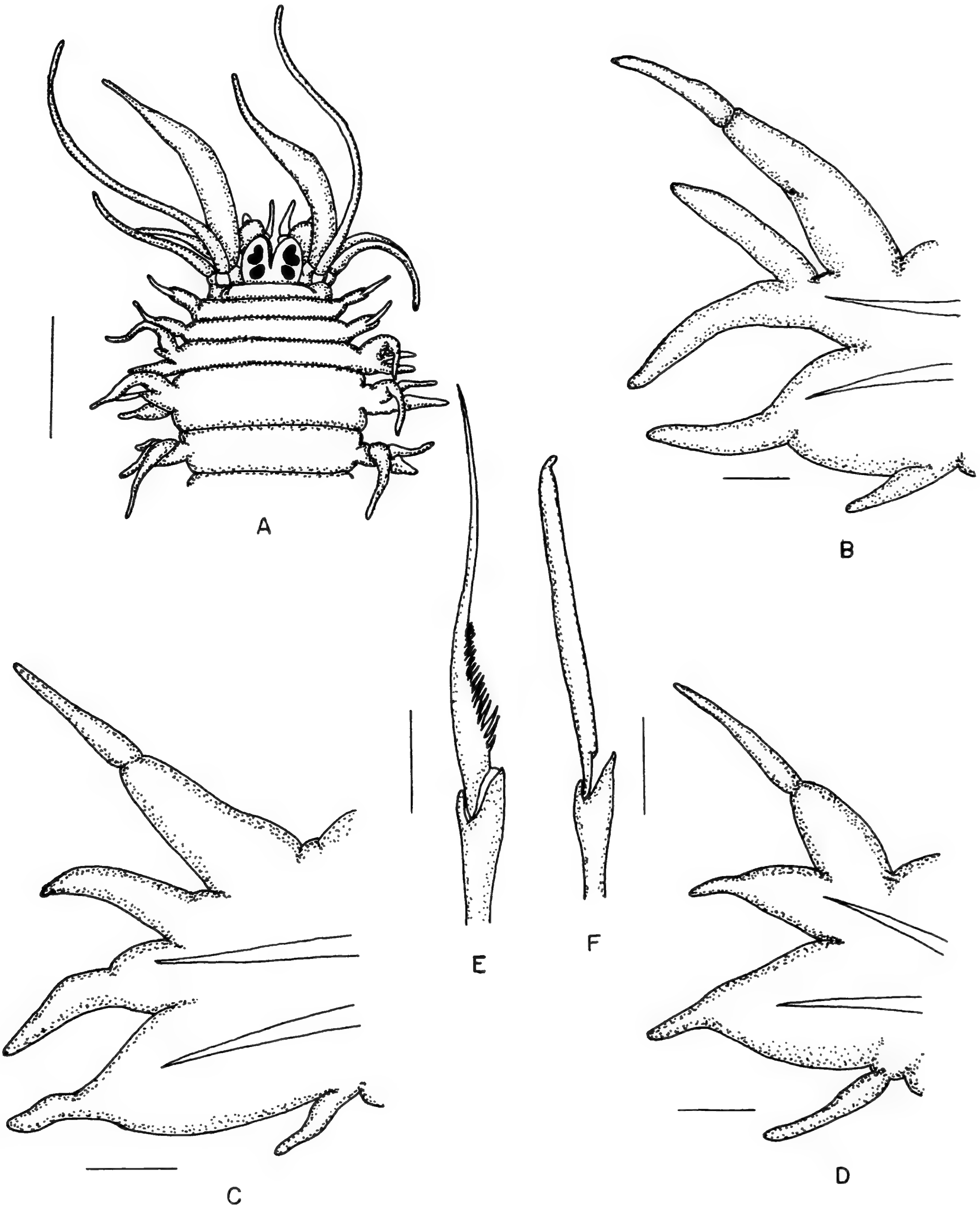

Fig. 2. *Stenoninereis tecolutlensis* new species A. Anterior end, dorsal view; B. 10th parapodium; C. 25th parapodium; D. Posterior parapodium; E. Neuropodial infracicular heterogomph spiniger from parapodium of middle segments; F. Neuropodial infracicular heterogomph falciger from parapodia of middle segments. (B, C, D: anterior view, setae omitted). Scale: A = 0.5 mm; B − D = 60 μm; E, F = 8 μm.

segments 1.5 times longer than the cirrostyles; on posterior parapodia cirrostyle 1.5 times longer than the cirrophore, but the cirrophore is basally stouter. Ventral cirri longer on posterior parapodia.

Setation is similar throughout the body. Notosetae are homogomph spinigers in supracicular position and two sesquigomph spinigers in subacicular position. Supracicular neurosetae are heterogomph and sesquigomph falcigers with smoothly serrated blades. Infracicular ones in dorsal position with one pair of heterogomph spinigers strongly denticulate (Fig. 2E), and heterogomph falcigers with elongate terminal hooked blades (Fig. 2F); inferior ones one third of superior ones' length.

Anus terminal, with two flat winglike expansions, and a pair of anal cirri.

Geographical distribution.—Known only from Estero de Larios, Tecolutla, Veracruz, Mexico, where it was collected under oyster shells attached to mangrove roots in very shallow estuarine waters.

Etymology.—Stenoninereis tecolutlensis is named after the type locality, Tecolutla, Veracruz.

Remarks.—The genus *Stenoninereis* was erected by Wesenberg-Lund (1958) for only one species: *S. martini. S. tecolutlensis* differs from the type species in the shape of the prostomium and the size of the eyes: in *S. martini,* the prostomium is rounded with small eyes while in *S. tecolutlensis* the prostomium is deeply incised frontally, with large eyes. They further differ in the shape and distribution of the supracicular double notopodial lobe (short and present to the end of the body in *S. martini,* long and missing on posterior parapodia in *S. tecolutlensis*); the relative length of the cirrophore and the cirrostyle, the number and size of teeth on the jaws, (nine in *S. martini* and five minute teeth in *S. tecolutlensis*), the difference in size and area covered by the denticulation of the heterogomph spinigers, *S. martini* have homogomph spinigers in infracicular position, while *S. tecolutlensis* have sesquigomph spinigers; and the relative size of the ventral cirri on posterior parapodia (short in *S. martini* and longer in *S. tecolutlensis*).

Key to *Stenoninereis*

1. Prostomium rounded, supracicular double notopodial lobes short, present throughout body, notopodium with homogomph spinigers in infracicular position .... *S. martini*

– Prostomium deeply incised frontally, supracicular double notopodial lobes missing on posterior parapodia, notopodium with sesquigomph spinigers in infracicular position .... *S. tecolutlensis*

Literature Cited

Gardiner, S. L., & W. H. Wilson, 1979 (1977). New records of polychaete annelids from North Carolina with the description of a new species of *Sphaerosyllis* (Syllidae).—The Journal of Elisha Mitchell Scientific Society 93(4):159–172.

Hartman, O. 1958. A new nereid worm from Warm Mineral Springs, Florida with a review of the genus *Nicon* Kinberg.—Journal of Washington Academic Science 48:263–266.

Hartmann-Schröder, G. 1977. Die Polychaeten del Kubanisch-Rumanischen Biospeologischen Expedition nach Kuba 1973.—Résultats des expéditions biospéologiques cubano-roumaines, Cuba 2:51–63.

Pettibone, M. H. 1971. Revision of some species refered to *Leptonereis, Nicon* and *Laeonereis* (Polychaeta: Nereididae).—Smithsonian Contributions to Zoology 104:1–53.

Wesenberg-Lund, E. 1958. Lesser antillean polychaetes chiefly from brackish water with a survey and a bibliography of fresh and brackish-water polychaetes.—Studies on the Fauna of Curacao and other Caribbean Islands 8:1–41.

Williams, G. E., M. J. Poff, & J. T. MzBee. 1976. Western Gulf of Mexico records of *Stenoninereis martini* Wesenberg-Lund 1958 (Polychaeta, Nereidae) with contributions to its habitat ecology.—Contributions in Marine Sciences 20:83–85.

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Boguea panwaensis, a new species from Thailand: the first member of the Bogueinae (Polychaeta: Maldanidae) to be found outside northeast America

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Abstract.—A new boguein polychaete species, *Boguea panwaensis,* is described from Cape Panwa, Phuket, Thailand. It is closely related to the North American *B. enigmatica,* but differs in number, arrangement and structural details of its chaetae.

The first species of the maldanid subfamily Bogueinae was described from Bogue Sound, North Carolina, by Hartman (1945), who first considered it as belonging to the Oweniidae. Later on (Wolf 1984) it was recorded from different localities around the coasts of North America at depths down to 100 m, usually between 2 and 20 m, in sand and sand-gravel. With the description of the closely related species *Boguella ornata* Hartman & Fauchald, 1971, the two authors erected the family Bogueidae and mentioned that it differs from oweniids in possessing avicular or terebelloid uncini (Hartman & Fauchald 1971). Wolf (1983) redescribed the taxon and reduced its rank to Bogueinae, a subfamily of the Maldanidae, emphasising that they share morphological and ontogenetic features especially characteristic of this family. Independently of Wolf (1983), Nilsen and Holthe (1985) argued in the same direction by stating that the boguein uncini could well be derived from those of the Rhodininae, a subfamily of the Maldanidae. Holthe (1986) confirmed this in his phylogenetic discussion of the Bogueidae. The new *Boguea* species presented is the first one occurring outside the North American area.

Boguea panwaensis, new species
Figs. 1, 2, 3 A–F, 4 A–E

Material examined.—Two complete specimens and one anterior end with 5 chaetigers. Location: Thailand, Phuket, Cape Panwa, near the Phuket Marine Biological Center (PMBC), at a depth of about 10–15 m in the centre of the bay west of the aquarium (7°52′N, 98°22′E); mature specimen and anterior end found in October 1994, immature specimen in March 1995. Probably living in a layer (1–3 cm) of very fine, mostly oozy organic material on top of fine sand with organic material, few shells and little gravel, partly with clay texture.

Methods.—Extraction of the polychaetes was carried out with a solution of 8% $MgCl_2$ isotonic to sea water. Specimens were observerd in living condition before they were fixed in Bouin's fluid, and then transferred to 70% ethanol. For SEM investigations the dehydrated specimens were critical-point dried with CO_2 as intermedium, mounted with a carbon film on aluminium stubs, sputter-coated with gold and examined in a Zeiss 962 SEM.

Type material.—Holotype with 24 chaetigers (length 10 mm), mature; deposited in the Phuket Marine Biological Center, Reference Collection, Thailand (No. PMBC 13577). Paratype with 23 chaetigers (length 4 mm), immature; SEM preparation, deposited in the collection of the Senckenberg Museum, Frankfurt (No. SMF 5633).

The new species was named after Cape Panwa in the southern region of the island

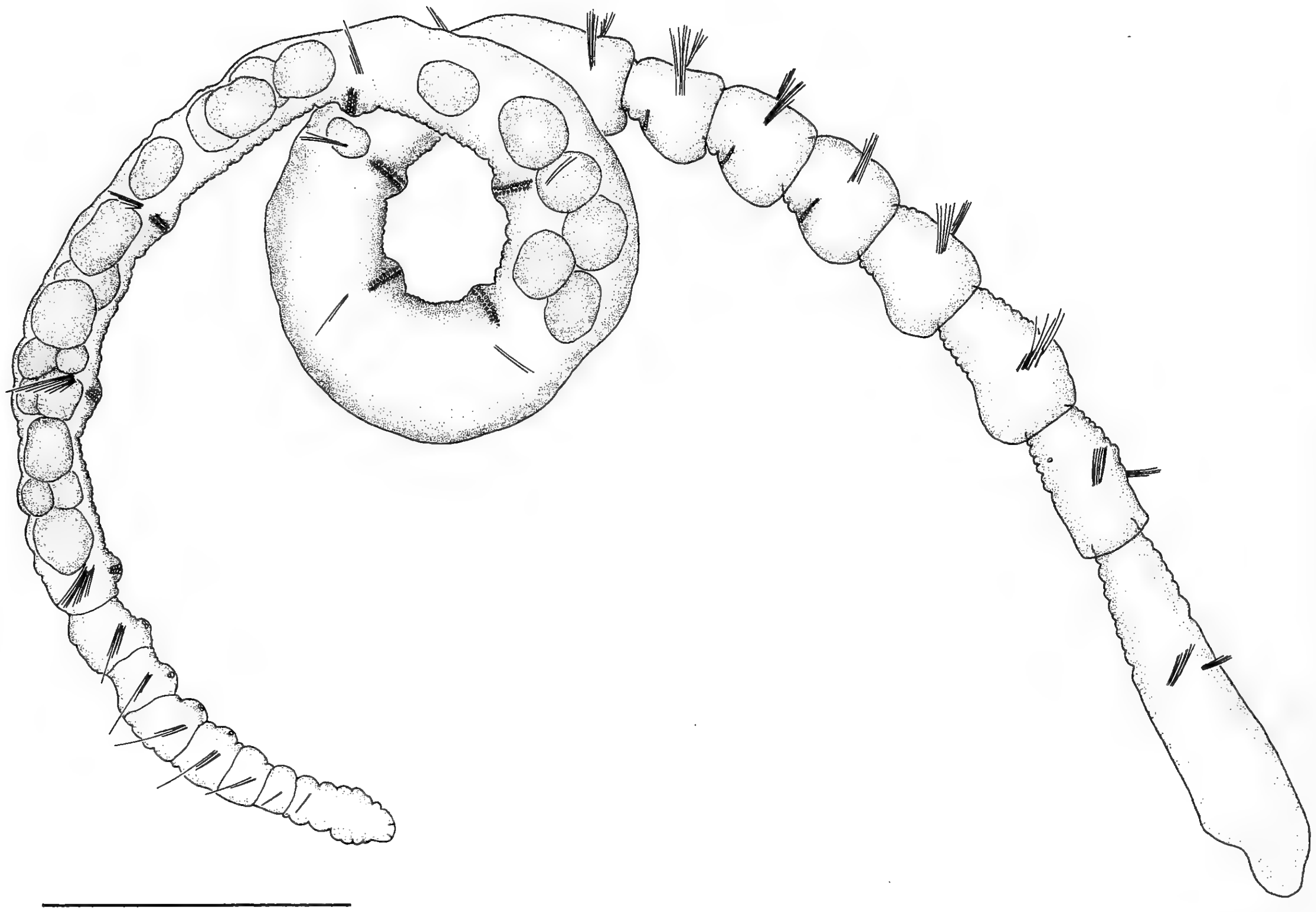

Fig. 1. *Boguea panwaensis,* new species. Holotype with oocytes, lateral view (on chaetiger 2 a single juvenile uncinus). Scale bar = 1 mm.

of Phuket, where it was found by the authors.

Material for comparison.—*Boguea enigmatica* Hartman, 1945 (extracted from: ZMUC-POL-541; Bogue Sound, North Carolina 6 Aug. 1962).

Description.—Length about 10 mm, up to 24 chaetigerous segments, width about 0.5 mm. Colour light brownish-translucent. Body divided into three regions differentiated by the shape of the segments and the distinctness of their boundaries, type and number of notochaetae, number of uncini and their arrangement in one or two rows. Prostomium, peristomium and pygidium without appendages.

Anterior region.—Through chaetiger 7. Prostomium and peristomium fused. Prostomium anteriorly rounded. No nuchal organs visible. Borderline between peristomium and first chaetiger indistinct. Chaetigers 2 to 7 contractible, so that their anterior part may be wider than their posterior part (Fig. 1) and the preceding chaetiger is partly recessed into the following one. When relaxed, chaetigers longer than wide. Parapodia absent, except groups of notopodial and neuropodial chaetae, emerging in the middle of each chaetiger, and arranged in one or two rows. Types of notopodial chaetae in this region include simple, smooth capillaries, serrated capillaries and short, stiff spines. In chaetiger 3 four serrated capillary chaetae with minute imbrications and one smaller additional capillary. In the following chaetigers only some of the capillaries show this special structure (Table 1). In chaetiger 3 one additional row of four short spines anterior to these capillaries.

Neuropodial chaetae may be present from chaetiger 2 backwards. One small rostrate uncinus in chaetigers 2 to 4 (Fig. 3D, E) in the juvenile specimen (Fig. 2). In the mature specimen (Fig. 1) the latter are miss-

Table 1.—Distribution of types of notopodial chaetae in the holotype of *Boguea panwaensis,* new species.

Chaetiger	Types of chaetae on the notopodia
1–2	smooth capillary chaetae
3	stiff, short spines; serrated capillary chaetae
4–7	serrated and smooth capillary chaetae
8–13	imbricated capillary chaetae
14–17	serrated capillary chaetae; capillary chaetae with triangular imbrications; slightly curved, flattened serrated chaetae
18–22	short spines; smooth capillary chaetae
23–24	short spines

ing, with the exception of one in chaetiger 2. The neuropodial chaetation commences in chaetiger 5, consisting of a single row of avicular uncini in chaetigers 5 to 7, their number varying between 7 and 12.

Middle region.—Borderlines between chaetigers 8 to 13 indistinct. Chaetigers longer than wide. Neuropodial chaetae resemble those in the anterior and posterior regions, and notopodial chaetae are capilleries with minute imbrications. These chaetae are shorter than in the anterior region and only up to four in number. From chaetiger 8 onwards two rows of neuropodial uncini on both sides. Anterior row comprising 3 to 6 on chaetiger 8, increasing in number up to 12 in the following chaetigers. Posterior row with 7 to 15 uncini in the mature specimen. Each uncinus with a rostrum and two rows of distinct teeth (=capitium in the terminology of Holthe 1986), several additional small teeth laterally and between the larger teeth, visible only by SEM. Additionally some hair-like projections emerging from the lateral side of the uncini cover the tip of the rostrum (Figs. 3F, 4D).

Posterior region.—From chaetiger 14 backwards. Number of notopodial chaetae

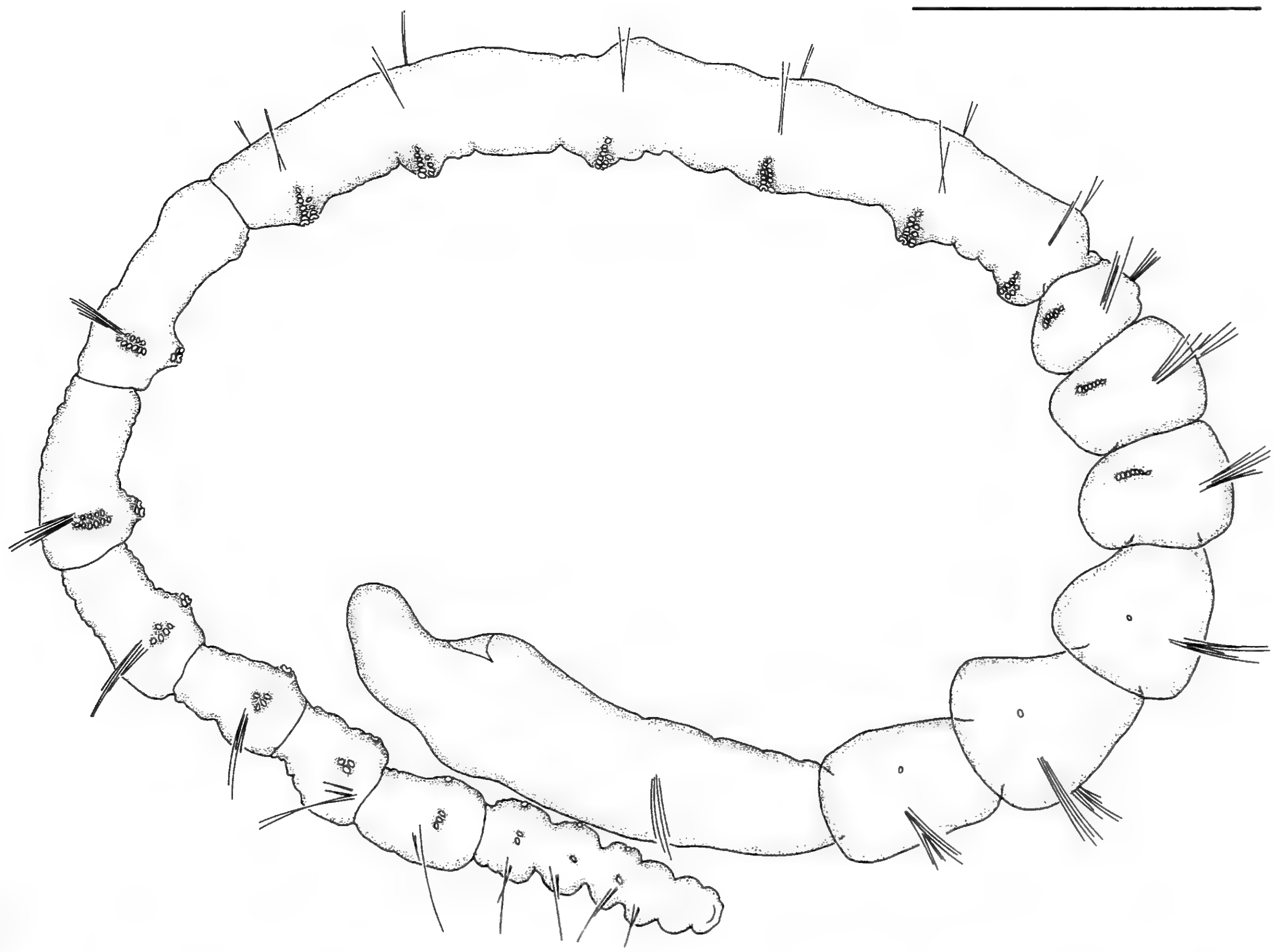

Fig. 2. *Boguea panwaensis,* new species. Paratype. Immature, lateral view. Scale bar = 0.5 mm.

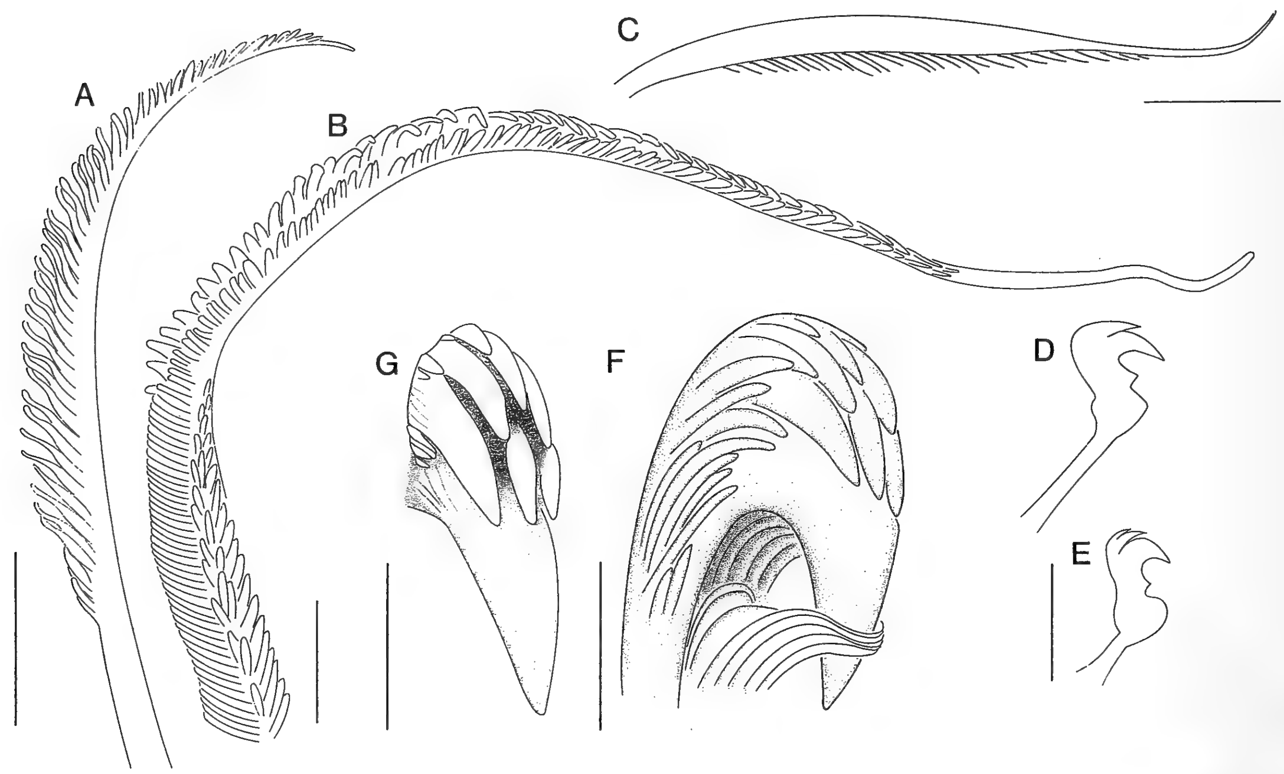

Fig. 3. A–F *Boguea panwaensis,* new species. A, Serrated capillary chaeta from chaetiger 15 with slender, curved imbrication. Scale bar = 5 μm. B, Capillary chaeta from chaetiger 16 with triangular imbrications in the middle region. Scale bar = 5 μm. C, Slightly curved, flattened serrate chaetae from chaetiger 14. Scale bar = 10 μm. D, Juvenile rostrate uncinus from chaetiger 4 (D and E from paratype). E, Juvenile rostrate uncinus from chaetiger 2. Scale bar in D and E = 10 μm. F, Uncinus from chaetiger 15. Scale bar = 2 μm. G, *Boguea enigmatica* Hartman, 1945. Paratype, uncinus from chaetiger 5. Scale bar = 2 μm.

first increasing up to 10, then decreasing in the posteriormost chaetigers, last two segments achaetous. Some of the imbricated capillary chaetae on chaetiger 14 to 17 possessing a specific structure not present in those of the anterior and middle region: in light microscopy these chaetae appear featherlike in lateral view with a series of fine pinnulated imbrications. From SEM preparations, pinnules from one type of chaetae revealed to be cylindrical in the proximal part of the chaetae; distally they are arranged in pairs, gradually forming triangular structures (Figs. 3B, 4E). The imbrications project dorsally from the ventral sides of the chaetal axes. The two rows of imbrications are covered on the ventral side with a series of additional forward directed imbrications, which build a characteristic keel (Fig. 4B). On chaetiger 14 to 17 another type of capillary chaetae with single rows of slender, slightly curved pinnules on each side exist (Figs. 3A, 4C). These pinnules are bent forward on the ventral side of the chaetae and directed dorsally. They differ from the chaetae with the triangular imbrications in that the appendages of these chaetae are longer and remain separated up to the distal end of the chaetae. There are also some curved, flattened serrated chaetae on these chaetigers (Fig. 3C; see also Wolf 1983, fig. 1i). In the following segments, from chaetiger 18 on, they are replaced by smooth and shorter capillary ones. From chaetiger 18 backwards relatively small spines occur, gradually decreasing in number; they are present even on one or two of the posteriormost segments, which bear no other chaetae. These spines resemble those of chaetiger 3, but are smaller.

Number of uncini reduced to approximately 8 in each row in chaetiger 14, decreasing gradually in number to chaetiger 23, with the 2 rows merging towards the posterior end of the body. Uncini in the last

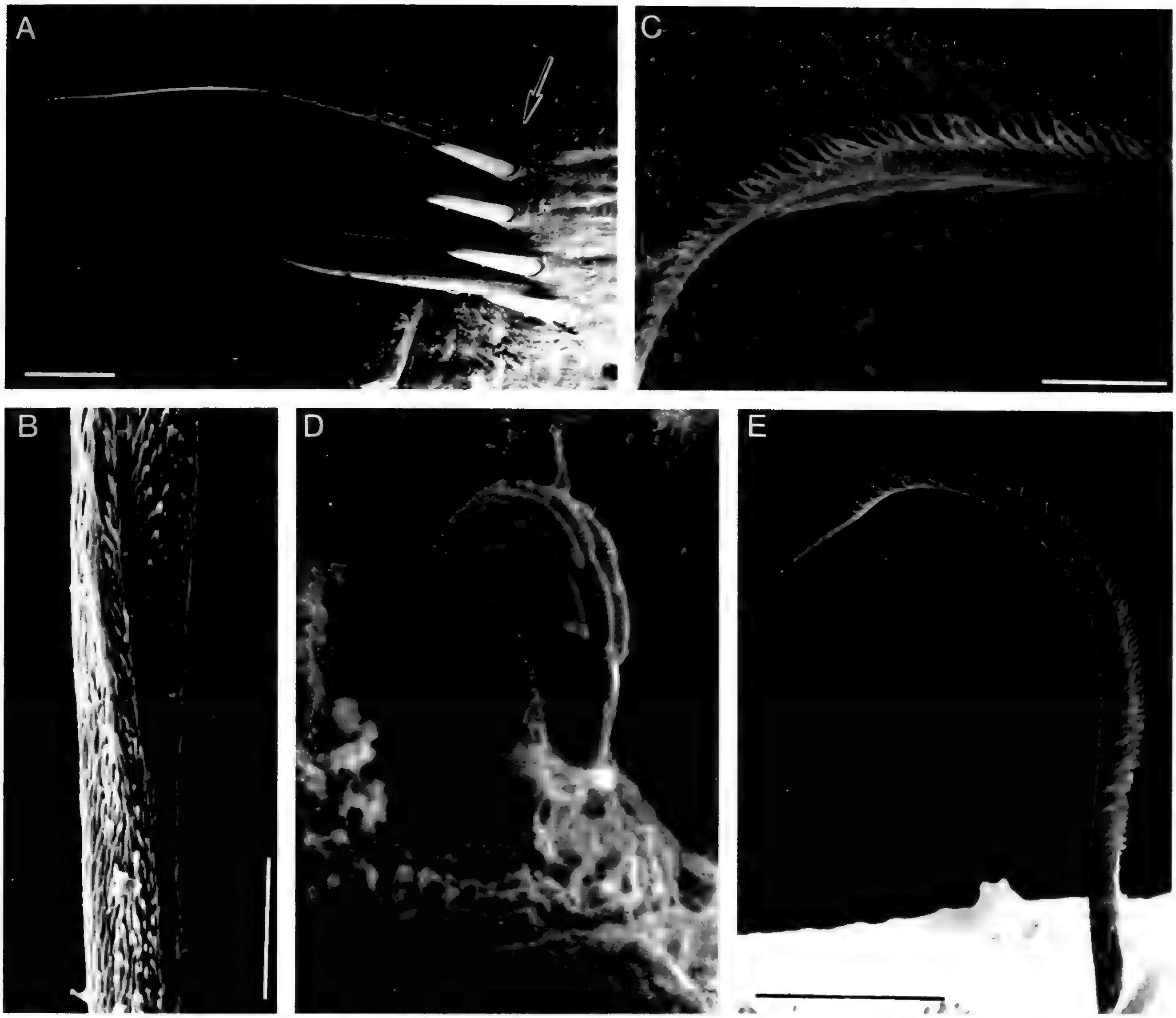

Fig. 4. *Boguea panwaensis,* new species. A, Spines and serrated capillary chaeta from chaetiger 3, arrow points to a broken-off additional capillary chaeta. Scale bar = 20 μm. B, Serrated capillary chaeta with view on the ventral edge formed of imbrications on ventral side. Scale bar = 5 μm. C, Capillary chaeta from chaetiger 15 with slender, curved imbrications. Scale bar = 5 μm. D, Uncinus from chaetiger 15 with several additional teeth on the lateral side. Scale bar = 2 μm. E, Chaeta from chaetiger 16 with triangular imbrications in the distal region. Scale bar = 5 μm.

segments of the juvenile specimen small and rostrate.

Pygidium without appendages, anus terminal. In mature animals eggs of light brownish colour can be seen from the middle region to the posterior chaetiger (Fig. 1).

Discussion.—The new boguein species was discovered at Phuket, Thailand. The two other described species (*Boguea enigmatica* Hartman, 1945; *Boguella ornata* Hartman & Fauchald, 1971) were recorded only from Northeast America. To our knowledge this is the first species found outside this region, with the exception of another undescribed species at the coast of Mauritania, probably belonging to *Boguella* (Dr. H. Michaelis, pers. comm.).

The new species from Thailand belongs to the genus *Boguea.* It shares the following characters with *B. enigmatica:* The body is divided into three regions. Distribution and types of chaetae are almost identical. A distinct borderline between peristomium and first chaetiger is not distinguishable, although Wolf (1983) mentioned slight lateral indentations. The chaetae on the anterior chaetigers show the same minute distally rounded imbrications. The first segment that bears a single row of uncini is the fifth chaetiger. Both species of *Boguea* possess posterior notopodial spines and small rostrate uncini.

The most characteristic difference of *Boguea panwaensis* is the double row of uncini starting on chaetiger 8, whereas *B. enigmatica* has double rows from chaetiger 9 backwards. In addition, on the third chaetiger of the new species four capillary chaetae and four spines exist, which were not described for *B. enigmatica.* Four to six acicular spines are also mentioned by Wolf (1984) in his description of *Boguea* sp. A from the Gulf of Mexico, however, his drawings differ from the structures observed by light microscopy in the specimens from Thailand. The length of the acicular spines in *B. panwaensis* is approximately the same, whereas *Boguea* sp. A (Wolf 1984) show spines of varying length. These characteristic spines occur in the holotype and in the incomplete specimen of the present material, but are missing in the immature specimen.

The specific structures of the capillary chaetae in the species from Thailand at first—when compared with the drawings of the corresponding chaetae published by Wolf (1983)—seemed clearly to differentiate it from *B. enigmatica.* However, examination of a paratype of the latter species by SEM made clear that these differences derive largely from the lower resolution achievable with light microscopy; the structure of the chaetae is fundamentally the same in the two species. Certain differences in detail nevertheless did appear in this SEM comparison: serrated capilleries with paired and triangular imbrications (Figs. 3B, 4E) could not be found in *B. enigmatica.* The uncini show a similar arrangement of teeth in both species, with additional small teeth between the larger teeth on the lateral side. In the area under the rostrum, several smaller teeth are also present, but they are much more numerous in *B. panwaensis* (Figs. 3F, 4D) than in *B. enigmatica* (Fig. 3G). The hair-like projections are only found on *B. panwaensis.* The small rostrate uncini are quite similar in both species.

Acknowledgments

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Literature Cited

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera.—Natural History Museum Los Angeles County Science Series 28:1–190.

Hartman, O. 1945. The marine annelids of North Carolina.—Bulletin of Duke University Marine Station 2:1–54.

———, & K. Fauchald. 1971. Deep water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas, Part 2.—Allan Hancock Monographs in Marine Biology 6:1–327.

Holthe, T. 1986. Evolution, systematics, and distribution of the Polychaeta Terebellomorpha, with a catalogue of the taxa and a bibliography.—Gunneria 55:1–236.

Nilsen, R., & T. Holthe. 1985. Arctic and Scandinavian Oweniidae (Polychaeta) with a description of *Myriochele fragilis* sp.n., and comments on the phylogeny of the family.—Sarsia 70:17–32.

Wolf, P. S. 1983. A revision of the Bogueidae Hartman and Fauchald, 1971, and its reduction to Bogueinae, a subfamily of Maldanidae (Polychaeta).—Proceedings of the Biological Society of Washington 96:238–249.

———. 1984. Family Bogueidae (Hartman & Fauchald, 1971). Chapter 16, Pp. 16-1 to 16-9 *in* J. M. Uebelacker & P. G. Johnson, eds., Taxonomic guide to the polychaetes of the Northern Gulf of Mexico, Vol 2. Final reports to the Minerals Management Service, Contract 14-12-001-29091. Barry A. Vittor & Associates, Inc. Mobile, Alabama.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(2):210–226. 1997.

Triathrix montagni and *T. kalki*, a new genus and two new species of Cletodidae (Crustacea: Copepoda: Harpacticoida) from California and the Gulf of Mexico

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Abstract.—*Triathrix* new genus (Copepoda, Harpacticoida, Cletodidae) is established to accommodate *T. montagni* new species from the California continental shelf and *T. kalki* new species from the Gulf of Mexico. The genus is characterised by a triangular, sharply pointed rostrum; a chitinous extension bearing four socles on the posterior border of the cephalothorax; no socles on the preanal somite; a median tube pore on the operculum; seta I of the caudal ramus implanted posterior to seta II; antennal exopod with three setae; mandibular palp with five setae; maxillulary coxal endite with one seta and basal complex with eight setae; maxillary proximal syncoxal endite with two elements, allobasal endite with a spine and two setae, endopodal setae not fused at base; maxillipedal syncoxa without seta; no sexual dimorphism on male P3; female P5 with baseoendopodal lobe and exopod long, rectangular and equal in length. The two species can be distinguished easily from each other by the size of the dorsal extension to the cephalothorax, the shape of the dorsal median socles on the free prosomites, the length of setae on the P1 and male P5 baseoendopodal lobe and the length to width ratio of the caudal rami and the female P5. *Enhydrosoma nicobarica* Sewell, 1940 is also included in the genus as *T. nicobarica* new combination.

Sewell (1940) described *Enhydrosoma nicobarica* Sewell, 1940 from a single immature specimen found in weed washings in Nankauri Harbour in the Nicobar Islands off the north coast of Indonesia. Within the genus *Enhydrosoma* Boeck this species is unique in that the exopod of the antenna has three setae: a large, plumose seta on the lateral margin along with a large, plumose and a small, naked seta on the distal margin. In his consideration of the genus, Gee (1994) dismissed *E. nicobarica,* in his preliminary assessment of the genus, on the grounds that it was a juvenile (copepodid V), although he considered that an antennal exopod bearing three setae was probably the plesiomorphic condition in Cletodidae based on this condition being found in *Limnocletodes,* Borutsky and, reportedly, in *Acrenhydrosoma perplexa* (T. Scott, 1899). More recently, Fiers (1996) has shown that a trisetose antennal exopod also occurs in the copepodid I stage of *E. lacunae* Jakubisiak, 1933 (and other *Enhydrosoma* species) but the small distal seta is lost in copepodid II and subsequent developmental stages. He concluded, from this, that the antennal exopod structure of *E. nicobarica* is not a juvenile feature and that the species should be removed from *Enhydrosoma* and placed as *species inquirenda* within the family.

During recent monitoring studies of the effects of oil and gas platforms on the surrounding benthic fauna on the Californian continental shelf (Hyland et al. 1990, Montagna 1991) and the northern part of the Gulf of Mexico (Montagna & Harper 1996), two new species of Cletodidae have been discovered which, in the adult, have an antennal structure exactly akin to that described by Sewell (1940) for *E. nicobarica.* In this paper, we describe these species and demonstrate that they, and *E. nicobarica,* should be placed in a new genus within the Cletodidae.

Methods

Before dissection the habit is was drawn, and body length measurements made, from whole specimens temporarily mounted in lactophenol. Specimens were dissected and the parts mounted in lactophenol under coverslips sealed with Bioseal. All drawings were prepared using a *camera lucida* on a Nikon Optiphot 20 differential interference contrast microscope. The terminology for body and appendage morphology follows that of Huys et al. (1996). Abbreviations used in the text and figures are P1–P6 for pereiopods 1–6 exopod (endopod)-1(-2-3) to denote the proximal (middle, distal) segments of a ramus. Body length was measured from the base of the rostrum to the median posterior border of the anal somite (i.e., excluding the caudal rami).

Family Cletodidae T. Scott, 1904

Our concept of the Cletodidae is based on that defined by Por (1986) after he removed many of the genera included in this family by Lang (1948).

Triathrix, new genus

Enhydrosoma Boeck, 1872, p. 53 (part.)

Diagnosis.—Cletodidae. Body semi-cylindrical with well defined somites, tapering posteriorly without clear distinction between prosome and urosome. Cephalothorax with distinct chitinous extension on dorsal posterior margin carrying 4 sensillum-bearing socles. Free-prosomites and urosomite-1 with 6 sensillum-bearing socles and 4 sensilla without socles, dorso-lateral socles usually very pronounced; urosomites-2 to -4 with 4 sensillum-bearing socles and 4 sensilla without socles. Female genital double-somite with a continuous cuticular rib marking line of fusion; genital field with vestigial P6s, bearing 1 seta, covering separate gonopores; minute copulatory pore adjacent to cuticular rib. Preanal somite without any socles. Urosomites, except anal somite, with a double row of spinules on ventral posterior margin and a pair of lateral tube pores; anal somite with additional pair of ventro-lateral tube pores, and single tube pore on operculum. Caudal rami much longer than wide, tapering posteriorly; minute seta I implanted posterior to seta II; seta III implanted more or less medially on outer margin and seta VII proximal to seta III on inner dorso-lateral margin; ventral and lateral tube pore present in median portion of ramus. Rostrum well-developed, distinctly triangular in shape with sharply pointed recurved tip. Female antennule 5-segmented; setal formula 1[1], 2[8], 3[8+aesthetasc], 4[1], 5[11+aesthetasc]. Male antennule 6-segmented. subchirocer; segment-4 swollen, with row of lanceolate setules but without modified setae; setal formula 1[1], 2[9+tube pore], 3[8], 4[13+aesthetasc], 5[2+tube pore], 6[9+aesthetasc]. Antennal allobasis with 2 pinnate setae on abexopodal margin; exopod a well-developed segment with 3 setae (1 pinnate seta on lateral margin and 1 pinnate and a small naked seta on distal margin). Labrum without central tuft of setules. Mandibular palp with 5 setae. Maxillulary coxal endite with 1 seta; basis with 8 setae. Maxilla with 2 syncoxal endites, proximal endite with 2 elements, distal endite with 3 elements; allobasal endite with fused spine and 2 setae; endopod represented by 2 setae not fused at base. Maxillipedal syncoxa without seta; endopodal claw pinnate with a long accessory seta and a short finger-like projection at base. Male P3 without sexual dimorphism. Setal formula of P1-P4 as follows:

	Exopod	Endopod
P1	0:0:022	0:0/111
P2	0:0:022	0:020
P3	0:0:122	0:021
P4	0:0:122	0:021

P5 exopod articulating with baseoendopod; in female endopodal lobe and exopod long, rectangular, equal in length and each with 3 setae; in male rami with 2 setae but endopodal lobe reduced. Male P6 a single asymetrical plate without setae. Sexual dimorphism in antennule, P5, P6, urosome. Females with 1 egg-sac, males with 1 spermatophore.

Type species.—*Triathrix montagni* new species, by designation.

Other species.—*Triathrix kalki* new species and *T. nicobarica* (Sewell 1940) new combination.

Etymology.—The generic name is derived from the Greek noun *treis* (plural *tria*) meaning three and *thrix* meaning hair and refers to the condition of the exopod of the antenna.

Gender.—Feminine.

Triathrix montagni, new species. Figs. 1–6C

Material examined.—Holotype, an adult female (dissected) USNM 278221; paratypes, 8 females (2 dissected) and 10 males (3 dissected) USNM 278822. All material collected by Dr. P. Montagna at CAMP site R4, 15 km off the central California coast, 34°43′N, 121°13′W, from a coarse silt sediment at approx. 90 m depth.

Female.—Body (Fig. 1). Length 0.59–0.67 mm ($\bar{X}$ 0.62 mm, $n = 6$), almost cylindrical but flattened ventrally in urosome; body surface glabrous. Cephalothorax tapering anteriorly, relatively deep dorso-ventrally; ornamented with sensilla and tube pores as in Fig. 1; anterior ventral borders with lateral extensions (Fig. 1A) slightly recurved dorsally (Fig. 1B); dorsal posterior border with large chitinous extension carrying 4 sensillum-bearing socles; lateral and ventral border with 14 sensilla. Posterior border of free prosomites and urosomite-1 with 6 sensillum-bearing socles and 4 sensilla without socles; dorso-lateral socles very pronounced, increasing in size posteriorly, each with an associated tube-pore. Genital double-somite with continuous median cuticular rib marking line of fusion, with 4 lateral sensillum-bearing socles and 2 dorsal sensilla; posterior border with, dorsally 2 sensilla, laterally 6 sensillum-bearing socles (ventral pair with an associated tube-pore) and, ventrally a double row of spinules and 2 sensilla (Fig. 2E). Urosomite-4 posterior border as for genital-double somite except that only 4 lateral sensillum-bearing socles. Pre-anal and anal somite without socles or sensilla except for a pair associated with smooth operculum (Fig. 1A); both somites with a pair of ventro-lateral tube pores; anal somite with additional pair of ventral tube-pores (Fig. 2C) and 1 tube pore on operculum (Fig. 1).

Rostrum (Figs. 1, 3E) well-developed, fused to cephalothorax, triangular, tapering to sharply pointed, strongly recurved tip; with 2 lateral sensilla but, apparently, no median ventral tube pore.

Caudal rami (Figs. 1, 2C) divergent, slightly swollen at base and tapering posteriorly; 4.1–4.4 times longer than maximum width; with tube pore mid-ventrally and laterally immediately posterior to seta III (Fig. 2C). Seta I inserted on ventro-lateral margin, posterior to seta II; seta III inserted laterally at 40% of ramus length; seta IV very small, fused at base to large seta V; seta VI small; triarticulate seta VII inserted at 28% of ramus length.

Genital field (Fig. 2D). Vestigial P6s extremely reduced with 1 seta. Gonopores

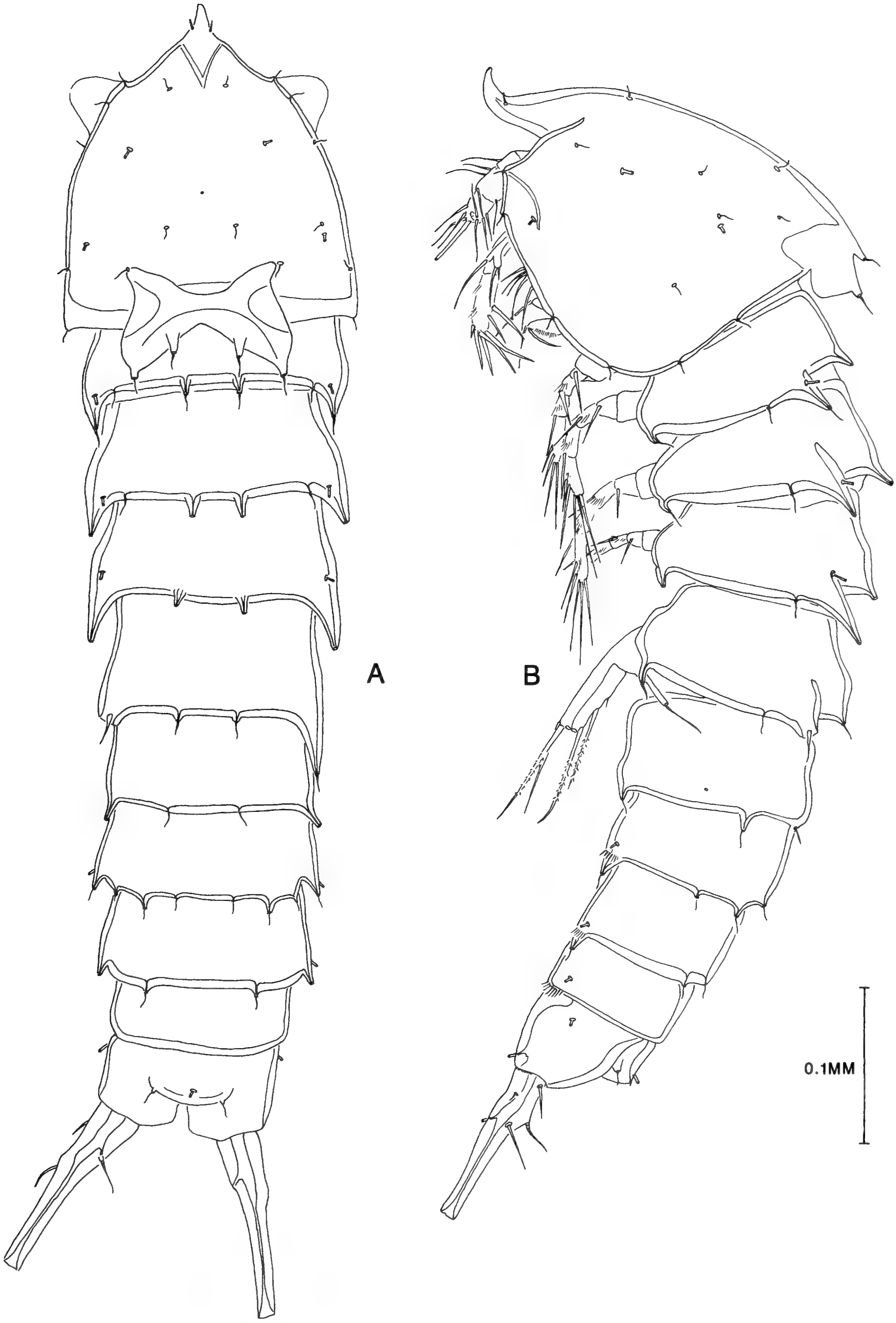

Fig. 1. *Triathrix montagni,* new species. Female body A, dorsal view; B, lateral view.

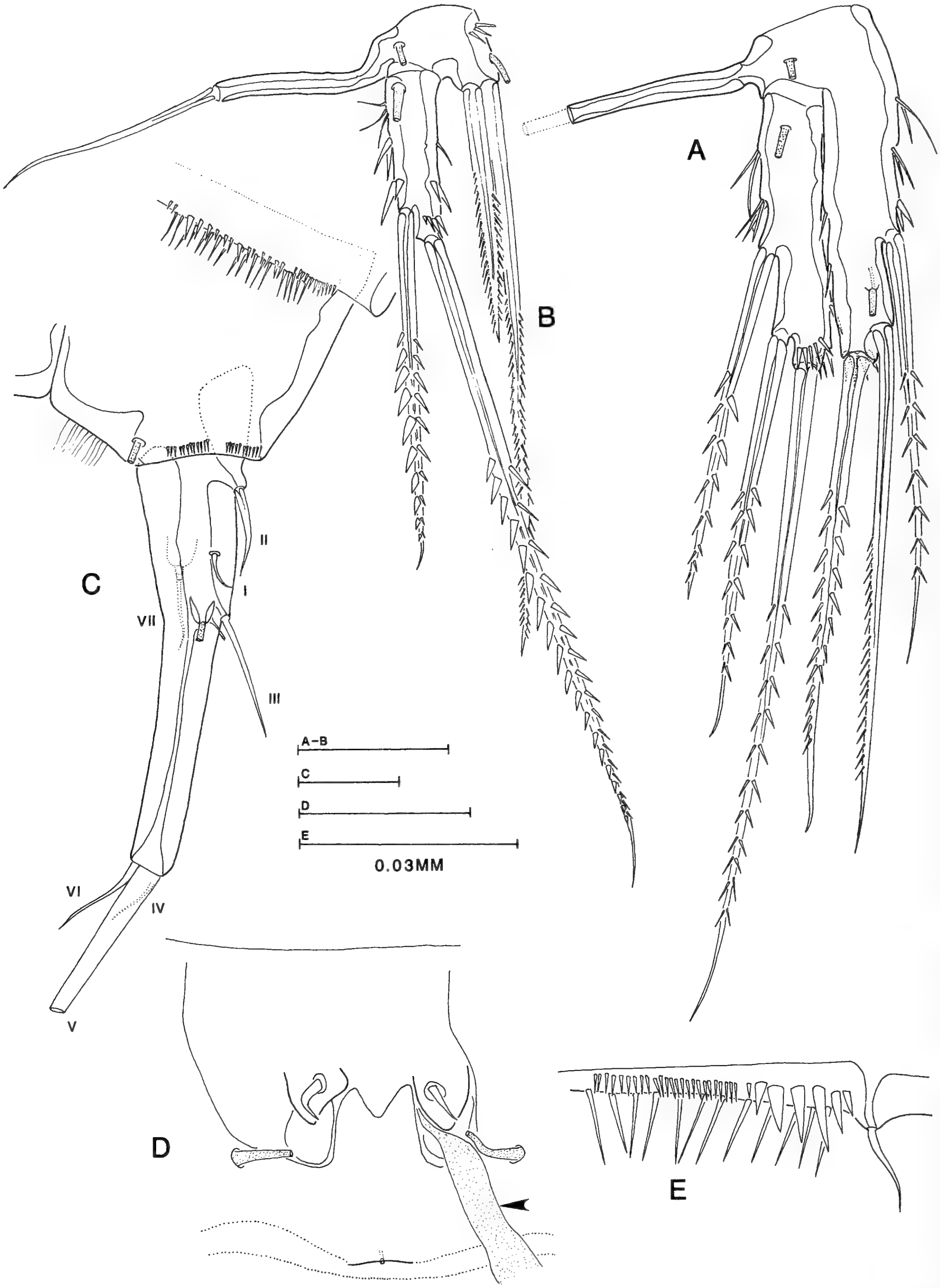

Fig. 2. *Triathrix montagni,* new species. A, female P5; B, male P5; C, female caudal ramus, ventral view; D, female genital field. E, portion of posterior border of female genital double-somite.

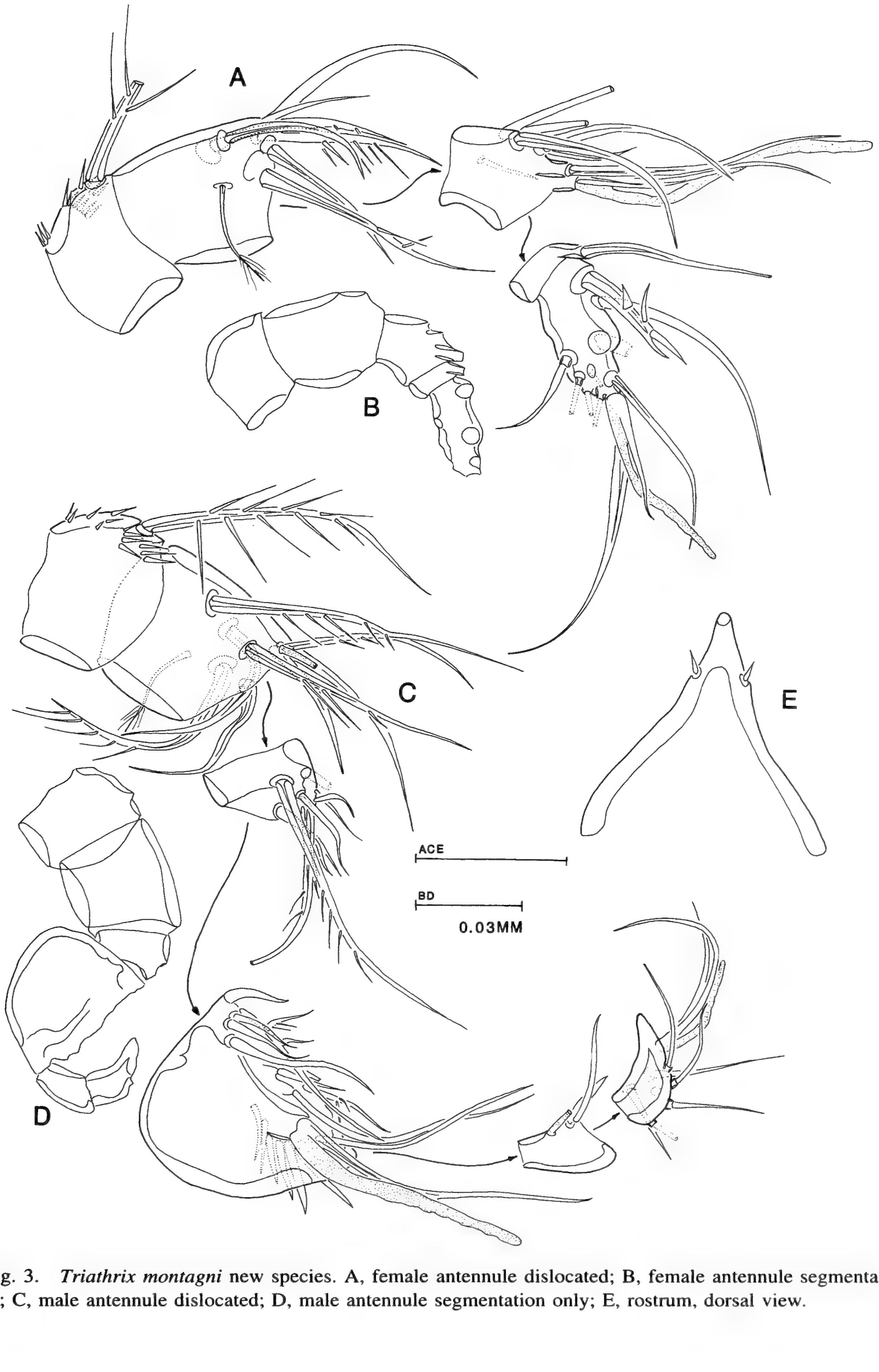

Fig. 3. *Triathrix montagni* new species. A, female antennule dislocated; B, female antennule segmentation only; C, male antennule dislocated; D, male antennule segmentation only; E, rostrum, dorsal view.

completely separate and under P6s (judging by attachment of remains of egg-sac arrowed in Fig. 2D). A pair of large tube-pores immediately posterior to gonopores. Copulatory pore well posterior near median cuticular rib, minute and maybe protected by integumental fold.

Antennule (Fig. 3A–B) short, stout, 5-segmented. Segment 1 with 3 rows of spinules and 1 large, bipinnate seta. Segment 2 with 4 pinnate and 4 naked setae. Segment 3 with 8 naked setae and an aesthetasc fused at base to one of setae. Segment 4 small with 1 naked seta. Segment 5 with 2 strongly pinnate setae and 7 naked setae on lateral margins; distal margin with a trithek of 2 naked setae and an aesthetasc.

Antenna (Fig. 4A). Coxa well-developed with row of setules. Allobasis with 2 strongly pinnate setae on abexopodal margin. Exopod well-developed, 1-segmented with row of setules round distal margin and with 3 setae (a large bipinnate seta on median lateral margin, a large bipinnate seta and a small naked seta in common socket on distal margin). Endopod with 2 rows of strong spinules on anterior margin and a dentate hyaline frill on posterior distal margin; armature consists of 2 spines and a seta subdistally and, on distal margin, 3 finely pinnate spines, 2 geniculate setae, a small seta fused to base of large inner spine, and a tube pore.

Mandible (Fig. 4B). Syncoxa robust with row of setules near base of palp; gnathobase with uni- and multi-cuspid teeth and 1 pinnate seta at distal inner corner. Palp well-developed, 1-segmented, with 5 bipinnate setae (3 on distal and 2 on inner margin).

Maxillule (Fig. 4C). Praecoxa with row of marginal setules; arthrite with 2 large tube setae on anterior surface, a row of setules on inner margin and, on distal margin, 4 cuspid teeth and a pinnate seta. Coxa well-defined with only 1 pinnate seta on distal margin. Basis with a row of spinules on anterior surface and 8 marginal elements (2 pinnate and 1 naked setae on distal endite, 2 naked setae on sub-distal endite, a pinnate seta representing endopod, and a pinnate and a naked seta representing exopod).

Maxilla (Fig. 4D). Syncoxa with 2 marginal rows of spinules and 2 endites; proximal endite with 1 fused pinnate spine and 1 slender seta, distal endite with a fused pinnate spine and 2 naked setae. Allobasal endite with a fused pinnate spine and 2 naked setae. Endopod represented by 2 setae not fused at base.

Maxilliped (Fig. 4E). Syncoxa with 2 rows of spinules but no seta. Basis relatively short, oval, with a row of spinules on palmar and outer margin. Endopod represented by a minutely pinnate, recurved spine, a long, well developed accessory seta, and a small finger-like projection.

P1–P4 (Fig. 5) exactly same in both sexes (Fig. 5B–C). Intercoxal sclerites slender, curved. Protopods ornamented on anterior face as in Fig. 5, same in P1–P4 except that P1 basis with a strong bipinnate seta on inner margin and P2–P4 coxa with an extra row of small spinules centrally. Exopods 3-segmented, segments not elongate; P1 (Fig. 5A) with plain inter-segmental hyaline frills, P2–P4 with dentate frills; no tube pores on any segments; exopod-1 to 3 with 3 rows of spinules on outer margin, exopod-2 and -3 with a row of setules on inner margin; outer terminal seta of exopod-3 much longer than distal outer spine and 2 terminal pinnate setae with a comb of pinnules at tip. Endopods 2-segmented, endopod-2 much longer than endopod-1; both segments with spinules on outer margin, endopod-2 with setules on inner margin; P1 endopod-2 with 3 armature elements, middle one a pinnate seta with a comb-like tip (Fig. 5A).

P5 (Fig. 2A). Limbs well separated and connected by slender intercoxal sclerite (not illustrated). Small basal part of baseoendopod with a tube pore on anterior surface; outer margin with long pedicel bearing outer seta; endopodal lobe long, slender (4 times longer than wide), rectangular in shape and reaching to distal margin of exopod, with 3 rows of spinules on inner and

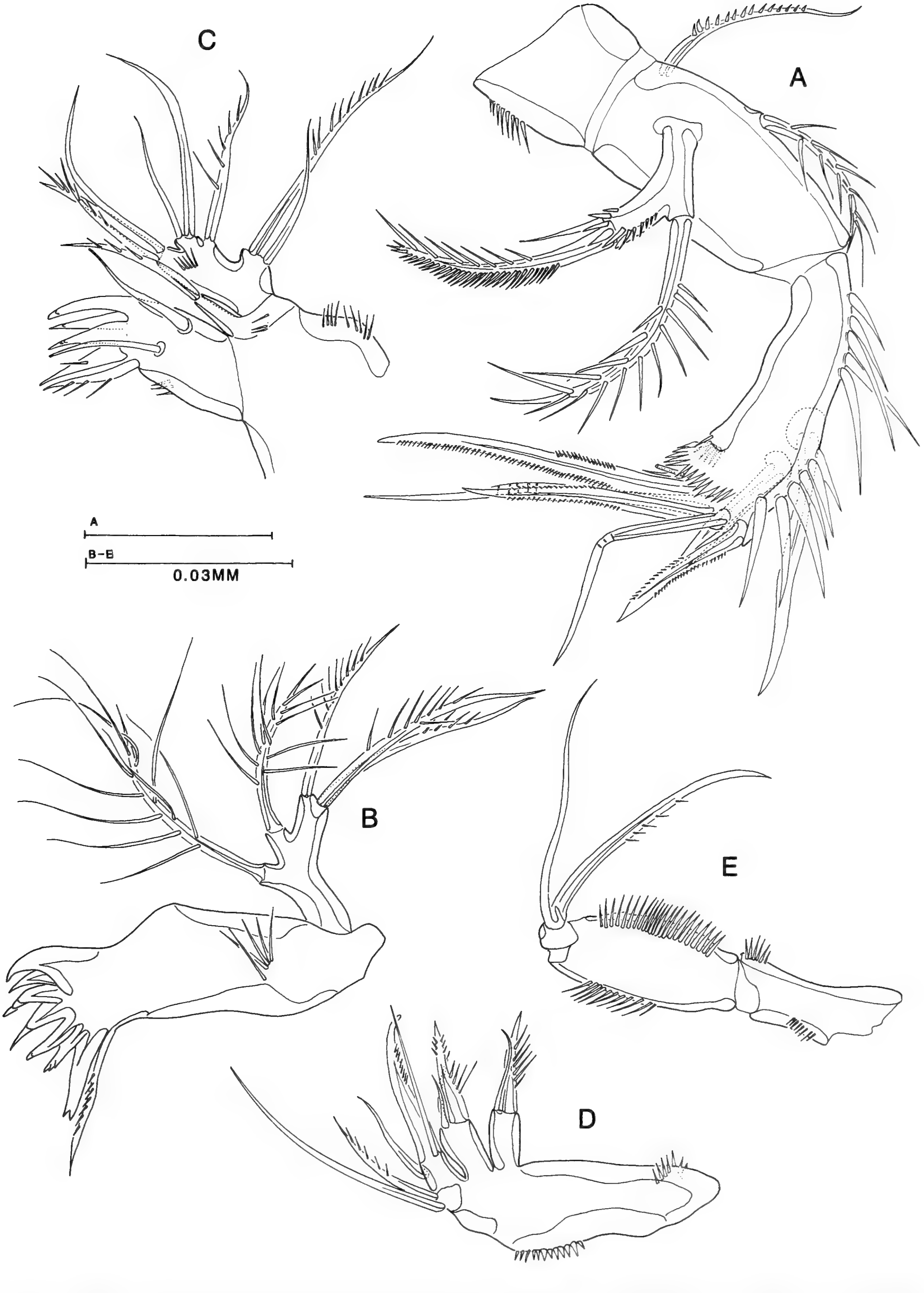

Fig. 4. *Triathrix montagni* new species. A, antenna; B, mandible; C, maxillule; D, maxilla; E, maxilliped.

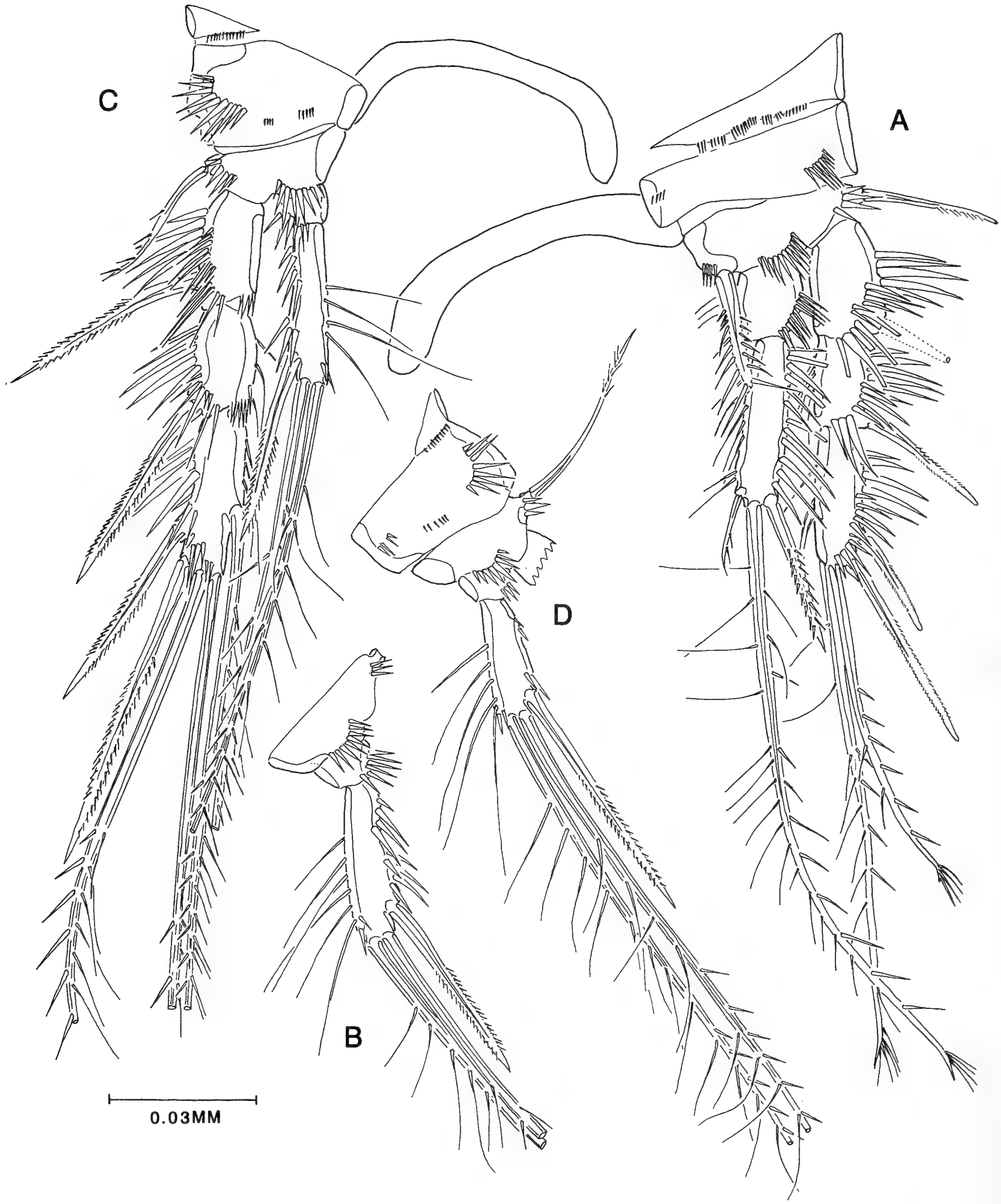

Fig. 5. *Triathrix montagni* new species. A, P1; B, female P3 basis and endopod; C, male P3; D, female P4 protopod and endopod.

outer margin, 1 row terminally on posterior surface, and tube pore on anterior surface between inner lateral and inner sub-distal seta; bearing 3 setae inserted and ornamented as in Fig. 2A. Exopod separate, articulating with margin of baseoendopod; long, slender (4 times longer than wide), rectangular; ornamented with 2 rows of setules on outer margin, 1 row around distal margin, and a tube pore proximally on anterior surface; bearing 3 setae inserted and ornamented as in Fig. 2A.

Male.—As female except in urosome, antennule, P5 and P6.

Body (Fig. 6) length 0.60–0.71 mm ($\bar{X}$ 0.64 mm, $n = 8$), slightly more slender than female. Urosomite-2 and -3 completely separate. P6 (Fig. 6C) on posterior margin of urosomite-2, an asymmetrical oval plate with row of small spinules but no setae.

Antennule (Fig. 3C–D) 6-segmented, sub-chirocer. Segment 1 with 3 rows of spinules and a large bipinnate seta on anterior margin. Segment 2 with nine setae (5 pinnate, 4 smooth) and a tube pore. Segment 3 with 8 setae ($^{2}/_{3}$? pinnate, $^{6}/_{5}$? smooth). Segment 4 strongly swollen with 13 setae and an aesthetasc fused to base of 1 seta on palmar margin; a row of strong setules on dorsal surface. Segment 5 with 2 setae and a tube pore. Segment 6 with a distal trithek and 7 other setae.

P5 (Fig. 2B). Elements well separated and connected by slender sclerite (Fig. 6C). Baseoendopod small, endopodal lobe virtually non-existant, with a tube pore on inner margin and 2 terminal setae, outer seta about half length of inner. Exopod separate, articulating with margin of baseoendopod, slender (3 times longer than wide), rectangular, with 3 rows of spinules on inner and outer margin and a tube-pore proximally on anterior face; with 2 bipectinate setae distally, outer about half length of inner.

Etymology.—This species is dedicated to our friend and colleague Dr. Paul Montagna who provided the specimens from his collections.

Variation.—Amongst the 19 specimens examined there was no variation in the structure and proportion of the appendages or the major features of the body ornamentation.

Triathrix kalki, new species
Figs. 6D–8

Material examined.—Holotype, an adult female (dissected) USNM 278223; paratypes, 4 females (1 dissected), 8 males (1 dissected) and 19 copepodids USNM 278224. All material collected by Dr. P. Montagna at Flower Gardens site, SE of Galveston Texas, in the Gulf of Mexico, 27°54′N, 93°34′W, from a silty sand sediment at 110–160 m depth.

The following description is confined to those characters either not described for, or which differ from, *T. montagni.*

Female.—Body (Fig. 7A–B) length 0.44–0.54 mm ($\bar{X}$ 0.51 mm, $n = 4$). Chitinous extension on posterior border of cephalothorax less pronounced and socles more equal in size than in *T. montagni.* Median dorsal sensillum-bearing socles on free prosomites and anterior urosomites fused together into Y-shaped structure, extended dorso-lateral socles without tube pore. Anal operculum (Fig. 8A) fringed with fine setules.

Caudal rami (Fig. 8A–B) slender, tapering posteriorly, 6 times longer than maximum width in ventral view. Setae II and VII inserted slightly more posteriorly (14% and 33% respectively) than in *T. montagni.*

Labrum (Fig. 8C). With a pore and small row of setules medially, oral margin with a short row of long spinules laterally and minute denticles medially.

P1–P4 (Fig. 8D–E). Outer terminal seta of P1 exopod-3 (arrowed in Fig. 8D) shorter than outer distal spine. Terminal setae of exopod-3 and endopod-2 without setule comb at tip. Median row of small setules on coxa of P2–P4 (Fig. 8E) slightly more proximal in position than in *T. montagni.*

P5 (Fig. 8F). Baseoendopodal lobe and exopod 6 times longer than wide. Distal inner seta on endopodal lobe shorter (in absolute length) than proximal inner seta.

Male.—As female except for urosome, antennule, P5 and P6.

Body length 0.45–0.52 mm ($\bar{X}$ 0.48 mm, $n = 8$) and slightly more slender than female. Urosomites-2 and -3 completely separate.

P5 (Fig. 7C). Exopod 4 times longer than wide (more slender than in *T. montagni*). Outer seta on endopodal lobe not reaching distal margin of exopod and only slightly shorter than inner seta.

Etymology.—The species is dedicated to

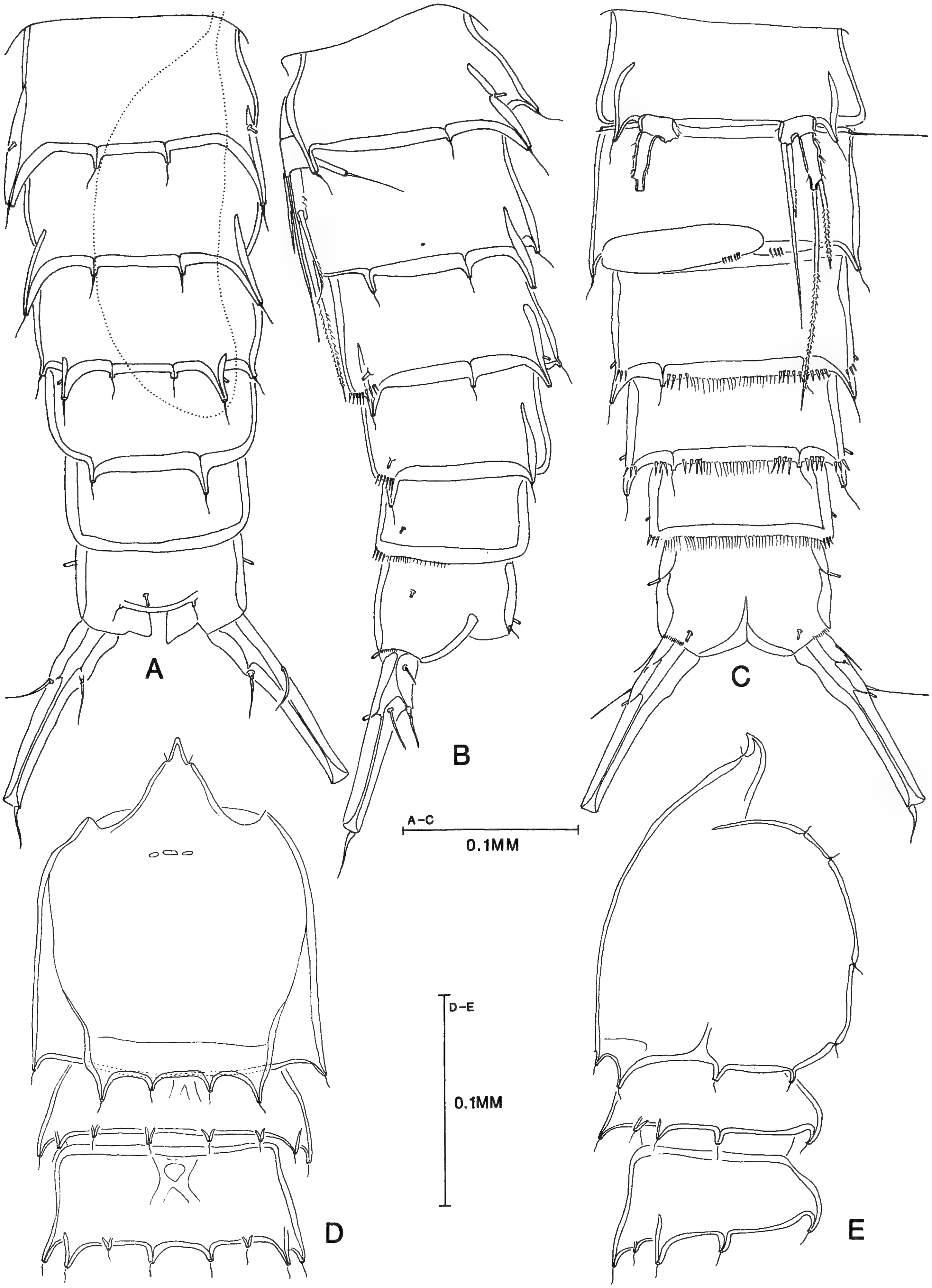

Fig. 6. *Triathrix montagni* new species, male urosome A, dorsal view; B, lateral view; C, ventral view. *Triathrix kalki* new species, female copepodid V cephalothorax and first two free prosomites, D, dorsal view, E, lateral view.

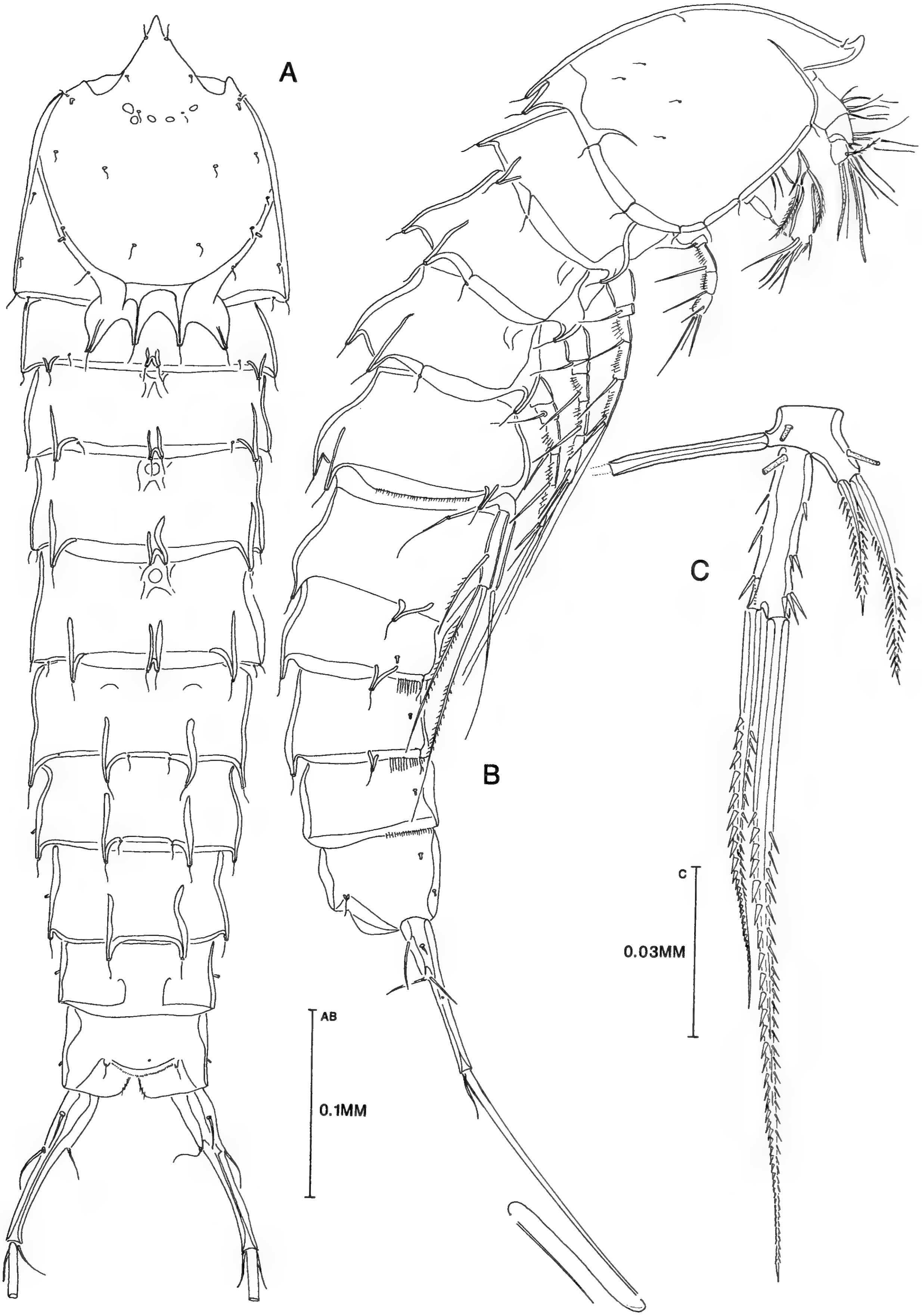

Fig. 7. *Triathrix kalki* new species. A, female body, dorsal view; B, female body lateral view; C, male P5.

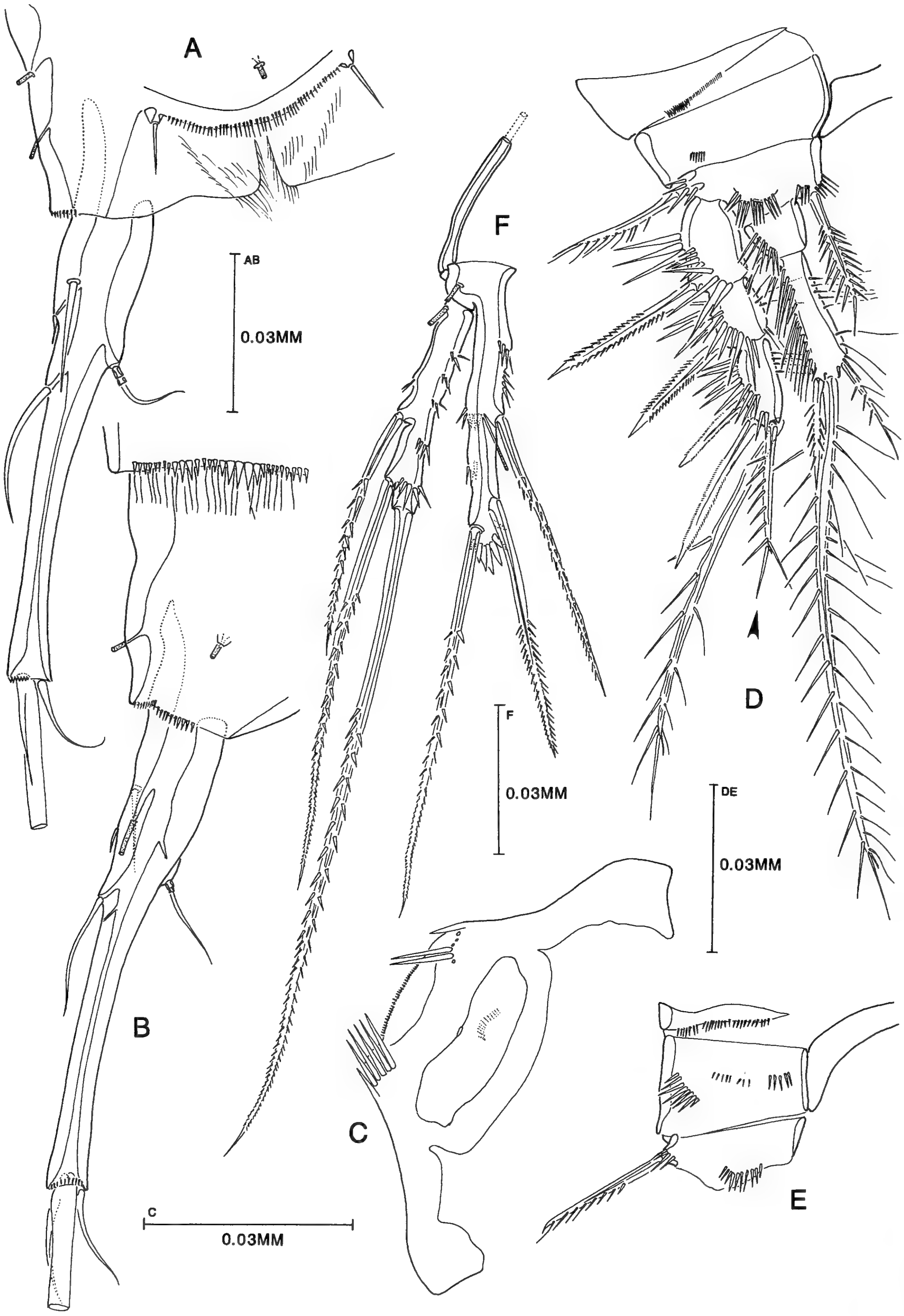

Fig. 8. *Triathrix kalki* new species. A, Female operculum and caudal ramus, dorsal view; B, female caudal ramus, ventral view; C, labrum; D, P1, E, P2 protopod; F, female P5.

our good friend and colleague Mr. Rick Kalke, the leader of the team engaged in the analysis of meiofauna samples from the GOMEX project.

Variation.—Amongst the 13 adult specimens examined there was no variation in the structure and proportion of the appendages or the major features of the body ornamentation.

Discussion

The specimens described above can be placed within the Cletodidae on the basis of the following combination of characters: well defined somites with no hyaline frills but with sensilla and socles on the posterior border; an operculum with a pair of associated sensillum-bearing socles; an antennule which is 5-segmented in the female and 6-segmented in the male; a 1-segmented antennary exopod with at most three setae; rami of the mandible and maxillule fused to the basis; a maxilla with two syncoxal endites; a chelate maxilliped without setae on the basis; the P1 with a 2-segmented endopod in which endopod-2 is much longer than endopod-1; endopod-1 of P1–P4 without an inner seta; P1 and P2 exopod-3 with four setae/spines; the P5s in both sexes not fused medially; the male P6 an asymetrical plate without armature elements.

Gee (1994) and Gee & Huys (1996) regard the structure of the antenna to be significant in phylogenetic considerations within the Cletodidae. The antenna of the above species (and of *E. nicobarica*) is the most primitive condition found in the family with two setae on the abexopodal margin of the allobasis and a 1-segmented exopod bearing three setae, two on the distal margin and one on the lateral margin. *Limnocletodes* also retains the primitive structure of the antennary exopod but has lost one seta on the abexopodal margin of the allobasis. In the original description of *Acrenhydrosoma perplexa,* Scott (1899) illustrates (plate XI, fig. 15) an exopod with three setae but this are not homologous with the above because there is only one seta on the distal margin and two setae on the lateral margin. Fiers (1996) is of the opinion that the proximal lateral seta may have been confused with a large spinule, especially in the light of the fact that the other two species of *Acrenhydrosoma* Lang (see Lang, 1965 and Schizas & Shirley 1994) have only one terminal and one lateral seta. All other genera within the Cletodidae have either (a) a well developed exopod with two setae (one distal and one lateral) and one or no setae on the abexopodal margin of the allobasis; or (b) a small cylindrical exopod with one seta and with two or one setae on the abexopodal margin of the allobasis.

Although the structure of the antenna in the species described in this paper is plesiomorphic they are placed in a separate genus on the basis of the following autapomorphies: A chitinous plate with four socles on the posterior margin of the cephalothorax. Most genera of cletodid usually have more than four socles arranged around the margin of the cephalothorax but in no species has a chitinous extension to the cephalothorax been described; No socles on the preanal somite. The arrangement of socles on the urosomites has not always been accurately recorded but for all species and genera that we have examined in detail there are always two non-sensillum bearing socles on the posterior border of this somite; A median tube pore on the operculum. The presence of a pore in this position has not been recorded before in the Cletodidae but again this could be the result of lapses in observation or resolution of microscopes used by previous workers; Seta I of the caudal ramus inserted posterior to seta II. In all other genera in the family, where the condition is known, seta I and seta II arise in very close proximity on the lateral margin of the ramus; The maxillulary coxal endite with only 1 seta. For many genera and species of Cletodidae the mouthparts are unknown. However, amongst those that are known, there are two setae on the coxal endite, except in species of *Enhydrosoma* where the coxal endite is fused to the basis and in *Cletodes millerorum* Hamond, 1973 and *C. pseudodissimilis* Coull, 1971; Maxillulary basal complex with eight setae; three on the distal endite, two on the proximal endite, one representing the endopod and two the exopod. It is thought that the primitive condition in the family is 10 or 11 setae on the basal complex, (six or seven on the basal endites and two each representing the exopod and endopod). This is the condition found in *Cletodes, Intercletodes* Fiers, *Strongylacron* Gee & Huys and *Schizacron* Gee & Huys. In *Enhydrosoma, Enhydrosomella* Monard, *Kollerua* Gee, *Stylicletodes* Lang and *Acrenhydrosoma* (referred to below as the *Enhydrosoma* group) there is a maximum of six setae on the basal complex (four on the basal endites and one each representing the exopod and endopod).

In addition to the above autapomorphies, the genus *Triathrix* is also characterized by the following features: The sharply pointed, triangular rostrum. The phylogenetic significance (and polarity) of this character is difficult to assess but no other cletodids have a rostrum shape identical to these species and there is evidence (Gee & Huys, 1996) that the rostrum has a characteristic shape in each genus; A mandibular palp with five setae. The primitive condition in the family is six setae on the mandibular palp (two on the inner, three on the distal and one medially on the outer margin), found in some species of *Cletodes, Intercletodes* and *Monocletodes. Triathrix* has lost the seta on the outer margin, as has *Strongylacron* and other species of *Cletodes* with five palp setae, except *C. millerorum,* which appears to have lost the proximal seta on the inner margin. *Enhydrosoma curticauda* Boeck, 1872, the remaining three species of *Cletodes, Schizacron* and *Acrenhydrosoma maccalli* Schizas & Shirley, 1994, have four setae on the palp, all having lost the seta on the outer margin and one on the distal margin. All other genera or species where the condition is known, have three setae on the palp, the additional lost seta beings the proximal seta on the inner margin; Proximal maxillary syncoxal endite with two armature elements. The primitive condition in the family is three elements on both syncoxal endites and is found in most species where the condition has been reliably reported. In a number of species of *Enhydrosoma* there are two elements on the distal endite but, except in *Cletodes reductus* Moore, 1977 there are no reliable reports of two elements on the proximal endite; Maxillary allobasal endite with a spine and two setae. Again the primitive condition within the family is a spine and three setae on this endite although all genera in the *Enhydrosoma* group appear to have the *Triathrix* condition; The two setae representing the maxillary endopod are not fused at the base. This is probably the primitive condition in the family and, as far as we know, the basal fusion of these two setae is only found in genera in the *Enhydrosoma* group; Maxillipedal coxa without a seta. Most genera in the family have retained the seta on the coxa but it has been lost in a large number of the species at present placed in *Enhydrosoma* (including the type species); The shape of the female P5 in which the baseoendopodal lobe and the exopod are rectangular in shape and equally long. Only in *Stylicletodes* is the P5 similarly shaped but in this genus there are four or five setae on each ramus compared to only three in *Triathrix.* The rami of the female P5 in *Strongylacron* and *Schizacron* are equal in length and bear three setae but are well separated (giving the limb a characteristic U-shape) and the exopod is fused to the baseoendopod. The female P5 exopod in most species of *Cletodes* is long and rectangular but always bears five setae and the endopodal lobe is usually much reduced. Within the family, the morphology and setal arrangement of the P5 in both sexes are important in defining generic boundaries and are undoubtably of great phylogenetic significance (Fiers, 1996) but at the moment the relationships of these characters are difficult to understand; No sexual dimorphism on swimming legs. Within the Cletodidae, sexual dimorphism, when present, is found on the P3 endopod, although in three species of *Enhydrosoma* (*E. longifurcatum* Sars, 1909, *E. latipes* (A. Scott, 1909) and *E. pericoense* Mielke, 1990) it is also found on the P3 exopod. The range of sexual dimorphism on the P3 endopod, its origins and homologies are discussed in detail by Gee (1994), Gee & Huys (1996) and Fiers (1996). Briefly however, the former two authors regard the 3-segmented P3 endopod in the male of *Cletodes, Strongylacron, Schizacron* and *Enhydrosoma curvirostre* (T. Scott, 1894) as a development (apomorphy) from an originally 2-segmented ramus (plesiomorphic condition) and interpret the absence of sexual dimorphism in some species of *Cletodes, Intercletodes* and *Monocletodes* as a secondary loss of sexual dimorphism. The latter author, on the other hand regards the 3-segmented ramus on the male P3 as the plesiomorphic condition and absence of sexual dimorphism as the most advanced state.

We have not examined the single known specimen of *E. nicobarica* which is a male copepodid V and the description of Sewell (1940) does not detail the structure of the mouthparts. Nevertheless, the shape of the rostrum, the setation of the antennal exopod and the caudal ramus, and the structure of the juvenile P5, all suggest that this specimen is a juvenile *Triathrix.* There is no evidence of the posterior extension to the cephalothorax in the drawing of the dorsal view of the body of *E. nicobarica* (Sewell, 1940 fig. 85A). However, it is known (F. Fiers, pers. comm.) that one of two further new species belonging to this genus from Campeche Bank, Yucatan Peninsula, southern Gulf of Mexico, has an even smaller dorsal extension than that of *T. kalki.* Further, an examination of the copepodid V specimens in our sample of *T. kalki,* shows that the posterior extension of the cephalothorax is not developed in the last juvenile stage (Fig. 6D–E). In addition, it should be noted from Fig. 6D–E, firstly, that there are eight socles on the cephalothorax and ten on the free prosomites in copepodid V rather than the four and six respectively found in the adult and, secondly that the median dorsal socles are well separated in copepodid V rather than fused as in the adult of this species. Thus, it is clear that the distinctive body features of the species described in this paper may only appear in the adult and that the copepodid V stage is the same as that drawn by Sewell (1940) for *E. nicobarica.* Further, Sewell illustrated the P1 endopod-2 of *E. nicobarica* with only two elements (Sewell, 1940, fig. 85F) and noted that the inner distal element of P2 exopod-3 was a spine-like element (rather than a normal seta as in *T. montagni* and *T. kalki*). Developmental studies on Cletodidae (Fiers, 1991, 1996) indicate that all setae present in the adult are also present in copepodid V but may differ slightly in appearance. Thus the absence of an inner seta on P1 endopod-2 in *E. nicobarica* clearly distinguishes it from the two species described above but the form of the distal elements on P2-endopod-3 may be just a juvenile precursor of a normal seta and not a distinguishing feature. Thus, it is clear that *E. nicobarica* should be transferred to the new genus *Triathrix* as *T. nicobarica* new combination.

Finally, *Triathrix* appears to be limited in its distribution to the Indo-Pacific Oceans and the western Atlantic with three species known to inhabit the Gulf of Mexico region east of the central American isthmus, one the Californian Pacific coast and one the Indian Ocean. Woodring (1966) presents evidence from the fossil molluscan record suggesting that the whole of the Caribbean area and tropical eastern Pacific formed a single biogeographic province during the Miocene. Jones & Hasson (1985) suggest that the Central American isthmus gradually emerged from about the time of the late Miocene with final closure ocurring in the southern part of the isthmus some three m.y.a. in the late Pliocene or early Pleistocene. The present known distribution of *Triathrix* suggests that the genus was in existence well before that date and that during more recent times speciation within the Gulf of Mexico region has been greater than that in the eastern Pacific region. However, it must be remembered that the harpacticoid copepod fauna of the Caribbean and Central American region is extremely poorly known, especially for sublittoral communities. Therefore the present known distribution of species on either side of the isthmus may be more a function of sampling effort than the pace of evolution.

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Literature Cited

Fiers, F. 1991. Three new harpacticoid copepods from the Santa Maria Basin off the Californian Pacific coast (Copepoda, Harpacticoida).—Beaufortia 42(2):13–47.

———. 1996. Redescription of *Enhydrosoma lacunae* Jakubisiak, 1933 (Copepoda, Harpacticoida); with comments on the *Enhydrosoma* species reported from West Atlantic localities, and a discussion of cletodid development.—Sarsia 81:1–27.

Gee, J. M. 1994. Towards a revision of *Enhydrosoma* Boeck, 1872 (Harpacticoida: Cletodidae sensu Por); A re-examination of the type species, *E. curticuada* Boeck, 1872, and the establishment of *Kollerua* gen. nov.—Sarsia 79:83–107.

———, & R. Huys. 1996. An appraisal of the taxonomic position of *Enhydrosoma buchholzi* (Boeck, 1872), *E. bifurcarostratum* Shen & Tai, 1965, *E. barnishi* Wells, 1967 and *E. vervoorti* Fiers, 1987 with definition of two new genera (Copepoda, Harpacticoida, Cletodidae).—Sarsia In press.

Huys, R., J. M. Gee, C. G. Moore, & R. Hamond. 1996. Marine and brackish water harpacticoid copepods Part 1. Synopses of the British Fauna (Ed. R. S. K. Barnes & J. H. Crothers), Field Studies Council Press, UK. 51:1–352.

Hyland, J., D. Hardin, I. Crecelius, D. Drake, P. Montagna, & M. Steinhauer. 1990. Monitoring long-term effects of offshore oil and gas development along the southern California outer shelf and slope: background environmental conditions in the Santa Maria Basin.—Oil and Chemical Pollution 6:195–240.

Jones, D. S., & P. F. Hasson. 1985. History and development of the marine invertebrate faunas separated by the Central American Isthmus. Pp. 325–356 *in* F. G. Stehli & S. D. Webb, eds., The Great American Biotic Interchange. Plenum Press.

Lang, K. 1948. Monographie der Harpacticiden I: 1–896, figs 1–361; II: 897–1682, figs. 362–607, maps 1–378. Håkan Ohlsson, Lund.

———. 1965. Copepoda Harpacitcoidea from the California Pacific Coast.—Kungliga Svenska VetenskapsAkademiens handlinger 10:1–560.

Montagna, P. A. 1991. Meiobenthic communities of the Santa Maria Basin on the California continental shelf—Continental Shelf Research 11: 1355–1378.

———, & D. E. Harper Jr. 1996. Benthic infaunal long-term response to offshore production platforms.—Canadian Journal of Fisheries and Aquatic Sciences. In Press.

Por, F. D. 1986. A re-evaluation of the family Cletodidae Sars, Lang, (Copepoda, Harpacticoida). *In* G. Schriever, H. K. Schminke, & C.-T. Shih eds., Proceedings of the Second International Conference on Copepoda, Ottawa, Canada, 13-17th August, 1984.—Syllogeus 58:420–425.

Schizas, N. V., & T. C. Shirley. 1994. *Acrenhydrosoma maccalli,* a new species from Auke Bay, Alaska (Copepoda, Harpacticoida).—Crustaceana 67:329–340.

Scott, T. 1899. Notes on recent gatherings of micro-Crustacea from the Clyde and the Moray Firth.—17th Annual Report of the Fisheries Board of Scotland for 1898, Part III: 248–273.

Sewell, R. B. S. 1940. Copepoda, Harpacticoida.—The John Murray Expedition 1933-34, Scientific Reports, British Museum (Natural History) 7: 117–382.

Woodring, W. P. 1966. The Panama land bridge as a sea barrier.—Proceedings of the American Philosophical Society 110:425–433.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(2):227–235. 1997.

New records of the genus *Hansenomysis* in Japan with description of a new species (Crustacea: Mysidacea: Petalophthalmidae)

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Abstract.—A new species, *Hansenomysis japonica,* and a species tentatively identified as ?*Hansenomysis lucifugus* (Faxon, 1893), of the mysid family Petalophthalmidae, were collected from Japanese waters. *Hansenomysis japonica* is clearly distinguishable from the nearest species of the genus, *H. violacea* (Birstein & Tchindonova, 1958), by the long acute horns of the eyeplate, the narrower antennal scale, the segmented carpopropodus of the endopod of the eighth thoracopod, and the longer and narrower telson. The new species is the fifth described species of *Hansenomysis* in the Pacific Ocean. ?*Hansenomysis lucifugus* has not previously been recorded from Japan and western Pacific, if the identification is correct. A key to the species of *Hansenomysis* is also included.

The genus *Hansenomysis* was established by Hansen in 1887, under the name *Arctomysis,* to incorporate *A. fyllae* collected southwest of Greenland. However, *Arctomysis* was already allocated to a different species (Czerniavsky 1883), and Stebbing (1893) changed the name to *Hansenomysis.* Since the establishment of the genus, the classification of its species has experienced notable changes. *Hansenomysis lucifugus* and *H. violacea,* were initially described as the two only species of the genus *Scolophthalmus.* Birstein & Tchindonova (1970) transferred these two species of *Scolophthalmus* to *Hansenomysis.* Later, Murano & Krygier (1985) transferred five *Hansenomysis* species to *Bacescomysis,* which was established by them for *B. pacifica,* based mainly on the exopod of uropod which is a 2-segmented plate in the former genus, but unjointed in the latter. The most recent species of *Hansenomysis, H. carinata,* was described by Casanova (1993) for a single male specimen from the New Caledonian area.

Presently, the genus *Hansenomysis* consists of 15 species. The new species, *Hansenomysis japonica,* is the 16th species of the genus. ?*Hansenomysis lucifugus,* is reported for the first time from Japan and the western Pacific. Table 1 shows the latitudinal occurrence, the adult body length, and the habitat of each species of *Hansenomysis.*

The type specimens of *H. japonica* are deposited in the National Science Museum, Tokyo (NSMT).

Order Mysidacea Boas, 1883
Suborder Petalophthalmida Tchindonova, 1981
Family Petalophthalmidae Czerniavsky, 1882
Genus *Hansenomysis* Stebbing, 1893

Arctomysis.—Hansen, 1887:210.
Scolophthalmus.—Faxon, 1893:219; 1895: 224–226.

Diagnosis.—Carapace very short. Eyes fused in single plate, without visual pig-

Table 1.—Latitude (n°), adult body length (mm), and habitat or depth (m) of the species of *Hansenomysis* Stebbing, 1893 (Mauchline & Murano 1977, Lagardère 1983, Casanova 1993).

Species	Latitude	Body length	Habitat/depth	Occurrence
H. angusticauda O. S. Tattersall, 1961	75S	>26	mesopelagic	Ross Sea, Palmer Archipelago
H. antarctica Holt & Tattersall, 1906	53S–76S	20–23	100–400	Antarctic
H. armata Birstein & Tchindonova, 1958	50N–35N	13	2960	Kurile-Kamchatka Trench
H. carinata J.-P. Casanova, 1993	23S		950–1000	New Caledonia
H. chini Băcescu, 1971	8S	>12	2000	Peru Trench
H. falklandica O. S. Tattersall, 1955	50S–53S	12–15	200–400	Southern Oceans
H. fyllae (Hansen, 1887)	70N–40N	16–17	150–1500	North Atlantic
H. japonica new species	35N	12	590	Japan
H. lucifugus (Faxon, 1893)	?35N–0	42	?742–2000	Off Galapagos, ?Japan
H. menziesi Băcescu, 1971	8S	22	2000	Peru Trench
H. nouveli Lagardère, 1983	56N–44N	14–18	1913–2498	Bay of Biscay
H. pseudofyllae Lagardère, 1983	48N–44N	14.4	1950–4829	Bay of Biscay
H. rostrata Birstein & Tchindonova, 1970	44N	32–35	bathypelagic	Kurile-Kamchatka Trench
H. spenceri Băcescu, 1971	8S	17	2000	Peru Trench
H. tropicalis Băcescu, 1967	8S	>8	2000	Peru Trench
H. violacea (Birstein & Tchindonova, 1958)	43N	19	bathypelagic	Kurile-Kamchatka Trench

ments or with small pigmented area. Dorsal surface of proximal region of antennular peduncle having what is identified as a sensorial organ called the "Tattersall organ" (Băcescu 1971). Antennal scale lanceolate with spines and setae. Maxilla and maxillule normal. First and 2nd thoracopods robust; endopods of 3rd–5th thoracopods slender, with chelate structure terminally; endopods of 6th–8th thoracopods slender with dactylus and nail together forming long slender claw. Pleopods of female uniramous; 1st–4th pleopods unsegmented; 5th pleopod longest, 2 or 3-segmented. Pleopods of male biramous; 1st with endopod unsegmented, exopod segmented; 2nd pleopod with exopod segmented and modified, endopod segmented. Endopod of uropod 2-segmented, without spines on its inner margin; exopod of uropod 2-segmented, proximal segment with spines on outer margin. Telson elongate, entire, without plumose setae on apex, posterior part of the lateral margins armed with long strong spines separated by groups of short spines.

Type species.—*Hansenomysis fyllae* (Hansen, 1887)

Hansenomysis japonica, new species

Figs. 1, 2, 3A–D

Type specimens.—Holotype (NSMT-Cr 11910), adult male 12.0 mm; paratype (NSMT-Cr 11911), juvenile 8.8 mm; 17 Oct 1990, Sagami Bay (35°09.0′N, 139°24.6′E), 590 m, sledge net.

Description of male.—Body robust, elongate. Carapace without spines, covering laterally part of 7th thoracic somite, and dorsally all but 6th–8th somites; anterior margin broadly rounded without rostral projection, leaving fused eyes uncovered (Fig. 1A); anterolateral corner sharply pointed.

Eyes fused in single plate with 2 acute median horns, outer margin undulated. Eyeplate with 2 fused rounded bulks of visual pigments away from eyeplate margin (Fig. 1A).

Antennular peduncle robust; first segment longest, basal dorsal surface with well-developed Tattersall organ (Fig. 1A), 2nd segment about same length as 3rd in dorsal view, shorter in ventral view (Fig. 1B), with blunt process armed with setae at distal outer corner. Outer flagellum very robust, clearly separated into subsegments, each subsegment with rounded inner margin armed with 2 rows of tight setae (Fig. 1B).

Antennal scale lanceolate, nearly 5 times as long as the maximum width, extending beyond distal end of antennular peduncle for 0.75 of its length, setose all round except for proximal 40% of outer margin. Outer distal edge of naked margin with 4 spines that gradually increase in length (Fig. 1C). Peduncle slightly shorter than scale but considerably longer than antennular peduncle, 3-segmented, 1st segment very short, 3rd segment about half length of 2nd. Sympod with one spine at base of scale (Fig. 1C).

Mandible with strong lacinia mobilis; palp large and slender, 3-segmented, 1st segment shortest, 2nd segment about twice as long as 3rd (Fig. 1D). Labrum symmetrical, pentagonal, wider than long, without frontal spiniform process (Fig. 1E). Maxillule with 7 spines and 1 seta on outer lobe. These spines bear small spinules on margins. Inner lobe with 7 setae, apical 3 large and plumose (Fig. 1F). Maxilla with distal segment of endopod longer than wide, densely setose on inner margin and scarcely setose on outer margin; proximal segment with 4 setae on inner margin; exopod large, with 26 setae on margin (Fig. 1G).

First thoracopod small and robust, without exopod; endopod with short preischium and dactylus, ischium, merus and carpopropodus similar in length; dactylus with 3 long plumose spines on distal margin, carpopropodus bearing single, long plumose spine on inner margin, merus with 5 plumose spines on inner margin, ischium with 5 shorter plumose spines on inner margin, preischium and basis with plumose setae but not spines on inner margins (Fig. 1H). Second thoracopod robust, endopod with 1 spine on outer margin of ischium, inner margin produced into very large lamellar lobe armed with many simple setae, preischium shortest, merus longest with expanded inner distal part, dactylus with long and slender nail (Fig. 2A). Third to 5th thoracic endopods long and slender, forming minute chelate structure terminally, but concealed by crown of long setae (Fig. 2B). Endopod of 3rd thoracopod with carpopropodus unsegmented and about equal to merus in length (Fig. 2C). Endopod of 5th thoracopod with carpopropodus longer than merus and divided in 2 subsegments by oblique articulation, proximal subsegment very short (Fig. 2D). Sixth to 8th thoracic endopods long and slender, dactylus and nail together forming long slender claw. Endopod of 8th thoracopod with carpopropodus separated into 3-subsegments by oblique articulations, proximal subsegment very short but 2nd shortest, merus longer than carpopropodus; penis cylindrical (Fig. 2E). Thoracic exopods distal to basal plate 9-segmented in 2nd limb, and 10-segmented in 3rd to 8th limbs; 1st segment longest.

Sixth pleonite about 1.7 times as long as 5th.

Pleopods developed, biramous. First pleopod with exopod 9-segmented, endopod unsegmented, expanded distally, not reaching distal end of 1st segment of exopod (Fig. 2F). Second pleopod (Fig. 2G) with 7-segmented exopod, 1st segment thick, 2nd segment extended, provided with 2 short simple setae and one strong spinous seta that is spinulose in distal part. This spinous seta extending beyond distal end of exopod. Endopod 9-segmented, 1st segment thick and long (Fig. 2G, H). Third pleopod with both rami 9-segmented (Fig. 2I). Fourth pleopod with 9-segmented exopod; 8-segmented endopod, 1st segment very long, almost reaching distal end of 3rd segment of exopod (Fig. 3A). Fifth pleopod with 9-segmented exopod; endopod unsegmented, almost reaching 6th segment of exopod (Fig. 3B).

Uropods slender, long. Endopod without statocyst, slightly extending beyond distal

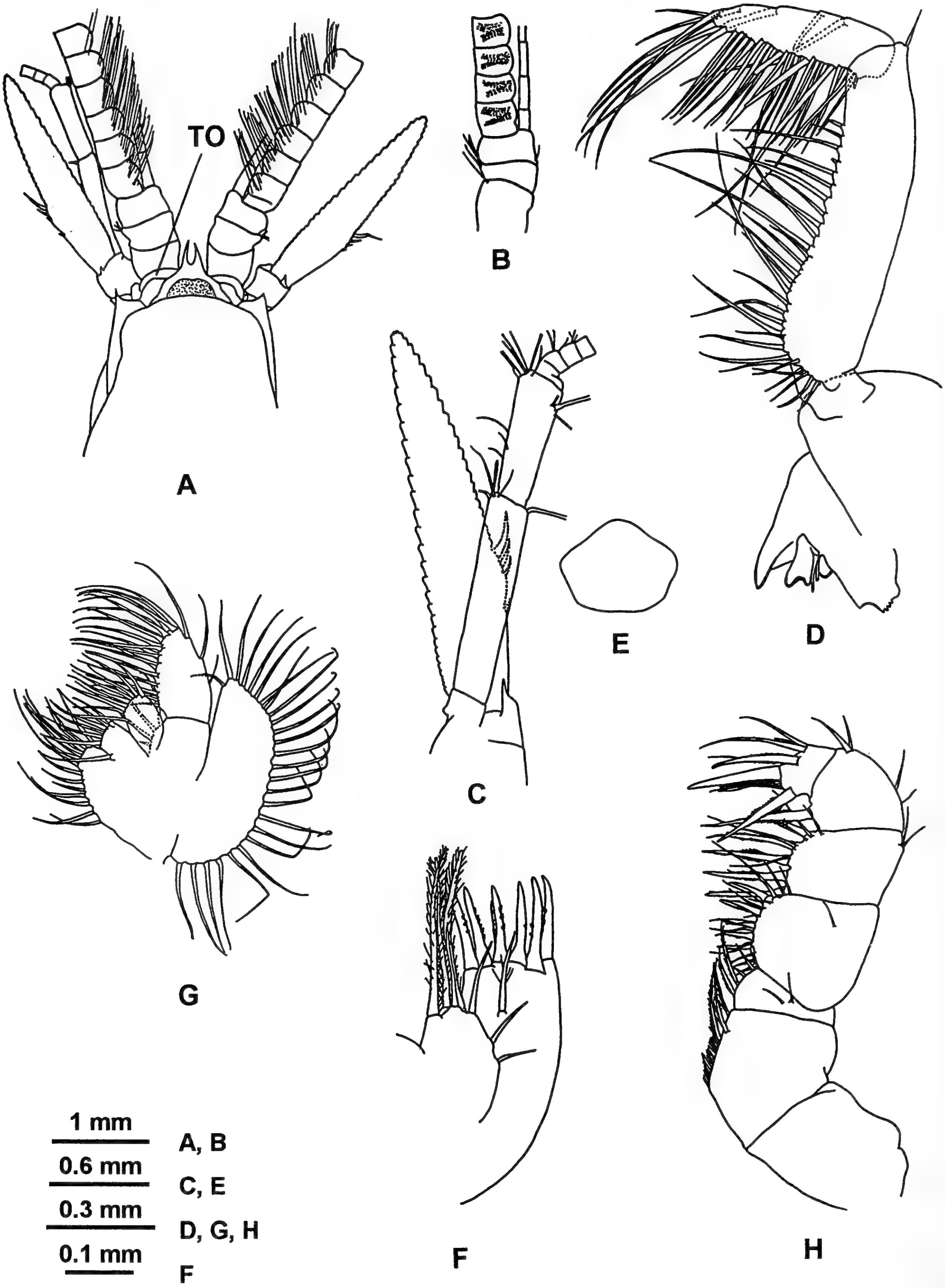

Fig. 1. *Hansenomysis japonica,* new species. Holotype, adult male. A, anterior part in dorsal view; B, antennular peduncle in ventral view; C, antenna; D, mandible; E, labrum; F, maxillule; G, maxilla; H, 1st thoracopod. Abbreviation, TO: Tattersall organ.

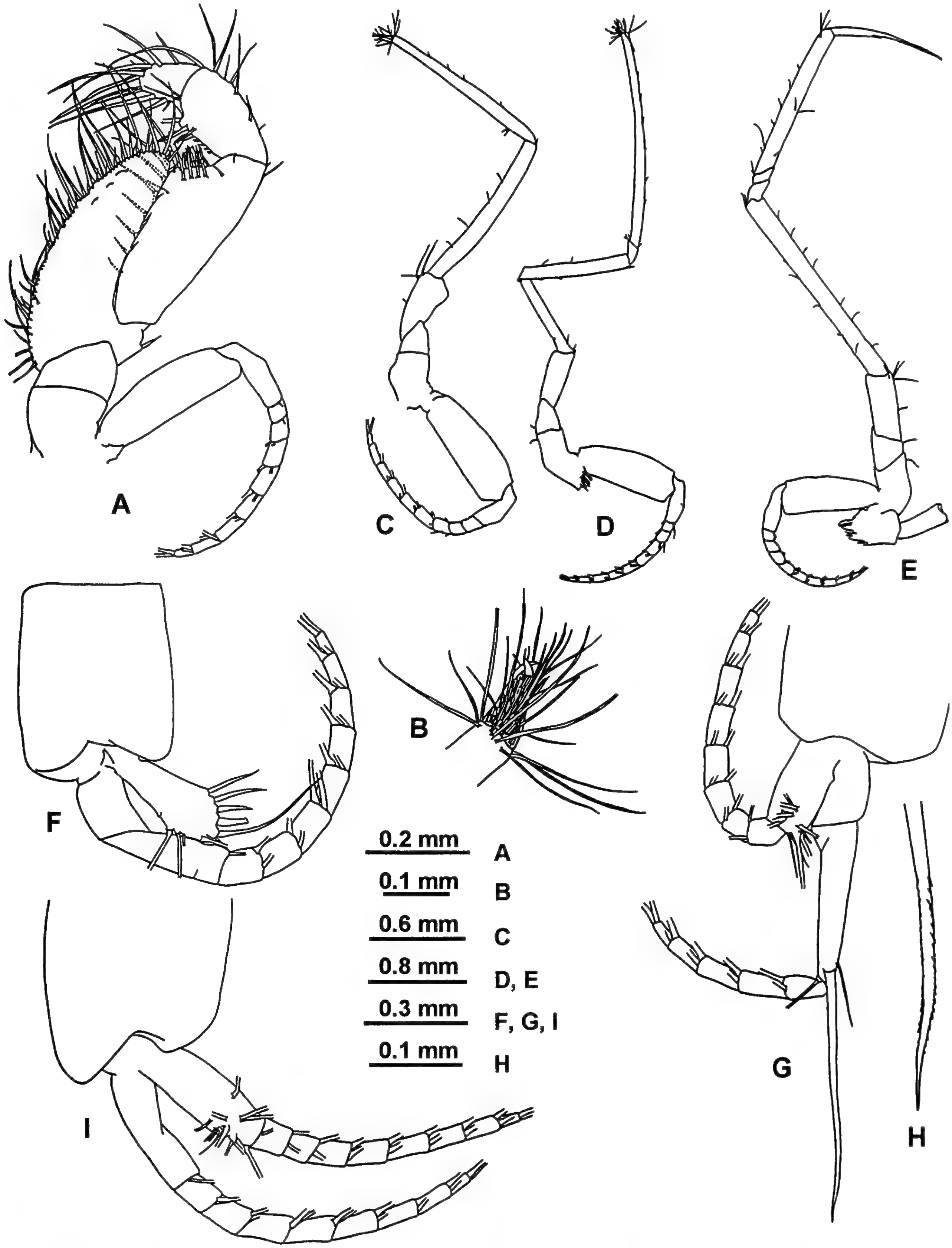

Fig. 2. *Hansenomysis japonica,* new species. Holotype, adult male. A, 2nd thoracopod; B, chela of endopod of 3rd thoracopod; C, 3rd thoracopod; D, 5th thoracopod; E, 8th thoracopod and penis; F, 1st pleopod; G, 2nd pleopod; H, distal part of modified seta on exopod of 2nd pleopod; I, 3rd pleopod.

edge of telson, 2-segmented, 1st segment 4.5 times longer than 2nd, which is lanceolated, setose all round without spines on inner margin. Exopod shorter than endopod, 2-segmented, 1st segment about 6 times longer than 2nd, armed in distal half of outer margin with 2 small, regularly spaced spines, and 3–4 closely set spines near distal end. The latter spines lengthen gradually towards extremity, inner margin setose, 2nd segment setose all round (Fig. 3C).

Telson entire (Fig. 3C), long and narrow, almost 3 times longer than 6th pleonite and about 4.2 times as long as broad, distal third tapered posteriorly in 3 steps, each step marked by strong spine; between these spines a series of 3–6 smaller spines. Remainder of lateral margin armed with 11–12 small spines regularly spaced, proximal 0.2 of lateral margin unarmed (Fig. 3C). Apex without plumose setae, truncate with 9 spines, central spine about same length as outermost spines; penultimate pair of terminal spines longest; two pairs of smaller spines on each side of central spine. Marginal spines moderately barbed (Fig. 3D).

Etymology.—The species name "japonica" refers to the collecting locality.

Remarks.—*Hansenomysis japonica* closely resembles *H. violacea* in general body form, but is easily distinguishable from it by the long acute horns of the eyeplate, the narrower antennal scale, the segmented carpopropodus of the endopod of the eighth thoracopod, and the longer and narrower telson. With *Hansenomysis armata* Birstein & Tchindonova, 1958, *H. lucifugus, H. rostrata,* and *H. violacea,* the new species is the fifth species of the genus recorded from the Pacific Ocean (Table 1).

?*Hansenomysis lucifugus* (Faxon, 1893)
Fig. 3E–G

Scolophthalmus lucifugus.—Faxon, 1893: 219; 1895:226, pl. LV, fig. 1.—Illig, 1930:556.—W. M. Tattersall, 1951:243.

Material.—Immature female 14.3 mm, 14 May 1995, Sagami Bay (35°05.9′N, 139°32.0′E), 742 m, sledge net.

Remarks.—*Hansenomysis lucifugus* was established by Faxon (1893) without illustrations, but a later redescription (Faxon 1895) included illustrations. His descriptions and illustrations, however, are brief, so that we cannot compare the present immature specimen with his type specimen. The following characters of the present specimen agree well with those of the type specimen: (1) carapace is produced to form an acute rostrum, anterolateral margins armed with two spines, one behind the external margin of the antennule, the other at the anterior inferior angle; (2) eyeplate bears two "spines"; (3) antennal peduncle with second and third segments about equal in length (Fig. 3E); (4) endopod of uropod slender with distal end extending beyond the telson and exopod (Fig. 3F). A difference is found in the fifth female pleopod. In the original description it is two-segmented whereas in the present our juvenile specimen it is unsegmented (Fig. 3G).

Hansenomysis lucifugus closely resembles *Hansenomysis rostrata*; they are the only two *Hansenomysis* species having the anterior margin of frontal carapace produced in an acute rostrum. *Hansenomysis rostrata,* however, differs from the former species in the telson which is ovate in shape and which does not bear large spines on the central region of apex.

Distribution.—Hitherto known only from the type locality, eastern Pacific off Galapagos. This is the first record of *Hansenomysis lucifugus* for Japan and western Pacific, if the identification is correct.

Key to species of the genus *Hansenomysis* (Modified from Băcescu 1971)

1\. Carapace with spines 2
   Carapace without spines 6
2\. Posterolateral angles of pleonites produced in form of spine-like processes 3
   Posterolateral angles of pleonites not

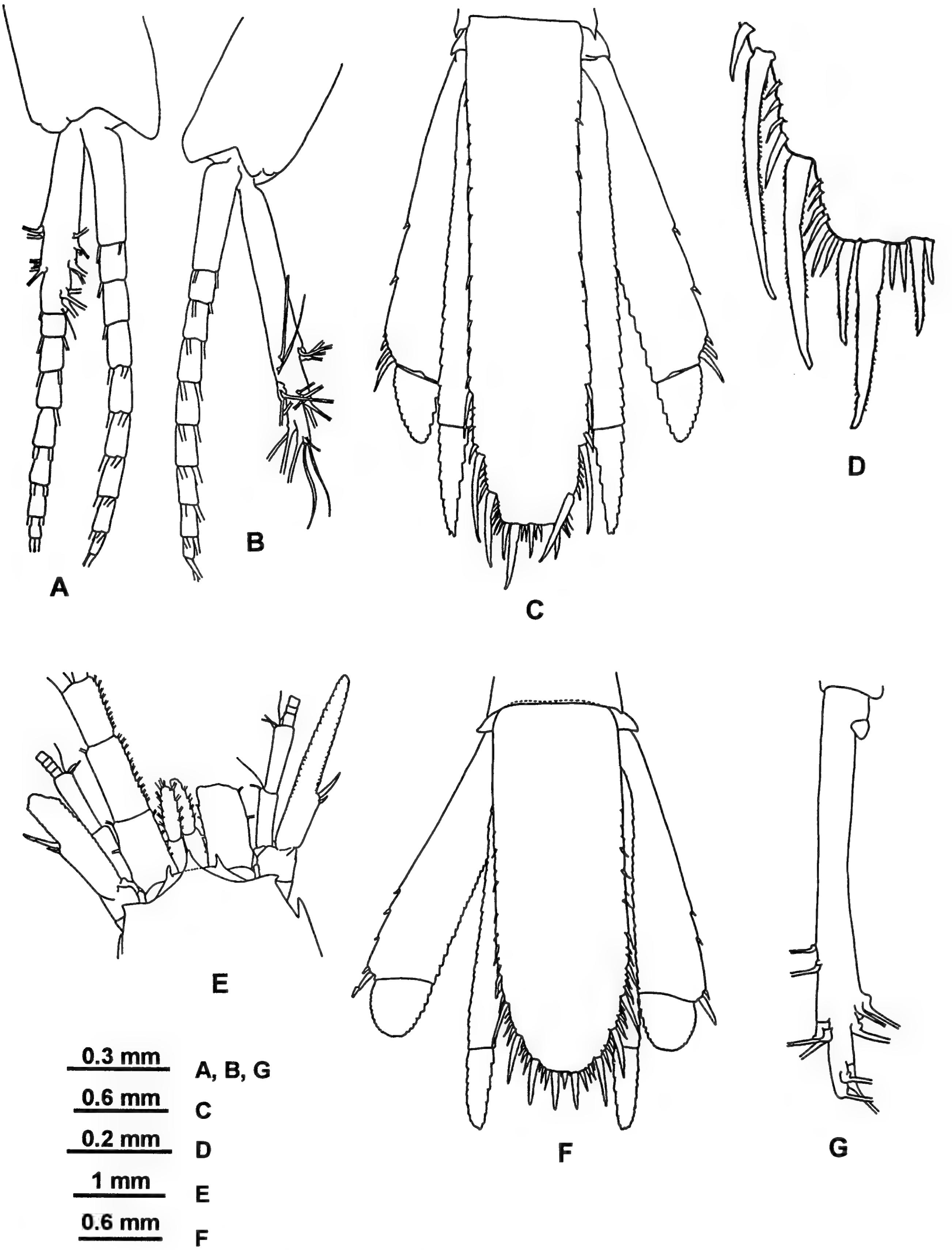

Fig. 3. *Hansenomysis japonica,* new species. Holotype, adult male. A, 4th pleopod; B, 5th pleopod; C, uropod and telson; D, apex of telson. ?*Hansenomysis lucifugus* (Faxon, 1893). Immature female. E, anterior part in dorsal view; F, uropod and telson; G, 5th pleopod.

produced in form of spine-like processes 4

3. Eyeplate with 2 lateral processes . . . . *H. menziesi* Băcescu, 1971
Eyeplate with 1 central process . . . . *H. nouveli* Lagardère, 1983

4. Outer margin of antennal scale with spines located among setae . . . . *H. armata* Birstein & Tchindonova, 1958
Outer margin of antennal scale without spines located among setae 5

5. Outer margin of antennal scale with 11–15 spines. Telson ovate . . . . *H. antarctica* Holt & Tattersall, 1906
Outer margin of antennal scale with 17–23 spines. Telson long and narrow . . *H. angusticauda* O. S. Tattersall, 1961

6. Eyeplate with anterolateral or median horns or processes 7
Eyeplate straight frontally or with weak lateral or median emargination 12

7. Anterolateral or median horns or processes of eyeplate not acute 8
Anterolateral or median horns or processes of eyeplate acute 9

8. Apex of telson rounded and narrow. Outer margin of antennal scale with spines located among setae . . . . *H. falklandica* O. S. Tattersall, 1955
Apex of telson broadly rounded. Outer margin of antennal scale without spines located among setae . . . . *H. violacea* . . . . (Birstein & Tchindonova, 1958)

9. Apex of telson somewhat rectangular with truncate apex. Carapace without rostral projection 10
Apex of telson rounded. Carapace with or without rostral projection 11

10. Antennal scale shorter than peduncle. Outer margin of exopod of uropod unarmed except for 2 spines confined near distal suture *H. tropicalis* Băcescu, 1967
Antennal scale longer than peduncle. Outer margin of exopod of uropod armed . . . . *H. japonica* new species

11. Outer margin of antennal scale without spines located among setae. Carapace with rostral projection . . *H. lucifugus* . . . . (Faxon, 1893)
Outer margin of antennal scale with spines located among setae. Carapace without rostral projection . . . . *H. pseudofyllae* Lagardère, 1983

12. Outer margins of antennal scale and exopod of uropod with spines located among setae . . . . *H. fyllae* (Hansen, 1887)
Outer margins of antennal scale and exopod of uropod without spines located among setae 13

13. Distalmost spine of outer margin of antennal scale and of exopod of uropod extending beyond apices of respective lamina. Outer margin of exopod of uropod with 8 spines . . . . *H. chini* . . . . Băcescu, 1971
Distalmost spine of outer margin of antennal scale and of exopod of uropod not extending beyond apices of respective lamina 14

14. Outer margin of exopod of uropod with less than 10 spines 15
Outer margin of exopod of uropod with more than 10 spines. Exopod of uropod longer than endopod . . . . *H. carinata* . . . . Casanova, 1993

15. Apex of telson rounded and narrow. Antennal scale with spines on distal half of outer margin . . . . *H. spenceri* . . . . Băcescu, 1971
Apex of telson broadly rounded. Antennal scale with spines on proximal half of outer margin . . . . *H. rostrata* . . . . Birstein & Tchindonova, 1970

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Literature Cited

Băcescu, M. 1967. Further mysids from the Pacific Ocean collected during the XIth cruise of R/V "Anton Bruun", 1965.—Revue Roumaine de Biologie, Série de Zoologie, 12(3):147–159.

———. 1971. Contributions to the mysid Crustacea from the Peru-Chile Trench (Pacific Ocean).—Anton Bruun Report 7:1–24.

Birstein, Y. A., & Y. G. Tchindonova. 1958. The deep sea mysids of the northwest Pacific Ocean.—Trudy Instituta Okeanologii, Akademiya Nauk SSSR 27:258–355.

———. 1970. New mysids (Crustacea, Mysidacea) from the Kuril-Kamchatka Trench.—Trudy Instituta Okeanologii 86:277–291.

Casanova, J.-P. 1993. Crustacea Mysidacea; les Mysidacés Lophogastrida et Mysida (Petalophthalmidae) de la région néo-calédonienne.—Mémoire d'Muséum national d'Histoire naturelle 156(0):33–53.

Czerniavsky, V. 1883. Monographia Mysidarum Imprimis Imperii Rossici. *in* Transactions of St. Petersburg Naturalists' Society, 18(3):1–102 + pls. 1–31.

Faxon, W. 1893. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steaner 'Albatross', during 1891, Lieut.–Commander Z. L. Tanner, U.S.N., Commanding. Preliminary descriptions of new species of Crustacea.—Bulletin of the Museum of Comparative Zoology 24:217–220.

———. 1895. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands to the Gulf of California in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross" during 1891. XV. The stalk-eyed Crustacea.—Memoirs of the Museum of Comparative Zoology 18:1–292.

Hansen, H. J. 1887. Oversigt over det vestlige Grönlands Fauna af Malakostrake Havkrebsdyr.—Videnskabelige Meddelelser fra Dansk Naturistrisk Forening i Kjøbenhevn 9:5–226, tables 2–7, 1 map.

Holt, E. W. L., & W. M. Tattersall. 1906. Preliminary notice of the Schizopoda collected by H.M.S. 'Discovery' in the Antarctic region.—The Annals and Magazine of Natural History, Ser. 7, 17(97):1–11.

Illig, G. 1930. Die Schizopoden der Deutschen Tiefsee-Expedition.—Deutschen Tiefsee-Expedition 1898-1899, 22(6):1–229.

Lagardère, J.-P. 1983. Les Mysidacés de la plaine abyssale du golfe de Gascogne I. Familles des Lophogastridae, Eucopiidae et Petalophthalmidae.—Bulletin d'Muséum national d'Histoire naturelle, Paris, 4^{e} sér, 5, section A, n° 3:809–843.

Mauchline, J., & M. Murano. 1977. World list of the Mysidacea, Crustacea.—Journal of the Tokyo University of Fisheries 64(1):39–88.

Murano, M., & E. E. Krygier. 1985. Bathypelagic mysids from the northeastern Pacific.—Journal of Crustacean Biology 5(4):686–706.

Stebbing, T. R. R. 1893. A history of Crustacea.—International Science Serie of London 74:1–466.

Tattersall, O. S. 1955. Mysidacea.—Discovery Reports 28:1–190.

———. 1961. Report on some Mysidacea from the deeper waters of the Ross Sea.—Proceedings of the Zoological Society of London 137(4):553–571.

Tattersall, W. M. 1951. A review of the Mysidacea of the United States National Museum.—The United States National Museum, Bulletin 201: 1–292.

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Nanomysis philippinensis, a new species (Crustacea: Mysidacea) from brackish waters of the Philippines

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Abstract.—A new species, *Nanomysis philippinensis,* is described based on specimens from the Philippines. *N. philippinensis* is easily distinguished from the two known species of the genus, *N. siamensis* and *N. insularis,* by the numbers of setae on the first segment of the exopods of the male third and fourth pleopods, the shape and the marginal spine number of the telson, and the size of body.

Specimens of a new species of *Nanomysis* were found in plankton samples collected with a scoop net at a cove in Panay Island, the Philippines and in those stored at the Southeastern Asian Fisheries Development Center (SEAFDEC) in Iloilo of the same island. In this paper, the description of the new species is given. The type specimens are deposited in the National Science Museum, Tokyo (NSMT).

Genus *Nanomysis* Tattersall, 1921

Nanomysis Tattersall, 1921: 408–409.—Ii, 1964: 426.

Diagnosis.—Carapace fringed with spinules on anterior margin.

First, second and fifth pleopods of male rudimentary, unjointed and of the same form as those in female. Third pleopod of male biramous with unjointed inner ramous and 3-jointed outer ramous; outer ramous longer than inner, third joint terminating in single strong seta. Fourth pleopod of male biramous; inner ramous unjointed; outer ramous very long, 4-jointed, penultimate joint with long seta, ultimate joint short, terminating in 2 long, slender setae.

Antennal scale narrowly lanceolate, 2-jointed, setose along entire margin, with apical part narrow but not pointed.

Carpopropodus of endopods of third to eighth thoracic limbs 3- or 4-jointed.

Endopod of uropod without spines on inner margin.

Telson short; posterior margin convex, straight or concave, not split, armed with a comb of spines between last lateral spines; lateral margins armed with spines.

Type species.—*Nanomysis siamensis* Tattersall, 1921.

Remarks.—The original diagnosis of the genus was given by Tattersall (1921) when the genus was established for *Nanomysis siamensis* and amended by Ii (1964) who took into account the description of the second species, *Nanomysis insularis,* described by Nouvel (1957). With the addition of the present new species, the generic diagnosis is modified again as mentioned above. Modifications are made in three points, the addition of character in the anterior margin of the carapace, the number of subsegments in the carpopropodus of thoracic endopods, and the shape of the posterior margin of the telson.

Nanomysis philippinensis, new species

Figs. 1, 2

Type material.—Holotype (NSMT-Cr 11912), adult female with embryos, 3.2 mm; allotype (NSMT-Cr 11913), adult male, 2.6 mm; paratypes (NSMT-Cr 11914), 5 adult females with embryos (2.8–3.0 mm) and 8 adult males (2.1–3.0 mm); Batan Bay, Panay Island, Philippines, 1 Dec 1979 collected with scoop net above eel grass bed at depth of about 1 m.

Other material.—Two adult females with embryos (3.0, 3.1 mm), 7 adult males (2.2–2.9 mm) and 1 immature male, Hamtik, Panay Is., 5 Apr 1976, 5 m deep, CM net (75 cm in diameter, 0.49 mm in mesh size); 2 immature females and 1 juvenile, off Negros Occidental School of Fisheries, Negros Is., Philippines, 28 Jun 1976, plankton net tow, 1 juvenile (1.4 mm), Oton Beach, Panay Is., 25 Aug 1976, plankton net tow; 10 immature females (up to 2.5 mm) and 4 immature males (up to 1.9 mm), same as type specimens; 3 adult females (2 with embryos) (2.9–3.2 mm), 11 adult males (2.2–2.8 mm), 11 immature females (up to 2.8 mm) and 3 immature males, mouth of Altavas River, Banga Cove, Batan, Panay Is., 2 Dec 1979.

Body length.—Adult female 2.8–3.2 mm, adult male 2.1–2.9 mm.

Description.—Carapace slightly produced into broadly rounded rostrum, frontal margin fringed with about 60 tiny spinules throughout (Fig. 1B); anterolateral corners rounded; posterior margin emarginate, leaving last thoracic somite exposed (Fig. 1A).

Eye large; cornea globular, slightly broader than eyestalk; eyestalk without papilliform process (Fig. 1B).

Antennular peduncle of female: first segment as long as following 2 segments together, armed at outer distal corner with several setae, one of which is plumose, longer and directed backward; second segment connecting obliquely with third segment, with single plumose seta at median distal corner; third segment with plumose seta at median distal corner (Fig. 1A, C). Antennular peduncle of male: more robust than that of female, first segment as long as third, third segment with processus masculinus small (Fig. 1B).

Antennal scale slender, lanceolate, extending beyond distal margin of antennular peduncle for ⅓ of its length in female and ¼ in male, 5 times as long as greatest width, setose all round, distal suture marked off at distal 2/9, distal segment more than 3 times as long as broad (Fig. 1D). Antennal peduncle more than half as long as scale, second segment longest, occupying about half of peduncle length (Fig. 1D). Antennal sympod with strong spinelike process at outer distal corner (Fig. 1D).

Mandibular palp relatively small, sparsely setose, second segment armed on external margin with 7 setae of which distal one differs slightly in shape from others, third segment about half as long as second, armed with 8 barbed setae arranged regularly on distal ⅔ of external margin (Fig. 1E). Coxa of mandibles as shown in Fig. 1F. Maxillule: outer lobe armed with 9 strong spines on distal margin and 3 thick setae on inner surface; inner lobe armed with 3 stout and one slender setae on apex, 2 setae on inner margin and 3 setae on outer margin (Fig. 1G). Maxilla: exopod small and slender, 3 times as long as broad, with only 2 setae, one at apex plumose, long and thick, the other on subapex of outer margin short, margin of exopod fringed with fine hairs; terminal segment of endopod oval, 1.2 times longer than broad (Fig. 1H).

Endopod of first thoracopod robust; endite of basis large, armed with 4 to 5 thick and hairy setae on inner margin and apex; preischium with 3 to 4 similar setae on inner margin (Fig. 1I). Endopod of second thoracopod robust; ischium fused with preischium, merus equal to combined length of carpopropodus and dactylus, carpopropodus becoming broader distally, twice as long as maximum breadth at distal end; dactylus broader than long, bearing 5 strong barbed setae in addition to slender setae (Fig. 1J). Endopods of third to eighth thoracic limbs becoming more slender towards posterior pairs; dactylus small, half length of slender terminal claw; in third to seventh pairs carpopropodus divided into 3 subjoints of which the middle is shortest

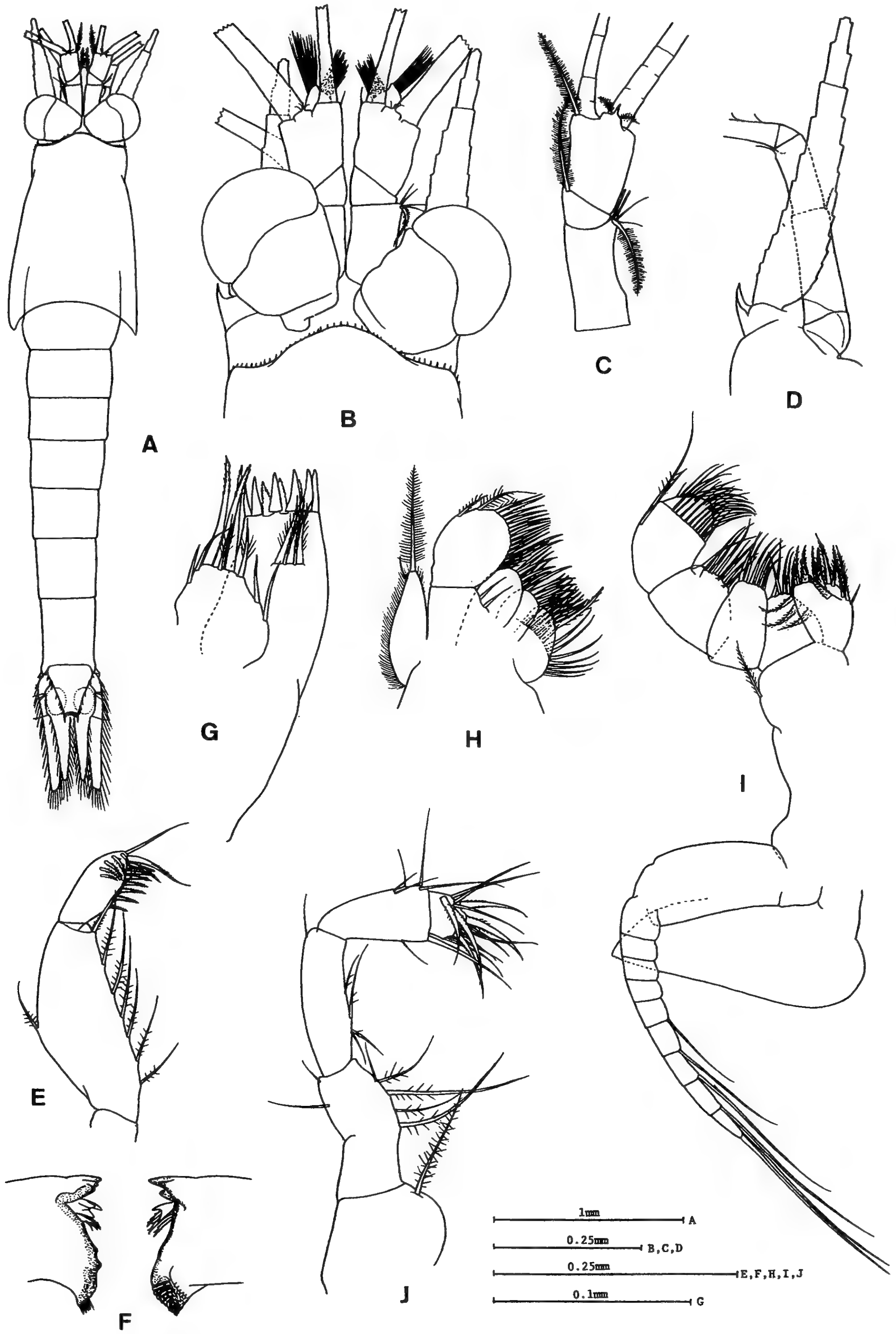

Fig. 1. *Nanomysis philippinensis,* new species. A, C–J, holotype (female); B, allotype (male). A, whole body, dorsal; B, anterior end, dorsal; C, antennular peduncle; D, antenna; E, mandibular palp; F, laciniae and molar parts of mandibles; G, maxillule; H, maxilla; I, first thoracic limb; J, endopod of second thoracic limb.

(Fig. 2A–C); in eighth thoracopod, carpopropodus divided into 4 subjoints, armed with strong antler-shaped spine at middle and distal end of outer margin of first subjoint and at outer distal end of second and third subjoints (Fig. 2D). Exopods of thoracic appendages 9-jointed in first to seventh pairs (Fig. 1I, Fig. 2A–C) and 8-jointed in eighth; basal plate with outer distal corner rounded.

Abdominal somites without furrows or spines, last somite slightly longer than preceding one, 1.3 times as long as broad (Fig. 1A).

Third and fourth pleopods of male modified. Third pair extending backwards beyond middle of sixth abdominal somite, biramous; endopod unsegmented and short; exopod 3-jointed: first joint somewhat curved outwardly much longer than second and third joints combined, armed with a small thin seta at outer distal corner, second joint 4 times as long as broad, armed with a small thin seta at outer distal corner, third joint ⅔ as long as second, terminating into long, stout, naked seta which is more than twice as long as joint (Fig. 2E). Fourth pair biramous; endopod unsegmented and short; exopod elongate, extending posteriorly near distal end of telson, 4-jointed: first joint longest, 2.5 times longer than endopod, furnished with 5 short setae regularly spaced on distal ⅗ of outer margin, second joint slightly shorter than first, unarmed, third joint slightly shorter than second, armed at outer distal corner with stout seta which is 1.5 times as long as joint and extending beyond tip of terminal setae, terminal joint short, armed on apex with 2 setae being equal in length but different in structure, one 2-jointed indistinctly near base, basal joint swollen (Fig. 2F).

Uropod setose along entire margin; endopod more than twice as long as telson, tapered, without spines on inner ventral margin; exopod slightly longer than endopod, with straight outer margin (Fig. 1A).

Telson short, trapezoid, 0.7 as long as last abdominal somite, 1.2 times longer than maximum width, posterior margin about ⅓ of maximum width at base, concave or straight, armed with long spine at each corner between which 5 to 10 short, slender spines are inserted, average number of distal inserted spines is 6.5 in male (n = 6) and 7.2 in female (n = 5); lateral margin straight or slightly concave, armed with 5–9 short spines along entire length (Fig. 2G).

Etymology.—The species is named after the locality in which it was collected.

Remarks.—The present specimens belong clearly to the genus *Nanomysis,* which was established by Tattersall in 1921, in having the carapace with spinules on the anterior margin, the slender antennal scale, 3-segmented exopod of the male third pleopod, 4-segmented exopod of the male fourth pleopod, and the trapezoid telson. *Nanomysis philippinensis,* new species, is clearly different from two known species of *Nanomysis, N. siamensis* Tattersall, 1921, and *N. insularis* Nouvel, 1957, as follows. The first segment of the exopod of the male third pleopod is armed with only a single thin seta at the outer distal corner in the new species, while armed on outer margin with 3 and 5 long setae in *N. siamensis* and *N. insularis,* respectively. The first segment of the exopod of the male fourth pleopod is armed with 5 setae on the outer margin in *N. philippinensis,* as against 3 in *N. siamensis* (Tattersall did not describe this character, but illustrated it in plate XV, fig. 10) and 7 setae in *N. insularis.* The posterior margin of the telson is concave or straight and with 5–10 shorter spines between longer spine at each corner in *N. philippinensis,* whereas it is convex and with 12 shorter spines in *N. siamensis* and 15 in *N. insularis.* The number of spines arming the lateral margin of the telson is 5–9 in *N. philippinensis* as against 10 in *N. siamensis* and 11–12 in *N. insularis.* The present new species is considerably smaller (2.8–3.2 mm in the adult

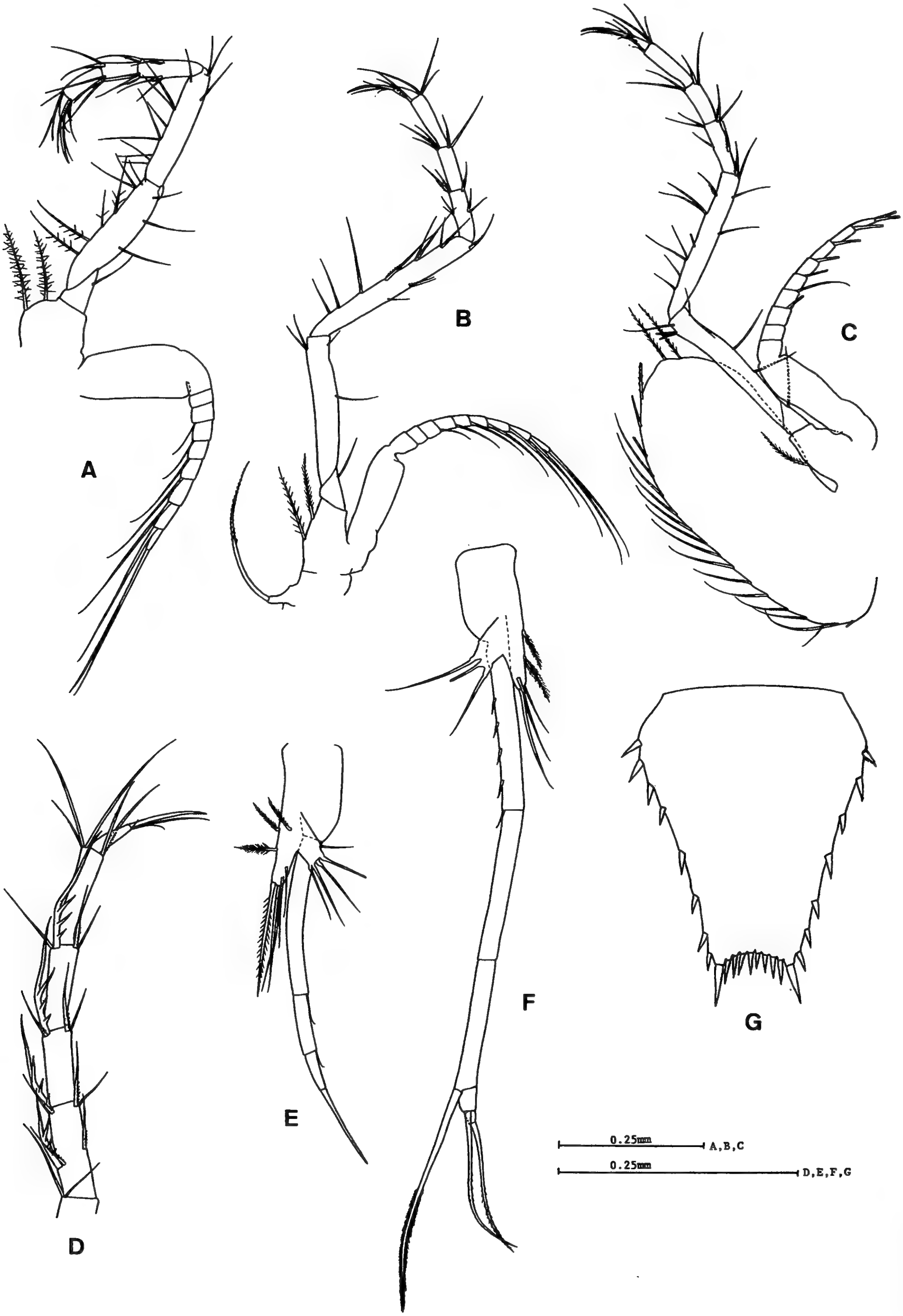

Fig. 2. *Nanomysis philippinensis,* new species. A–D, G, holotype (female); E, F, allotype (male). A, third thoracic limb; B, sixth thoracic limb; C, seventh thoracic limb; D, extremity of endopod of eighth thoracic limb; E, third pleopod (seta of first and second joint closely oppressed to following segment); F, fourth pleopod; G, telson.

female, 2.1–2.9 mm in the adult male) than the two known species (5 mm in the adult male of *N. siamensis* and 4.5 mm in *N. insularis*).

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Literature Cited

Ii, N. 1964. Fauna Japonica, Mysidae (Crustacea). Biogeographical Society of Japan, Tokyo, 610pp.

Nouvel, H. 1957. Mysidacés provenant de deux échantillons de ⟨⟨Djembret⟩⟩ de Java.—Zoologische Mededelingen 35:315–331.

Tattersall, W. M. 1921. Zoological results of a tour in the Far East. Mysidacea, Tanaidacea and Isopoda.—Memoirs of the Asiatic Society of Bengal 6:403–433, pls. 15–17.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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A new species of bopyrid isopod, *Pseudione chiloensis,* a parasite of *Nauticaris magellanica* (A. Milne-Edwards, 1891) (Crustacea: Decapoda: Hippolytidae)

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Abstract.—*Pseudione chiloensis* sp. nov., is described from the central-southern Chilean region, parasitic on the hippolytid shrimp *Nauticaris magellanica* (A. Milne-Edwards, 1891). Females of *Pseudione chiloensis* are similar to *Pseudione affinis* (Sars, 1882), *Pseudione indica* Chopra, 1930 and *Pseudione parviramus* Adkison, 1988 in having a wide frontal lamina, first antennae 3-segmented, 5 pairs of biramous pleopods, uropods uniramous, and eyes present; *Pseudione chiloensis* differ from these species in the absence of ornamentations on internal crest of oostegite 1, female's size, and setose maxillipedal palp. Males of *Pseudione chiloensis* are similar to those of *Pseudione affinis, Pseudione indica,* and *Pseudione parviramus* in having eyes present, first antennae 3-segmented, pleon of six pleomeres, midventral tubercules present on pereomeres, 5 pairs of uniramous pleopods, and last pleomere bifurcated; but differ from these species in having the second antennae 6-segmented, (7-segmented in the former species). Although males and females of *Pseudione chiloensis* share some characters with these species, the morphological differences and host lead us to propose a new species.

Resúmen.—*Pseudione chiloensis* n. sp., es descrita de la región centro-sur de la costa chilena, parásito del hipolítido *Nauticaris magellanica* (A. Milne-Edwards, 1891). Las hembras de *Pseudione chiloensis* son similares a *Pseudione affinis* (Sars, 1882), *Pseudione indica* Chopra, 1930 y *Pseudione parviramus* Adkison, 1988 en que tiene la primera antena 3-segmentada, 5 pares de pleópodos birrámeos, urópodos unirrámeos y ojos presentes. *Pseudione chiloensis* difiere de esas especies en la ausencia de ornamentaciones en la cresta interna del oostegito 1. *Pseudione magna* Shiino, 1951 difiere de *Pseudione chiloensis, Pseudione affinis, Pseudione indica,* y *Pseudione parviramus* en que tiene la segunda antena 4-segmentada, lámina frontal angosta y ausencia de ojos. Los machos de *Pseudione chiloensis* son similares a los de *Pseudione affinis, Pseudione indica* y *Pseudione parviramus* en la presencia de ojos, primera antena 3-segmentada, pleón de seis pleómeros, tubérculos medio-ventrales en los pereómeros, 5 pares de pleópodos unirrámeos y el último pleómero bifurcado. Los machos de *Pseudione chiloensis* difieren de *Pseudione magna* en la primera y segunda antenas que son 2- y 4-segmentadas, respectivamente, en la última especie; en *Pseudione parviramus* las segundas antenas son 7-segmentadas, y 6-segmentadas en *Pseudione chiloensis.* Aunque esta especie comparte características con las especies mencionadas, al mismo tiempo presenta caracteres y hospedero particulares para ser propuesta como una especie nueva.

Three species of the genus *Pseudione* have been described from the Chilean waters: *Pseudione tuberculata* Richardson, 1904 parasitizing *Neolithodes diomedae* (Benedict); *Pseudione paucisecta* Richardson, 1904 parasitic on *Munida curvipes* Benedict, and *Pseudione battstroemi* Stuardo, Vega, & Céspedes, 1986 parasitic on *Callianassa uncinata* H. Milne-Edwards. We report a new species of *Pseudione* parasitizing *Nauticaris magellanica* (A. Milne-Edwards, 1891), an hippolytid shrimp from the South American coasts including the Falkland Islands (Boschi 1979).

In Chile *Nauticaris magellanica* is one of the most abundant shrimps associated with mussel raft cultures (Aracena & López 1973, Wehrtmann & Albornoz 1997), and has been collected from holdfasts of the kelp *Macrocystis pyrifera* from the southern region (Ojeda & Santelices 1984). However, despite intensive sampling efforts over the past 4 years along the entire coast of Chile, only eleven parasitized individuals of *N. magellanica* were obtained exclusively from Putemún, Chiloé, central southern Chile.

Nauticaris marionis Bate, has been recorded in New Zealand (Page 1985) as a host for *Pseudione affinis,* this being the first record of Pseudionidae parasitizing the genus *Nauticaris.* Although our specimens share attributes with other species of *Pseudione,* there are differential characters which justify a new species. Two individuals male and female, were chosen as type specimens and prepared for SEM photographs.

Order Isopoda
Suborder Epicaridea
Family Bopyridae Rafinesque, 1815
Subfamily Pseudioninae R. Codreanu, 1967
Genus *Pseudione* Kossmann, 1881
Pseudione chiloensis, new species
(Figs. 1–15)

Holotype female (dry).—USNM-274301; allotype male (dry): USNM-274302 (both male and female, mounted on a stub for MEB).

Material examined (Paratypes).—USNM-274256 (2 specs.), USNM-274257 (1 spec.); ICMyL-UNAM-4999 (1 spec.), ICMYL-UNAM-5000 (7 specs.).
One adult male and 1 female, 5 Jun 1993; 1 female with cryptoniscus larvae associated, 5 Jun 1993; 2 males and 2 females, 12 May 1994; 1 male and 1 female, 5 Jun 1994; 5 males and 5 females, 13 May 1994; 1 male and 1 female, 26 Jun 1994. Two fully developed individuals male and female, were used for descriptions and selected as type specimens.

Type locality.—Putemún (42°25′S; 73°43′W), Chiloé Island, central-southern Chile.

Host.—*Nauticaris magellanica*; most infected individuals were males ($n = 10$; total length varying between 14.93 and 19.15 mm; $\bar{X} = 17.96$ mm); the only non-ovigerous female infected measured 22.61 mm total length.

Habitat.—The shrimps parasitized were associated with massive cultures of *Mytilus chilensis,* and were collected from approximately 5 m depth (salinity 29.5–29.7 ppm; temperature 9.0–10.5°C).

Description of female (Figs. 1–8).—Length 4.0 mm, width 2.9 mm; head triangular, slightly wider than long, deeply set into first pereomere but discernable (Fig. 2); barbula with two lateral projections on each side; anterolateral borders of head almost rounded, frontal lamina wide, rounded (Figs. 1, 2); maxilliped anterolaterally rounded, falcate, 3–4 setae on upper border, unarticulated palp (Fig. 3). First antenna 3 segmented; basal segment globose; second segment cylindrical, almost as high as former, 5 small aesthetascs on upper border; third segment cylindrical, smooth, 0.75 slender than previous, 5 aesthetascs on tip (Fig. 4). Second antenna 5 segmented, basal segment subovoid, other segments cylindrical, almost as high as the former but slender; fourth and fifth segments smooth, apical segment with a tuft of 5 setae (Fig. 5);

distal segment projects slightly beyond the border of frontal lamina; squamous structures on surface of both antennae; eyes present. Pereon margins forming smooth curve; thin, conspicuous rectangular coxal plates on pereomeres 1–4 conspicuously exceeding border; tergal projections narrow, pigmented on short side. Oostegite 1 covering head and partially anterior portion of brood pouch; anterior lobe rounded, higher than posterior, no ornamentation on internal ridge (Fig. 6). Strong pigmentation on oostegites of short side; some chromatophores dispersed on oostegites 2–4 of opposite side. Oostegites 2–4 foliate, fifth oostegites fringed, slender, extending across posterior region of brood pouch, and overlapping opposite one. First two pereopods smaller than last five, small subcuadrangular carina on basis of first four pairs (Fig. 7); last three pairs of pereopods not carinated. All articles distinct, small scales on ventral surface of legs, four small setae on carpus, dactyli deeply set into propodi. Pleomeres completely separated dorsal and laterally, ending in lateral, foliate, and rounded plates. Five pairs of biramous foliate pleopods, partially covering ventral surface of pleon (Fig. 1); border of pereomeres 5–7 dorsally folded and directed forward on short side (Fig. 8); endopods shorter and narrower than exopods, lanceolate, both rami progresively larger from first to fifth pleopods; uropods uniramous present.

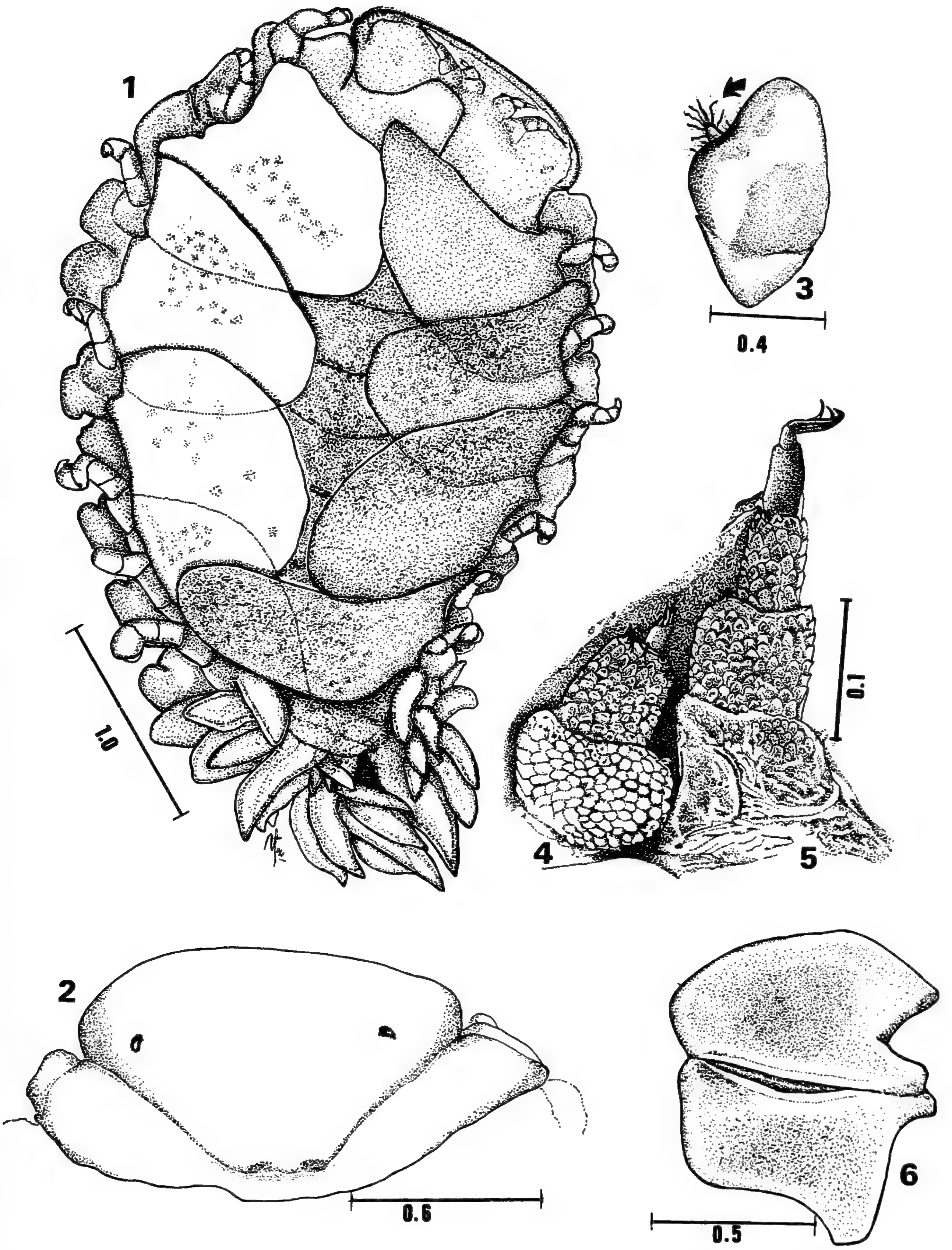
Description of male (Figs. 9–15).—Length 0.96 mm, width 0.26 mm. Head anteriorly rounded, wider than long, partially fused with first pereomere but clearly discernable; anterolateral borders rounded; eyespots irregular, conspicuous (Fig. 9). First antenna three segmented, globose basal segment with 2 small setae on external surface; cylindrical medium-sized, second segment; third segment 0.6 smaller than second, ending in a tuft of 6 aesthetascs, small scales on surface (Fig. 10). Second antenna 6-segmented, almost 3 times larger than first one. Basal segment truncated, subpyramidal; second one higher than first; third and fourth segments cylindrical, smooth, slender than former, some setae on upper border; fifth segment slender and shorter than previous; distal segment with tuft of 5–6 setae (Fig. 11) reaching first pereomere; both antennae with scarce scales on surface. Pereomeres all similar, deeply separated laterally and ventrally, tips rounded and reflexed ventrally, with small scales on borders, mid-ventral tubercules on pereomeres (Fig. 12). All pereopods similar in size, not carinated (Fig. 13); dactyli inserted into propodi (Fig. 14). Five distinct pleomeres separated dorsal, ventral, and laterally; five pairs of sessile tuberculiform pleopods on pleomeres 1–5, prominent and conspicuous in ventral view, anal cone present; sixth pleomere bifurcated, ending in short setae, sparse small scales on the tips (Fig. 15); no uropods.

Etymology.—The specific name is in reference to Chiloé, the type location. Gender masculine.

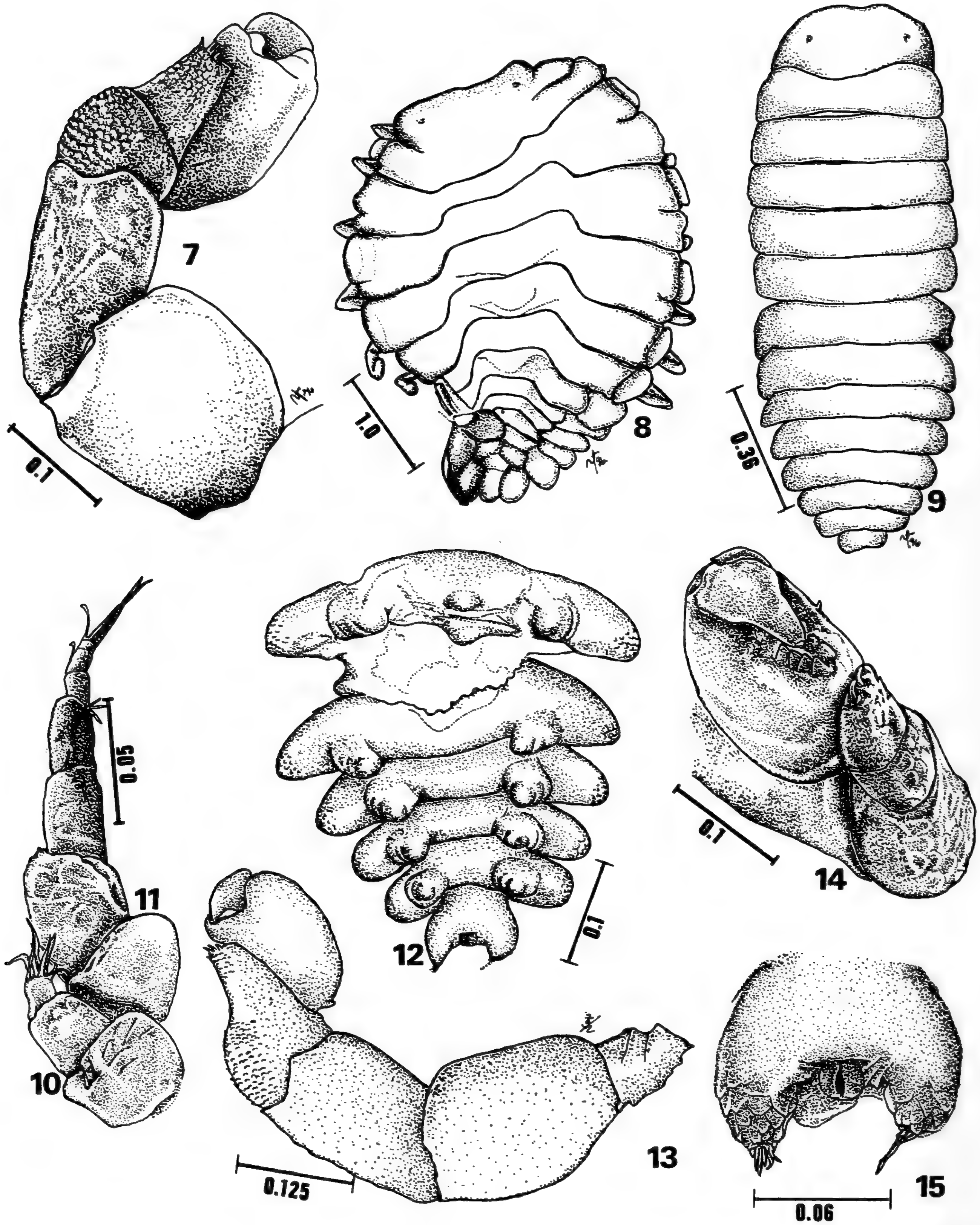
Variations.—Females varied in pigmentation patterns with oostegites 1–5 totally pigmented, and other individuals with oostegites only partially pigmented on the short side; in males the sixth pleomere are bilobed, but others with button-shaped or Y-shaped pleomere.

Discussion

This century many authors have cited the need for a revision for the genus *Pseudione.* The literature shows an immense diversity of forms and the genus parasitizes many families of Anomura and Brachyura, but a few species are known to infect certain genera of Caridea (Chopra 1930). We decided to include our material in the genus *Pseudione* because of the morphological characteristics are in agree with Sars (1899), Bourdon (1968), and Markham's (1985) descriptions; and, although Danforth (1971) quoted that "approximately 60 species of *Pseudione* so far described, identification of a new form is quite difficult", many species of *Pseudione* have since been described



Figs. 1–6. female. ***Pseudione chiloensis,*** new species. Fig. 1, paratype (ICMYL-UNAM-4999), ventral view. Fig. 2, head of same, dorsal view. Fig. 3, maxilliped with setose palp (arrow). Figs. 4–5, first and second antennae. Fig. 6, first oostegite, internal view (scales in mm).



Figs. 7–15. *Pseudione chiloensis*. Fig. 7, second pereopod (female) Fig. 8, holotype female (dry; USNM-274301), dorsal view. Figs. 9–15 male. Fig. 9, allotype, dorsal view (dry; USNM-274302). Fig. 10–11, first and second antennae. Fig. 12, pleon (broken) in ventral view. Figs. 13–14, seventh leg. Fig. 15, sixth pleomere and anal cone; (scales in mm).

from American waters (Stuardo et al. 1986, Adkison 1988, Adkison & Heard 1995).

Females of *Pseudione chiloensis* are similar to those of *Pseudione affinis, Pseudione indica* Chopra, 1930 and *Pseudione parviramus,* in having a wide frontal lamina, eyes present, first antennae 3-segmented, five pairs of biramous pleopods, and uropods uniramous (Sars 1899, Chopra 1930, Bourdon 1968, Adkison 1988). *Pseudione chiloensis* is similar to *Pseudione magna* Shiino, 1951 in that the first antennae is 3-segmented, pleopods biramous, and uropods uniramous; but the second antennae are 4-segmented, the frontal lamina narrow, and the eyes are absent in the later species. *Pseudione chiloensis* differs from *P. parviramus, P. affinis, P. indica,* and *P. magna* in the absence of ornamentation on internal crest of oostegite 1, and presence of setose maxillipedal palp.

The body size of females is different in the former species as follows: 10.0 and 14.5 mm in *P. affinis* (Sars 1899, Bourdon 1968), 20.2 mm in *P. magna* (Shiino 1951), and 9.0–11.0 mm in *P. parviramus* (Adkison 1988). *Pseudione chiloensis* however, is smaller (4.0 mm) than the former species and more similar in size to *P. indica* (2.0 mm; Shiino 1951).

Males of *P. chiloensis* are similar to those of *P. affinis, P. magna, P. parviramus,* and *P. indica* in having eyes present, pleon six-segmented, and five pairs of tuberculiform pleopods; although the males of *P. magna* differs from *P. chiloensis, P. affinis, P. indica,* and *P. parviramus* in having the first antennae 2-segmented, while these structures are 3-segmented in the remaining species. The second antennae of the males of *P. chiloensis* are 6-articulated, 7-segmented in *P. affinis, P. indica* and *P. parviramus,* and 4-segmented in *P. magna.*

The males of *P. chiloensis* have conspicuous midventral tubercles on pereomeres sixth and seventh, and on the first two pleomeres, and the final pleomere produced into bifurcated and setose structure, similarly to *P. indica* (Markham 1994), but not uropods in Adkison & Heard's sense (Adkison & Heard 1995). In addition, the males of *P. indica* closely resembles that of *Pseudione cognata* Markham, 1985 (Markham 1994).

Acknowledgments

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Literature Cited

Adkison, D. L. 1988. *Pseudione parviramus* and *Aporobopyrus collardi,* two new species of Bopyridae (Isopoda: Epicaridea) from the Gulf of Mexico—Proceedings of the Biological Society of Washington 101:576–584.

———, & R. W. Heard. 1995. *Pseudione overstreeti,* new species (Isopoda: Epicaridea: Bopyridae), a parasite of *Callichirus islagrande* (Decapoda: Anomura: Callianassidae) from the Gulf of Mexico.— Gulf Research Report 9(2):105–110.

Aracena, P. O., & M. T. López. 1973. Observaciones biológicas en organismos encontrados en substratos artificiales. Caleta Leandro, Talcahuano, Chile. I. Crustácea, Decápoda, Macrura.—Trabajos V Congreso Latinoamericano de Zoología 1:40–48.

Boschi, E. E. 1979. Geographic distribution of Argentinian marine decapod crustaceans.—Bulletin of the Biological Society of Washington 3: 134–143.

Bourdon, R. 1968. Les Bopyridae des Mers Européennes.—Mémories du Muséum National D'Histoire Naturelle, Paris. Serie A, Zoologie, Tome L, Fascicule 2:76–424.

Chopra, B. 1930. Further notes on Bopyrid isopods parasitic on Indian Decapoda Macrura.—Records of the Indian Museum 32(2):113–147.

Danforth, Ch. G. 1971. Two Bopyrids (Isopoda) from New Guinea.—Bulletin Southern California Academy of Sciences 70(2):99–102.

Markham, J. C. 1985. A review of the Bopyrid Isopods infesting Caridean shrimps in the Northwestern Atlantic Ocean, with special reference to those collected during the Hourglass cruises in the Gulf of Mexico.—Memoirs of the Hourglass Cruises 7(3):1–156.

———. 1994. Crustacea Isopoda: Bopyridae in the MUSORSTOM collections from the tropical Indo-Pacific I. Subfamilies Pseudioninae (in part), Argeniinae, Orbioninae, Athelginae and Entophilinae. Pp. 225–253 *in* A. Crosnier, ed., Résultates des Campagnes MUSORSTOM, Volume 10—Mémoirs du Muséum national d'Histoire Naturelle, París 161:225–253.

Ojeda, F. P., & B. Santelices. 1984. Invertebrate communities in holdfasts of the kelp *Macrocystis pyrifera* from southern Chile.—Marine Ecology Progress Series 16:65–73.

Page, R. D. M. 1985. Review of the New Zealand Bopyridae (Crustacea: Isopoda: Epicaridea).—New Zealand Journal of Zoology 12:185–212.

Richardson, H. 1904. Contributions to the natural history of the Isopoda.—Proceedings of the United States National Museum 27(1350):1–89.

Sars, G. O. 1882. Oversight af Norges Crustaceer med Forelobige Bemaerkninger Over de Nye Eller Mindre Bekjendte Arter. I. (Podophthalmata-Cumacea-Isopoda-Amphipoda).—Christiana Videnskabelige Solk. Forhandling 18:1–124.

———. 1899. An account of the Crustacea of Norway. II. Isopoda.—Publications of the Bergen Museum, Bergen, pp. 195–205.

Shiino, M. S. 1951. Some bopyrid parasites found on the Decapod Crustaceans from the waters along Mie Prefecture.—Report of Faculty of Fisheries, Prefectural University of Mie 1(1):26–40.

Stuardo, J., R. Vega, & I. Céspedes. 1986. New bopyrid isopod parasitic on *Callianassa uncinata* H. Milne-Edwards: with functional and ecological remarks.—Gayana Zoología 50(1–4):3–15.

Wehrtmann, I. S., & L. Albornoz. 1997. Larval development of *Nauticaris magellanica* (A. Milne-Edwards, 1891) (Decapoda, Hippolytidae), reared under laboratory conditions.—Bulletin of Marine Science. (in press).

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(2):249–255. 1997.

Observations on *Hexapanopeus schmitti* Rathbun from Brazil (Crustacea: Decapoda: Xanthidae)

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Abstract.—Observations are presented on members of a population of *Hexapanopeus schmitti* Rathbun from Pitangui, Rio Grande do Norte, Brazil. This species is very small, apparently not exceeding 10 mm in carapace length. It is illustrated in detail as are the gonopods of the four species of *Hexapanopeus* known from Brazil. A key to Brazilian species of *Hexapanopeus* is provided.

Field studies along the coast of Rio Grande do Norte, Brazil by one of us (C.S.) yielded a series of specimens of *Hexapanopeus schmitti* Rathbun, 1930, originally described from material from localities in Brazil and Uruguay. The population recorded here shows wide variation in color pattern that has not been recorded previously. Gonopods are illustrated for the four Brazilian species of *Hexapanopeus,* and a key to those species is presented.

Abbreviations used in the accounts below include: cb, carapace breadth; cl, carapace length; mm, millimeter; P1-5, first to fifth pereopods (P1 is the cheliped, P2-5 the walking legs). USNM is an acronym for the National Museum of Natural History, Smithsonian Institution, Washington, D.C., where some of the newly-collected specimens are deposited. The majority of the specimens are in the collections of the Museu do Mar "Onofre Lopes" at the Universidade Federal do Rio Grande do Norte, Natal, Brazil.

Family Xanthidae MacLeay, 1838
Hexapanopeus Rathbun, 1898
Hexapanopeus schmitti Rathbun, 1930
Figs. 1–4, *5e–h*

Hexapanopeus schmitti Rathbun, 1930:393, pl. 169, figs. 3–5. Type locality Bay of Rio de Janeiro [22°54′S, 43°14′W], Rio de Janeiro State, Brazil.—Coelho & Ramos, 1972:191 [listed].—Melo, 1985:105 [Pernambuco, Rio de Janeiro, and São Paulo states, Brazil].—Melo et al., 1989: 15 [Paraná].—Bakker et al., 1989:137, figs. 1–10 [Paraná; larval development].—Melo, 1996:360 [Brazil].

Material.—Brazil: Rio de Janeiro State, bay of Rio de Janeiro (22°54′S, 43°14′W), leg. W. L. Schmitt, 1925: 1 ♂ (holotype, USNM 59831).—Rio Grande do Norte State, intertidal region of Pitangui and estuary of River Potengi (5°47′S, 35°16′W), leg. C. Sankarankutty, 1995: 12 ♂♂, 12 ♀♀ (Museu do Mar "Onofre Lopes"; 1 ♂, 1 ovigerous ♀, USNM 284138).

Size.—Males, 3.4 by 4.6 mm (cl by cb) to 5.7 by 7.5 mm; non-ovigerous females, 3.0 by 3.8 mm to 5.7 by 7.8 mm; ovigerous females 4.1 by 5.3 mm to 5.3 by 7.7 mm. The holotype measures 9.4 by 12.8 mm (Rathbun, 1930:394).

Color (Fig. 4).—Variable but most live specimens are greenish-grey or pink in color; fronto-orbital border and anterolateral margins of carapace often bordered with white; fingers of chelae black except for tips.

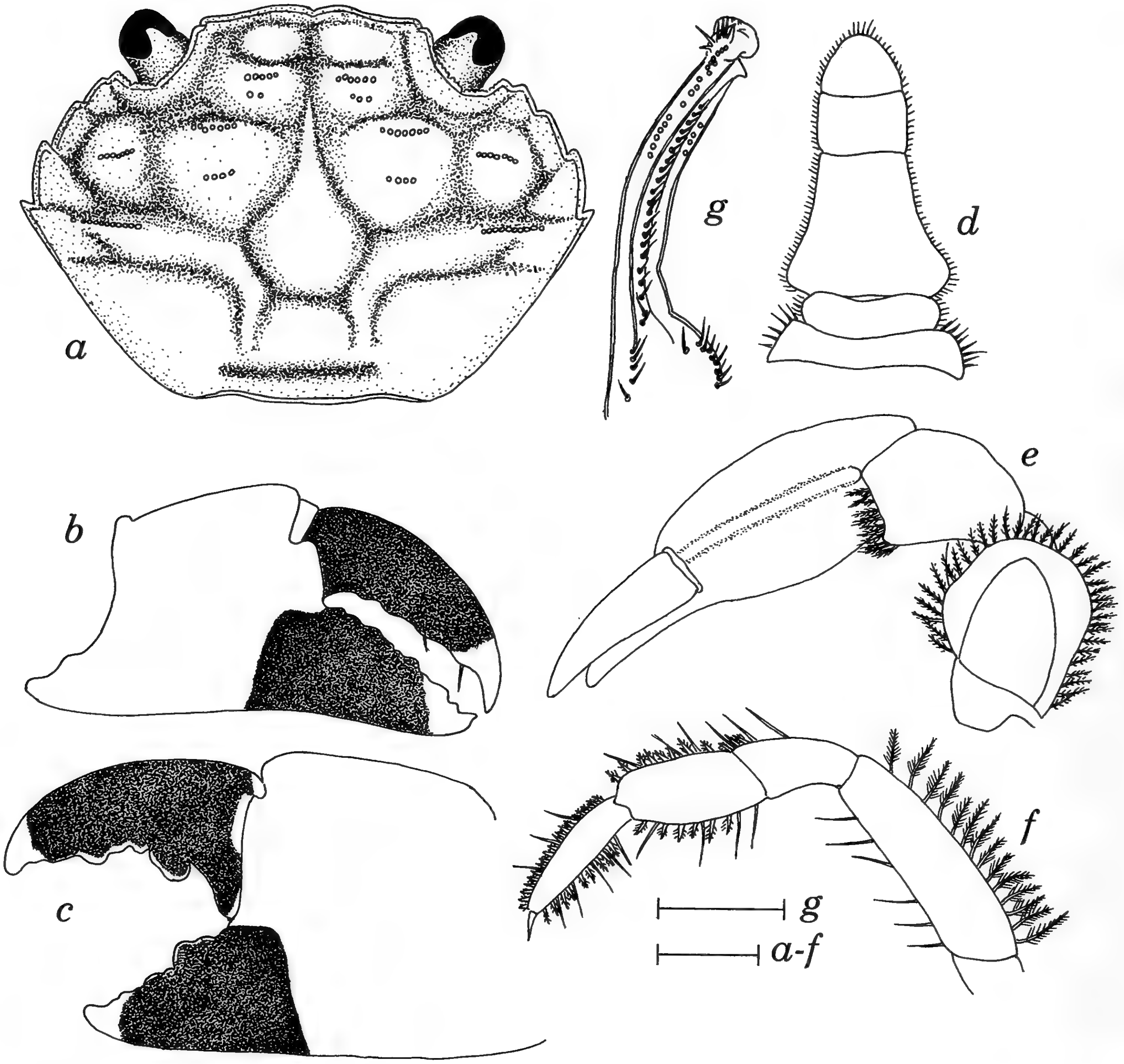

Fig. 1. *Hexapanopeus schmitti* Rathbun. Composite figure based on several specimens. Pitangui. *a,* Carapace showing rim around anterolateral and frontal margins; *b,* Right chela, outer face; *c,* Left chela, outer face; *d,* Abdomen of male; *e,* Cheliped (P1), dorsal view; *f,* Third walking leg (P4), posterior face; *g,* Gonopod. Scale *a–f,* 1 mm; scale *g,* 0.5 mm.

The majority of the freshly preserved specimens presented a uniform greyish green coloration while it was not uncommon to see a large variety of color patterns, some of which are depicted in Fig. 4. The carapace may be totally whitish with a few dark spots as in Fig. 4*b*; greyish green on most of its surface with a broad whitish band across the frontal and anterolateral regions (Fig. 4*c, e*). The carapace may also have a greenish background with a range of stripes extending posteriorly (Fig. 4*a, d*). Chelipeds normally assume the color of the carapace, but in some cases both chelae were whitish or in one rare case only the small chela was whitish. In a majority of cases, the merus, carpus, and the exopod of the third maxilliped had a fine whitish border. Dactyli of all of the walking legs were whitish and in some cases the distal half of the propodus also was whitish.

Remarks.—Martin & Abele (1986) surveyed gonopods (first male pleopods) of crabs related to *Panopeus* H. Milne Edwards,

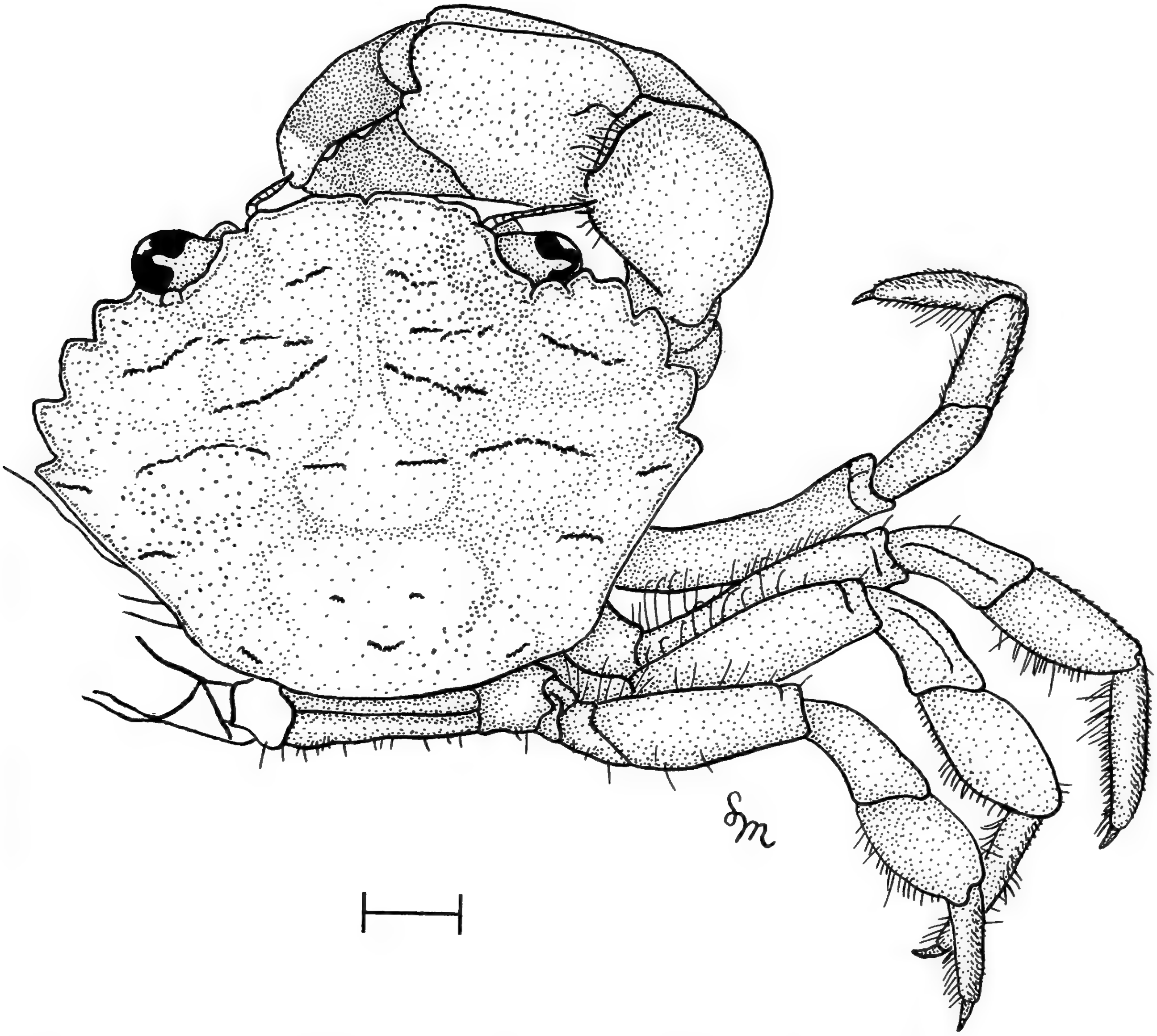

Fig. 2. *Hexapanopeus schmitti* Rathbun. Male, cl 5.0 mm, Pitangui. Dorsal view. Scale = 1 mm.

1834, and they pointed out that the tips of the gonopods of two species of *Hexapanopeus* Rathbun, 1898, the type species, *H. angustifrons* (Benedict & Rathbun, 1891), and *H. paulensis* Rathbun, 1930, differ from those of *Panopeus* s.s. The apices of the gonopods of those species of *Hexapanopeus* do not resemble those of *Panopeus* s.s., as they lack the strongly trilobed apex, with a long, sharp accessory process, a shorter rounded process, and a lateral tooth, often bifid. The apices of the gonopods of the holotype of *H. schmitti* Rathbun, 1930 (Fig. 5*e–h*), shown here, are similar in shape to those of *H. angustifrons* (Fig. 5*i*) but differ in having apical spines. The gonopod of *H. paulensis* (Fig. 5*c, d*) differs from that of species of *Panopeus* s.s. in having a trilobed apex with much smaller lobes.

In contrast, the apices of the gonopods of *H. beebei* Garth, 1961, from the eastern Pacific, have a long, tapering lateral tooth, a similarly shaped accessory process, and a rounded median process with three terminal spines (Martin & Abele 1986:fig. 3d). This agrees with the shape of the tip of the gonopods in the western Atlantic *H. caribbaeus* (Stimpson 1871) (Fig. 5*a, b*), the fourth nominal species of *Hexapanopeus* from Brazilian waters, in which the median process is ornamented with more terminal spines. As pointed out by Martin & Abele (1986:185), *Hexapanopeus* as currently understood contains at least two very distinct

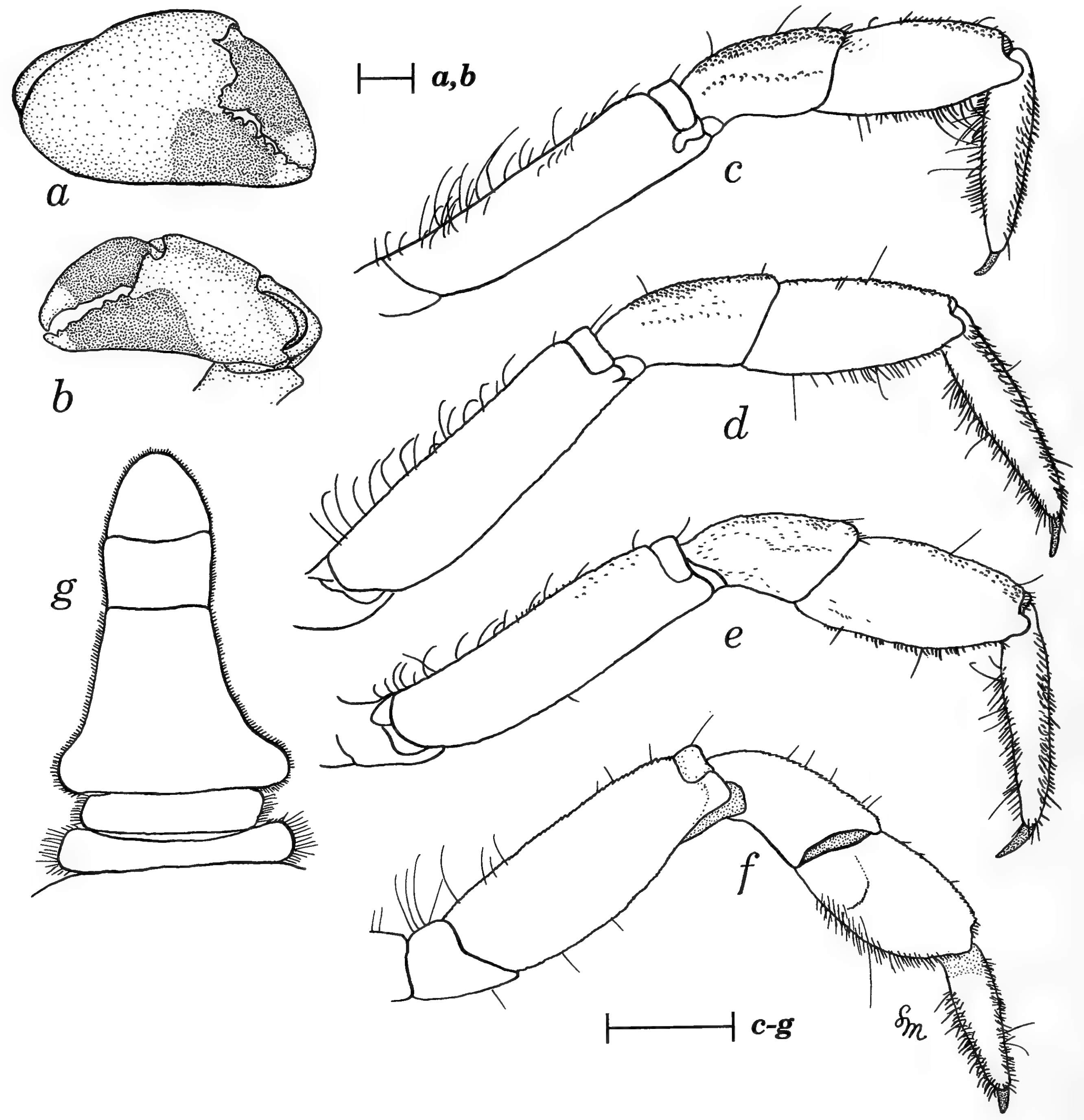

Fig. 3. *Hexapanopeus schmitti* Rathbun. Male, cl 5.0 mm, Pitangui. *a,* Right chela, outer face; *b,* Left chela, outer face; *c,* First walking leg (P2); *d,* Second walking leg (P3); *e,* Third walking leg (P4); *f,* Fourth walking leg (P5); *g,* Abdomen. Scales = 1 mm.

types of gonopods, that found on *H. angustifrons* and that found on *H. caribbaeus.* Indeed, as pointed out below, there may be three types of gonopod in different representatives of the genus.

The gonopod of *H. paulensis* from Brazil resembles that of *H. paulensis* from North America (see Williams 1984:410, fig. 331o) in shape but differs in ornamentation. In the Brazilian specimens the accessory process is covered with much larger spines. The gonopod of *H. paulensis* illustrated in Williams (1965:200, fig. 183E) apparently is based on another, undetermined species; it resembles that of *H. schmitti.*

The gonopod of *H. angustifrons* (from Williams 1965:200, fig 183D) is shown here (Fig. 5*i*) for comparison with the gonopods of the other three species of the genus known from Brazil. It appears to rep-

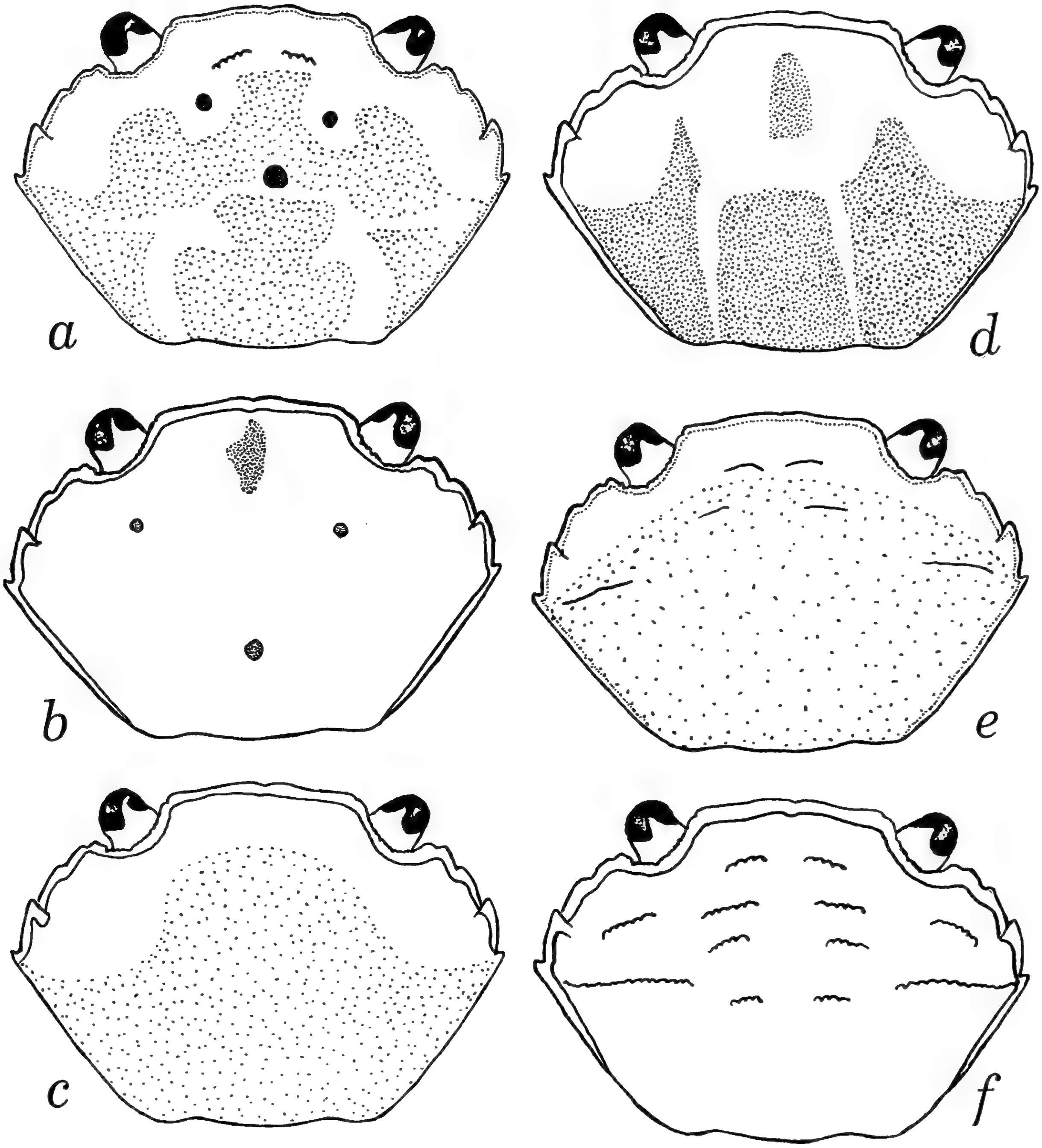

Fig. 4. *Hexapanopeus schmitti* Rathbun. Diagrammatic representation of common color patterns of specimens from Rio Grande do Norte.

resent a third type of gonopod within the genus, one with poorly developed lobes that also lacks distal spines. We have seen no material of *H. angustifrons* from Brazil, but it has been recorded from Maceio, Bahia, Rio de Janeiro, and Santa Catarina by Melo (1985), and from Pernambuco by Coelho Filho, Coelho Santos, & Coelho (1994). Melo (1996:357) gave its range in Brazil as from Pernambuco to Santa Catarina.

Rathbun (1930:393) commented on the thick, beveled front in *H. schmitti.* Actually the margin of the front is a continuation of a margin or shelf (Figs. 1*a,* 2), 0.1 mm wide, that extends across the front from the base of each fifth anterolateral tooth. The surface of the carapace rises from the inner edge of this shelf. The shelf is evident in *H. paulensis* but not on *H. angustifrons* or *H. caribbaeus.* It is much more prominent in our smaller specimens of *H. paulensis* than in ones as large as the holotype.

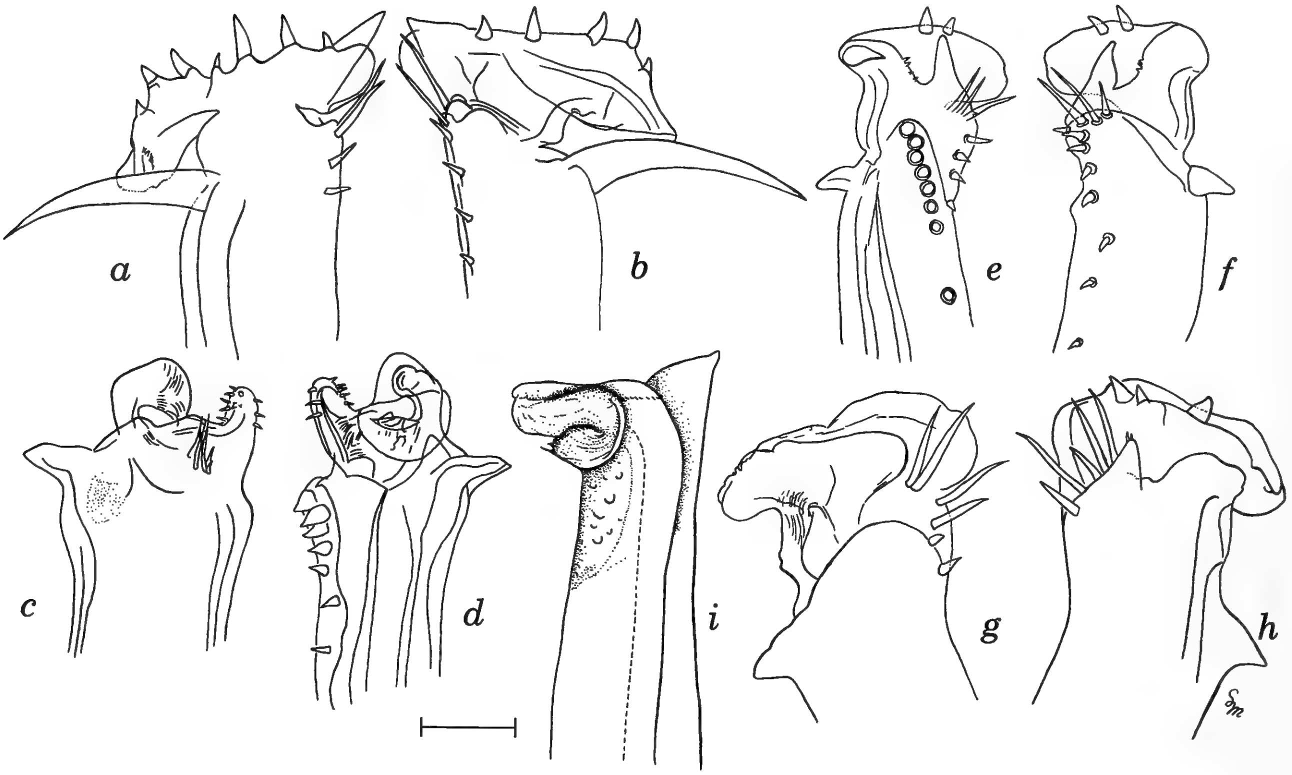

Fig. 5. Sternal (*a, c, e, g, i*) and abdominal views (*b, d, f, h*) of apex of gonopod of species of *Hexapanopeus* from Brazil. *a, b, Hexapanopeus caribbaeus* (Stimpson), male, cl 7.0 mm, Santa Catarina, USNM 61803; *c, d, Hexapanopeus paulensis* Rathbun, male holotype, cl 7.0 mm, Santos, USNM 61136; *e, f, Hexapanopeus schmitti* Rathbun, male holotype, cl 9.4 mm, Bay of Rio de Janeiro, USNM 59831; *g, h, Hexapanopeus schmitti* Rathbun, male, cl 5.0 mm, Pitangui; *i, Hexapanopeus angustifrons* (Benedict & Rathbun, 1891) (from Williams 1965:fig. 183D; not based on specimen from Brazil). Scale = 0.2 mm (*a–h* only).

Hexapanopeus caribbaeus lacks the large basal tooth on the dactylus of the cheliped that is found in *H. angustifrons, H. paulensis,* and *H. schmitti.*

Most species of *Hexapanopeus* have five well developed anterolateral teeth. The two species that have the anterior four teeth well developed and the fifth vestigial, *H. beebei* and *H. caribbaeus,* also have a long, tapering lateral process on the apex of the gonopod, and in these two characteristics differ from the type species of *Hexapanopeus,* H. *angustifrons.* This suggests that these two species should be removed from *Hexapanopeus* and placed in a new genus, an action that is beyond the scope of the present paper.

Rathbun (1930:394) pointed out that "Small specimens are easily mistaken for *Panopeus permudensis* on account of the similarity of the granulate lines of the carapace, but they can be identified by the character of the lateral teeth, the thick front, the texture of the palms, and the extension of the color of the finger in the male."

Key to Brazilian species of *Hexapanopeus*

1. Anterolateral teeth 5, fifth well developed, lateral. Apex of gonopod blunt, lacking long, tapering lateral process 2
– Anterolateral teeth 4, fifth minute, almost posterolateral. Apex of gonopod with long, tapering lateral process . . . . *H. caribbaeus*
2. Carpus of cheliped not markedly tuberculate. Color of fixed finger of chela extending proximally and dorsally onto palm 3
– Carpus of cheliped with about 15 irregularly placed tubercles. Color of fixed finger of chela barely extending onto palm. [Apex of gonopod trilobate] . . . . *H. paulensis*
3. Edge of front thick, beveled. Apex of gonopod a single rounded lobe, with 2–3 apical spines . . . . *H. schmitti*

– Edge of front not thick or beveled. Apex of gonopod subtriangular, lacking apical spines . . . . *H. angustifrons*

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Literature Cited

Bakker, C. de, M. Montú, K. Anger, & L. Loureiro Fernandes. 1989. Larval development of *Hexapanopeus schmitti* Rathbun, 1930 (Decapoda, Brachyura, Xanthidae) reared in the laboratory.—Nerítica, Pontal do Sul, PR 41/2:137–164.

Benedict, J. E., & M. J. Rathbun. 1891. The genus *Panopeus.*—Proceedings of the United States National Museum 14:35–385, pls. 19–24.

Coelho, P. A., & M. de Araújo Ramos. 1972. A constituição e a distribuição da fauna de decápodos do litoral leste da América do Sul entre as latitudes de 5°N e 39°S.—Trabalhos Oceanográficos, Universidade Federal de Pernambuco, Recife 13:133–236.

Coelho Filho, P. A., Coelho Santos, M. A., & Coelho, P. A. 1994. Estudo dos Xanthidae (Crustacea-Decapoda-Brachyura) da Praia de Piedade, Jaboatã—PE.—Revista Nordestina de Zoologia 1(1):125–151, pls. 1-6.

Garth, J. S. 1961. Brachygnatha Brachyrhyncha. Nonintertidal brachygnathous crabs from the west coast of tropical America, Part 2. Eastern Pacific Expeditions of the New York Zoological Society, XLV.—Zoologica 46(3):133–159, pl. 1.

Martin, J. W., & L. G. Abele. 1986. Notes on male pleopod morphology in the brachyuran crab family Panopeidae Ortmann, 1893, sensu Guinot (1978) (Decapoda).—Crustaceana 50(2): 182–198.

Melo, G. A. S. de. 1985. Taxonomia e padrões distribucionais e ecológicos dos Brachyura (Crustacea: Decapoda) do litoral sudeste do Brasil. Unpublished Ph.D. Dissertation, Instituto de Biociências, Universidade de São Paulo, 215 pp., 32 figs., 27 tables.

———. 1996. Manual de identificação dos Brachyura (caranguejos e siris) do litoral Brasileiro. São Paulo, Plêiade, FAPESP: 604 pp.

———, V. G. Veloso, & M. C. de Oliveira. 1989. A fauna de Brachyura (Crustacea, Decapoda) do litoral do Estado do Paraná. Lista preliminar.—Nerítica, Pontal do Sul, PR 41/2:1–31.

Milne Edwards, H. 1834. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Agasse, 1:xxv + 468 pp.

Rathbun, M. J. 1898. The Brachyura of the Biological Expedition to the Florida keys and the Bahamas in 1893.—Bulletin from the Laboratories of Natural History of the State University of Iowa 4(3):250–294, pls. 1–9.

———. 1930. The cancroid crabs of America.—United States National Museum Bulletin 152:xvi + 609 pp., pls. 1–230.

Stimpson, W. 1871. Notes on North American Crustacea in the museum of the Smithsonian Institution, No. III.—Annals of the Lyceum of Natural History of New York 10(4–5):92–136.

Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas.—Fishery Bulletin, U.S. 65(1):1–298.

———. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., xvii + 550 pp.

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Eunephrops luckhursti, a new deep-sea lobster from Bermuda (Crustacea: Decapoda: Nephropidae)

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Abstract.—*Eunephrops luckhursti,* the fourth species of the genus, is described from material trapped at depths of about 800 m off Bermuda. It resembles *E. cadenasi* Chace, from the Bahamas and Caribbean Sea, in having a median carina on the second to fifth abdominal somites, but differs in having much shorter scaphocerites, more acute pleura on the abdominal somites, and in color in life.

The species named below was taken during exploratory trapping operations in deep water off Bermuda conducted by John P. (Sean) Ingham, Pathfinder Fisheries Ltd., and Brian Luckhurst, of the Division of Fisheries, Bermuda. William McCallan, another local fisherman using deep water traps, has been documenting and studying the catches from these traps since 1984. The traps used off Bermuda are described in Luckhurst (1986:209): "The traps used for this exploratory fishing are Antillian (sic) arrowhead traps of the type presently employed for catching reef fish and spiny lobsters in inshore waters. Several different trap sizes have been tested ranging in size from 3 × 3 × 1.5 feet (91 × 91 × 46 cm) to 8 × 8 × 4 feet (244 × 244 × 122 cm) ... The traps are constructed of 2 inch (5 cm) hexagonal mesh wire, either galvanized or vinyl coated. The frames are made principally of steel reinforcing rod with some stick supports. Traps are baited with various chopped reef fish ... The traps have been fished over a wide depth range to the west and south of the Bermuda platform."

Types are deposited in the National Museum of Natural History, Smithsonian Institution (USNM) and the Bermuda Natural History Museum (BNHM).

Abbreviations used in the account below include: A1, antennule; A2, antenna; cl, postorbital carapace length; cm, centimeters; fm, fathoms; m, meters; mm, millimeters; MXP3, third maxilliped; P1-5, pereopods (P1-3 are chelate, P1 is the major cheliped, P4-5 are walking legs); sta, station; tl, total length, measured from tip of rostrum to posterior margin of telson. All measurements are in millimeters.

Family Nephropidae Dana, 1852
Subfamily Nephropinae Dana, 1852
Eunephrops Smith, 1885
Eunephrops luckhursti, new species

Figs. 1, 2, 3*a, b,* 4

Type material.—Holotype: Off Bermuda, 32°14.55′N, 64°47.74′W, depth 450 fm (824 m), leg. S. Ingham, crab trap, 18 Feb 1991: 1 ♀, cl 51 mm (USNM 284136).

Paratypes: Off south shore of Bermuda, depth 820 m, S. Ingham sta 7, 7 Dec 1991: 1 ♂, cl 57 mm (BNHM 1991-090-012).—Off Bermuda, 1992, no other data: 3 ♀♀, cl 39 and 54 mm (USNM 284137) and cl 44 mm (BNHM).

Diagnosis.—Carapace lacking submedian postcervical spines. A2 peduncle with outer spine at base of scaphocerite. Scaphocerite minute, extending to or barely overreaching base of penultimate segment of A2. P2 and P3 with fingers about ⅓–¼ as long as palm. Abdominal somites 2–6 each with longitudinal median carina dorsally.

Description.—Rostrum extending beyond end of antennular peduncle. Lower margin of rostrum unarmed, appearing smooth, with few, very low, serrations visible only under magnification. Anterior pair of lateral rostral teeth larger than and directed more anterolaterally than posterior pair. Postsupraorbital spines smaller than supraorbital, 1 placed behind each supraorbital, both situated anterior to small postorbital and small postantennal spines. Supraorbital ridge absent. Postcervical spines absent. Carapace covered with tubercles, larger anteriorly; surface sparsely pubescent between tubercles.

First abdominal somite with shallow, transverse groove. Anterolateral angle of pleuron acute, sharp but not spiniform. Abdominal somites 2–6 each with longitudinal median carina dorsally. Longitudinal groove over bases of pleura faint. Pleura of somites 3–6 acute, forming sharp point.

Telson longer than wide, lateral margins bulging slightly near midlength, tuberculate there. Posterolateral spines strong.

Scaphocerite minute, barely extending to or overreaching base of penultimate segment of A2 peduncle. Apex usually rounded, rarely acute. Larger spine present on A2 peduncle at base of scaphocerite.

MXP3 extending about to end of rostrum. Merus and carpus each with blunt, lower distal spine, that of merus larger.

Major chelipeds (P1) very strong, heavy, subequal, longer than carapace and rostrum combined, extending beyond rostrum with distal part of merus. Chela length about 3 times width; lateral surfaces with broad longitudinal carina formed by tubercles, distalmost on inner surface largest, each carina bordered by upper and lower shallow, longitudinal depressions. Upper margin of palm formed by single carina, irregularly tuberculate, lower margin bicarinate to about middle of fixed finger. All carinae ornamented with large and small blunt spines. Dactylus tuberculate dorsally, slightly shorter than palm, shorter than fixed finger. Cutting edge of chela evenly tuberculate or with some larger teeth and smaller, uniform tubercles. Carpus about half as long as chela (measured dorsally), with 2 rows of spines on outer face, distalmost spines largest; dorsal surface with low row of rounded spines; upper, inner margin sparsely spined, distalmost largest of all spines on carpus; lower margin with single row of spines; other spines of various sizes placed on surface and distal margin. Merus as long as palm (measured on outer edge), inner and outer edges each with irregular row of spines, each with distal tooth.

P2 extending beyond rostrum with chela. Fingers about ⅓–¼ palm length. Carpus twice as long as dactylus. Merus more than twice as long as carpus.

P3 extending beyond rostrum with chela and distal part of palm. Fingers about ⅓–¼ palm length. Carpus about ¾ as long as palm and half as long as merus, latter as long as chela.

P4 extending beyond rostrum with dactylus. Carpus about twice as long as dactylus. Merus twice as long as carpus.

P5 short but overreaching penultimate segment of A2 peduncle.

In both sexes, sternite of P2 ending in narrow, acute, bifid process, sharper in males; sternites of P3 and P4 wider, longer, and rounded.

Gonopod as figured.

Color (Fig. 4).—Carapace, A1 and A2 peduncles, and chelipeds almost uniform red. A1 and A2 flagellae pink proximally, beige or clear distally. Ischium and basal part of merus of P2-5 red, carpus and propodus clear, extremities pink. Ridges on abdominal somites, telson, and uropods red, uropodal setae clear.

Measurements.—Male, cl 57 mm (cl plus rostrum 81 mm; tl 170 mm); females, cl 39, 44, 51, and 54 mm (cl plus rostrum 55, 57, 70, and about 63 mm, respectively; tl 11.7, 12.5, 15, ca. 15 cm, respectively). The largest specimen, the male, is 170 mm long; other measurements of largest male: P2

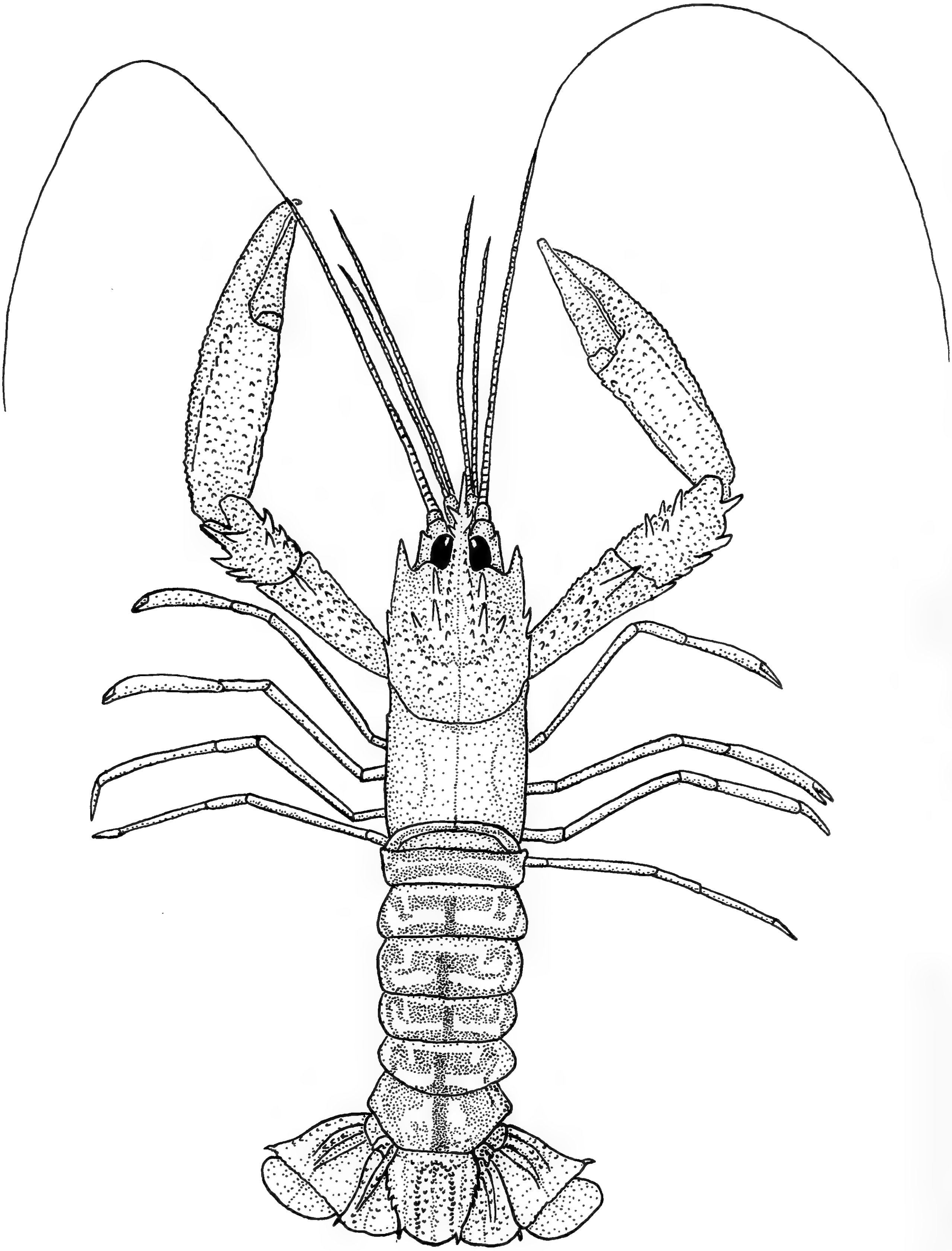

Fig. 1. *Eunephrops luckhursti,* new species, female holotype, cl 51 mm. Dorsal view.

palm length 24.2 mm, movable finger length 6.9 mm; P3 palm length 25.8 mm, movable finger length 5.9 mm.

Distribution.—Known only from Bermuda in depths of 800–824 m.

Etymology.—Named for Brian Luck-

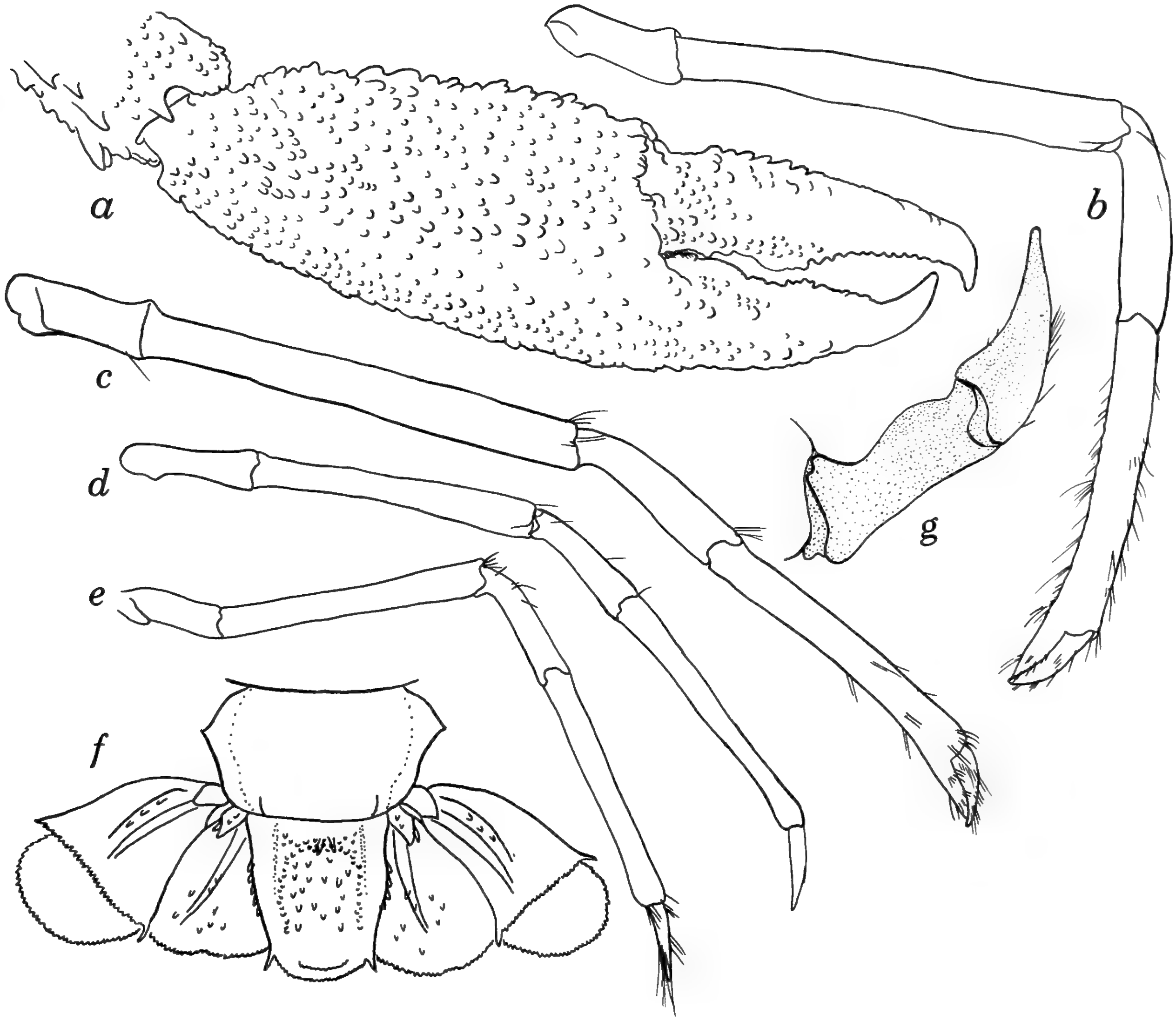

Fig. 2. *Eunephrops luckhursti,* new species, *a–f,* Female holotype, cl 51 mm; *g,* Male paratype, cl 57 mm. *a,* Chela; *b,* P2; *c,* P3; *d,* P4, *e,* P5; *f,* Tail fan; *g,* Gonopod. (Setae omitted).

hurst, a fishery scientist with the Bermuda Division of Fisheries, whose interest in exploratory deep trapping off Bermuda led to the discovery of this species. Other species taken in these trapping operations off Bermuda are reported in Luckhurst (1986) and Manning & Holthuis (1986), and Luckhurst & Manning (pers comm).

Remarks.—The species of *Eunephrops* are all known from localities in the northwestern Atlantic. *Eunephrops luckhursti* is the fourth species of *Eunephrops* to be recognized. It agrees with *E. cadenasi* Chace, 1939, and differs from both *E. bairdii* Smith, 1885 and *E. manningi* Holthuis, 1974, in having a distinct median carina on abdominal somites 2–5. It also differs from *E. cadenasi* in having much shorter scaphocerites (Fig. 3*b, E. luckhursti*; 3*d, E. cadenasi*) and in color as well (see below). *Eunephrops luckhursti* is a smoother species than *E. cadenasi,* with much smaller tubercles on the carapace and chelipeds; the spinulation of the major chelae is much less pronounced than in *E. cadenasi.* The pleura of abdominal somites 2–6 are acute and more pointed in *E. luckhursti* (Fig. 3*a*) than in *E. cadenasi* (Fig. 3*c*).

The color of *E. luckhursti* is quite different from that of *E. cadenasi* (see Paulmier 1993:pl. 24; Poupin 1994:pl. 2a,b). In *E. cadenasi* the chelipeds and abdominal ridges are primarily beige or yellow; the carapace is marked with yellow anteriorly; and the walking legs are clear or beige proximally, red distally. In *E. luckhursti* the car-

Fig. 3. *a, c,* Outline of abdominal pleura 2–5 in lateral view; *b, d,* Basal segment of antenna in oblique dorsal view to show antennal scale (indicated by arrow). *a, b, Eunephrops luckhursti,* new species, female holotype, cl 51 mm; *c, d, E. cadenasi* Chace, ovigerous female, cl 66 mm, Caribbean Sea, USNM 170675.

apace, chelipeds, and abdominal ridges are red (Fig. 4).

The five known specimens of *E. luckhursti* are somewhat smaller than those of *E. cadenasi,* the largest specimen having a total length of 170 mm, a carapace length (including rostrum) of 81 mm. The holotype of *E. cadenasi* is 224 mm long (Chace 1939). Holthuis (1974) reported males with carapace lengths (including rostrum) of 46 to 135 mm, with the carapace lengths of females somewhat smaller, 40 and 50 mm. Paulmier (1993) recorded a specimen 490 mm long; that specimen has a carapace length of 110 mm. Poupin (1994) reported specimens with a carapace length (including rostrum) of 39 to 116 mm.

The smallest female, cl 39 mm, has an extra rostral spine on the right side, both scaphocerites very small and rounded, and both major chelae evenly toothed. The female with cl 44 mm has the rostrum bifid at the apex and the left scaphocerite longer than the right, extending about to the middle of the penultimate segment of the peduncle. The largest female, cl 54 mm, has a broken rostrum; the scaphocerite is rounded on one side, pointed on the other; both chelae have enlarged teeth as well as evenly spaced smaller ones.

The length of the fingers and palm of both P2 of all available specimens of *E. luckhursti* (*n* = 5 specimens, 9 legs) and *E. cadenasi* (*n* = 8 specimens, 13 legs) were measured. In *E. luckhursti* the propodus ranged from 3.1 to 3.8 times as long as the dactylus (mean 3.4 times). In *E. cadenasi* ranged from 2.9 to 3.9 times as long as the dactylus (mean 3.5 times). These two species and *E. manningi* cannot be separated using this feature, but it can be used to distinguish all three of these species from *E. bairdii.*

The depth ranges of *E. luckhursti* and *E. cadenasi* are similar, the former having been taken in depths around 800 m, the latter in slightly shallower water. The holotype of *E. cadenasi* was taken at a depth of 300–315 fm (549–576 m), the allotype at 250 fm (458 m) (Chace 1939). Holthuis (1974) noted that *E. cadenasi* had been taken in depths between 373–434 and 591 m. Paulmier (1993) suggested that its optimal depth was below 450 m, and Poupin (1994) studied one lot taken at 607 m. Specimens of *E. cadenasi* in the USNM collections were

Fig. 4. *Eunephrops luckhursti,* new species. Female holotype, cl 51 mm. Off Bermuda. Color in life. Photo by Brian Luckhurst.

taken in depths of 275 to 340–380 fm (503 to 622–695 m).

Material of *E. luckhursti* was compared directly with the following specimens of *E. cadenasi* from the Leeward Islands in the USNM collections: USNM 170673, female, cl 65.3 mm, west of St. Martin, depth 360 fm (659 m); USNM 170674, ovigerous female, cl 76.3 mm, northeast of Nevis, depth 317 fm (580 m); USNM 170675, ovigerous female, cl 66.4 mm, northeast of St. Kitts, depth 344 fm (630 m); USNM 170676, male, cl 53.6 mm, north of St. Kitts, depth 365 fm (668 m); USNM 170677, male, cl 78.5 mm, off Dominica, depth 275 fm (503 m); USNM 170678, female, cl 85.9 east of St. Kitts, depth 350–370 fm (641–677 m); USNM 170679, 2 females, cl 57.9 and 89.9

mm, north of St. Kitts, depth 340-380 fm (622–695 m).

Key to Species of *Eunephrops* (modified from Holthuis 1974)

1. Carapace with submedian postcervical spines. No spine present on antennal peduncle at base of scaphocerite. P2 with fingers slightly less than half length of palm . . . . *E. bairdii*
– Carapace lacking postcervical spines. A spine present on antennal peduncle at base of scaphocerite. P2 with fingers less than ⅓ length of palm 2
2. Abdominal somites 2–5 with single transverse groove, lacking distinct median carina . . . . *E. manningi*
– Abdominal somites 2–5 with distinct median carina 3
3. Scaphocerite pointed anteriorly, long, extending to base of ultimate segment of antennal peduncle. Pleura of abdominal somites rounded . . . . *E. cadenasi*
– Scaphocerite usually rounded anteriorly, short, not extending to middle of penultimate segment of antennal peduncle. Pleura of abdominal somites pointed . . . . *E. luckhursti,* new species

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I thank John P. (Sean) Ingham, William McCallan, Brian Luckhurst, and Lisa Greene, Bermuda Museum of Natural History, for their help in the field and for making these specimens available for study. Brian Luckhurst provided color photographs of *E. luckhursti.* The line drawings were prepared by Lilly King Manning. My studies on the systematics of western Atlantic lobsters have been supported by the Smithsonian Marine Station at Link Port, Florida, a facility of the National Museum of Natural History. This is contribution 418 from that facility. This is contribution No. 8, Bermuda Biodiversity Project (BBP), Bermuda Aquarium, Natural History Museum and Zoo.

Literature Cited

Chace, F. A., Jr. 1939. Preliminary descriptions of one new genus and seventeen new species of decapod and stomatopod Crustacea. Reports on the scientific results of the first Atlantis Expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University.—Memorias de la Sociedad Cubana de Historia Natural 13(1):31–54.

Holthuis, L. B. 1974. The lobsters of the superfamily Nephropidea of the Atlantic Ocean.—Biological Results of the University of Miami Deep-Sea Expeditions, 106.—Bulletin of Marine Science 24(4):723–884.

Luckhurst, B. 1986. Discovery of deep-water crabs (*Geryon* spp.) at Bermuda—a new potential fishery resource.—Proceedings of the Thirty-Seventh Annual Gulf and Caribbean Fisheries Institute, Cancun, Mexico, November 1994: 209–211.

Manning, R. B., & L. B. Holthuis. 1986. Notes on *Geryon* from Bermuda, with the description of *Geryon inghami,* new species (Crustacea: Decapoda: Geryonidae).—Proceedings of the Biological Society of Washington 99:366–373.

Paulmier, G. 1993. Crustacés profondes capturés aux casiers aux Antilles françaises.—Catalogue de l'Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), February 1993: 1–34.

Poupin, J. 1994. Faune marine profonde des Antilles Françaises. Récoltes du Navire *Polka* faites en 1993. Paris, ORSTOM Éditions, Collection Études et Thèses, 79 pp., colored pls. 1–5.

Smith, S. I. 1885. Description of a new crustacean allied to *Homarus* and *Nephrops.*—Proceedings of the United States National Museum 8:167–170.

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A new crayfish of the genus *Orconectes* from western Tennessee (Decapoda: Cambaridae)

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Abstract—A new crayfish, *Orconectes pagei,* is described from northern and eastern flowing tributaries of the Tennessee River in western Tennessee. The species occurs in small to medium streams with sand substrate. Form I males of *O. pagei* differ from all other members of the genus *Orconectes* in being both pigmented and possessing a first pleopod with a short, laterally flattened central projection and a short, dorsoventrally flattened mesial process.

Recent re-examination of crayfishes collected from western Tennessee in the late 1970's and early 1980's housed in the Illinois Natural History Survey's Crustacean Collection, revealed the presence of several unidentifiable form II males and females from two locations in the Big Sandy River drainage. Subsequent field work in that drainage in 1996 resulted in the collection of several form I males of that unidentifiable taxon. That species, described herein as *Orconectes pagei,* is assigned to the nonimate subgenus *Orconectes.* This subgeneric assignment is based on the overall similarity in the shape of the form I male pleopod of *O. pagei* to other members of the subgenus. *O. pagei* represents the only epigean member of this subgenus and raises the total number of taxa assigned to it to seven. The remaining members of *Orconectes* (*Orconectes*) are *Orconectes* (*O.*) *australis australis* (Rhoades, 1941), *O.* (*O.*) *australis packardi* Rhoades, 1944, *O.* (*O.*) *incomptus* Hobbs & Barr, 1972, *O.* (*O.*) *inermis inermis* Cope, 1872, *O.* (*O.*) *inermis testii* (Hay, 1891), and *O.* (*O.*) *pellucidus* (Tellkampf, 1844). A subgenus that contains both epigean and troglobitic members is not uncommon in the family Cambaridae. Other described subgenera with both ecotypes include *Cambarus* (*Erebicambarus*), *C.* (*Jugicambarus*), *Procambarus* (*Austrocambarus*), and *P.* (*Ortmannicus*).

Orconectes pagei, new species
Figs 1 & 2, Table 1

Diagnosis.—Body and eyes pigmented. Rostrum flat anteriorly, slightly concave posteriorly, terminating in long acumen; median carina absent. Rostral margins thickened, slightly converging distally; terminating in spines (see Variation). Areola 25.0–31.5% ($\bar{X}$ = 28.3, n = 40, *SD* = 1.4) of total length of carapace. Narrowest part of areola just anterior of midpoint, 5.8–15.0 ($\bar{X}$ = 9.2, n = 40, *SD* = 1.9) times as long as wide with 2 to 4 (mode = 3, n = 40, *SD* = 0.5) punctations across narrowest part. One large cervical spine on each side of carapace. Postorbital ridges well developed, terminating in large spines. Suborbital angle weakly developed. Antennal scale broadest slightly proximal to midlength. Ischia of third pereiopods of form I and form II males with hooks; hooks overreaching basioischial articulation in form I males only. Chela with 3 rows of tubercles along mesial margin of palm; small tufts of setae over mesial margin of palm, fingers, and dorsomesial surface; dorsal surfaces of fingers with well defined longitudinal ridges. Ventral surface of chela with tubercle at base of dactyl. First pleopods of form I male symmetrical, extending to bases of third pereiopods when abdomen flexed. First pleopod of form I male without distinct shoulder on cephalic surface at base of central projection; central projection corneous, constituting 8.0–11.0% ($\bar{X}$ = 9.2, *n* = 4, *SD* = 1.3) of total length of first pleopod, flattened laterally and bladelike, tapering rapidly to a sharply pointed tip; mesial process equal in length and corneous, flattened dorsoventally and bladelike, tapering to acute tip. Central projection and mesial process of form I first pleopod divergent, forming wide gap between distal tips. Annulus ventralis immovable, subrhomboidal; cephalic half with median trough, lateral prominences forming anterior margin of fossa; fossa shallow with narrow lateral width; sinuate sinus running from center of fossa to caudal edge.

Description of holotypic male, form I.— Body slightly compressed laterally, thorax slightly wider than abdomen (16.3 and 14.8 mm, respectively). Greatest width of carapace slightly larger than height at caudodorsal margin of cervical groove (16.3 and 14.4 mm respectively). Postorbital carapace length 91.0% of length of carapace. Areola 9.7 times longer (10.7 mm) than wide (1.1 mm) with 2 punctations across narrowest part: length of areola 30.9% of length of carapace. Rostrum with scattered punctations and setae, posterior half slightly excavated; margins slightly converging anteriorly, fringed with setae and terminating in small rounded tubercles. Acumen terminating in corneous spine reaching nearly to end of antennular peduncle. Postorbital ridges well developed, terminating in corneous spines. Suborbital angle poorly developed. Cervical spine large and corneous; dorsal and branchiostegal areas of carapace punctate.

Abdomen longer than carapace (40.5 and 34.6 mm, respectively). Cephalic section of telson with 1 movable and 1 immovable spine in each caudolateral corner. Protopodite of uropod with spine extending over endopodite and spine in caudolateral corner extending over exopodite. Caudal margin of cephalic section of exopodite with numerous spines (15) and 1 movable spine in caudolateral corner. Lateral margin of endopodite terminating in spine; endopodite with prominent median ridge terminating in premarginal spine. Dorsal surfaces of telson and uropods setiferous.

Antennal scale broadest slightly proximal to midlength; thickened lateral margin terminating in large corneous spine. Left antennal scale 8.5 mm long, 3.7 mm wide.

Mesial surface of palm of left chela with 3 rows of tubercles, 10 tubercles in middle row, 6 in dorsal-most row, and 4 in ventral-most row; dorsal and lateral surfaces of palm covered with many small setiferous punctations. Ventral surface of palm of chela with corneous spine at base of dactyl. Dorsal and ventral surfaces of finger of propodus with submedian longitudinal ridges flanked by setiferous punctations, small tuft of setae at base; basal half of opposable margin with 5 weakly developed tubercles. Dorsal and ventral surfaces of dactyl with submedian longitudinal ridges flanked by setiferous punctations. Fingers with subterminal corneous tips.

Carpus with deep oblique furrow dorsally; mesial surface with 1 tubercle at distal end, large corneous procurved spine just distal to midlength, small corneous spine at midlength; ventral surface with 2 corneous spines at midlength of distal margin. Dorsodistal surface of merus with 2 large corneous spines; ventral surface with 2 large corneous spines just distal to midlength of ventrolateral margin and mesial row of 9 tubercles, some corneous; row terminating in large corneous spine. Ischium with 2 small corneous spines on mesial margin.

Hook on ischium of third pereiopod only; hook simple, overreaching basioischial articulation and not opposed by tubercle on basis. Right fifth pereiopod absent. First pleopod as in Diagnosis, reaching just cephalic to bases of third pair of pereiopods when abdomen flexed.

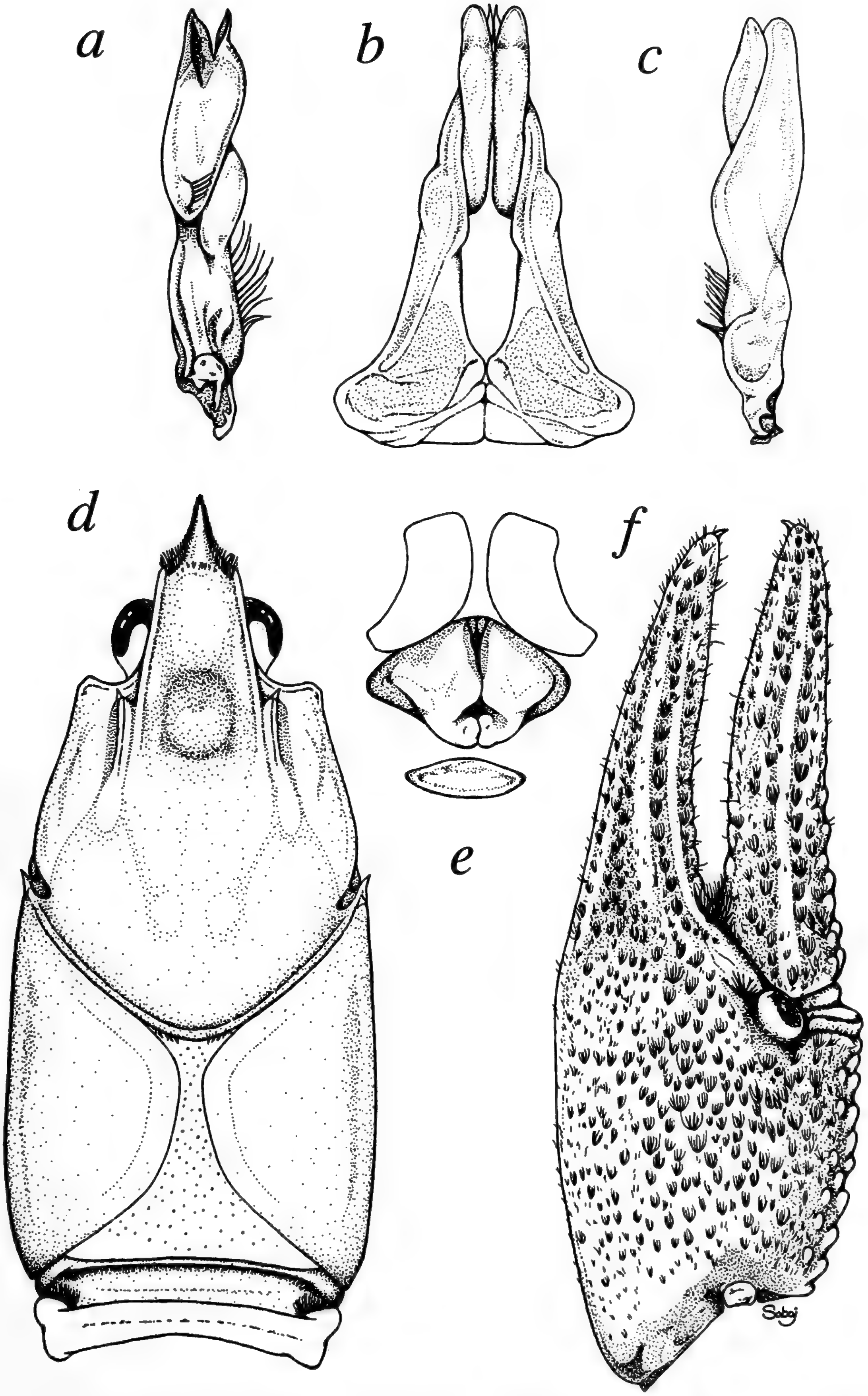

Fig. 1. *Orconectes pagei,* new species: a, Mesial view of first pleopod of form I male; b, Caudal view of first pleopods of form I male; c, Lateral view of first pleopod of form II male; d, Dorsal view of carapace; e, Annulus ventralis; f, Dorsal view of left chela. Figures 1a, 1b, 1d, and 1f are of holotype (INHS 5785); figure 1c is of morphotype (INHS 5777); figure 1e is of allotype (INHS 5772).

Description of allotypic female.—Differing from holotype as follows. Areola constituting 28.5% of length of carapace and 8.7 times longer than wide. Margins of rostrum terminating in corneous spines. Mesial margin of palm of left chela with secondary row of 5 weakly developed tubercles on dorsal surface lateral to primary row of 7 tubercles. Ventral surface of left merus with large spine in distolateral corner, mesial margin with row of 7 spines terminating in large corneous spine. Ventral surface of right merus with 2 spines in distolateral corner, 2 spines at midlength, and a mesial row of 4 weakly developed spines terminating in 2 large corneous spines.

Sternum between third and fourth pereiopods narrowly V-shaped. Postannular sclerite ½ as wide as annulus ventralis (described in Diagnosis). First pleopod uniramous, barely reaching annulus when abdomen flexed.

Description of morphotypic male, form II.—Differing from holotype as follows. Areola constituting 28.0% of length of carapace and 14.8 times longer than wide. Margins of rostrum terminating in corneous spines. Mesial margin of palm of left chela with secondary row of 6 weakly developed tubercles on dorsal surface lateral to primary row of 6 tubercles, mesial margin of palm of right chela with secondary row of 6 weakly developed tubercles on dorsal surface lateral to primary row of 8 tubercles. Ventral surfaces of meruses with mesial row of 7 tubercles terminating in large corneous spines.

Hook on ischium of third pereiopod not overreaching basioischial articulation. Left second pereiopod detached. First pleopod of uniform texture; both terminal elements noncorneous and of equal length with rounded distal ends.

Size.—The largest specimen examined is the holotype, a 34.6 mm CL form I male. Females (*n* = 6) range in size from 20.0 to 27.4 mm CL. Form I males (*n* = 4) range in size from 16.3 to 34.6 mm CL. Form II males (*n* = 30) range in size from 15.6 to 29.8 mm CL.

Color.(Fig. 2).—Dorsal and lateral surfaces of cephalothorax and abdomen tan to light brown and mottled with dark brown patches of varying size. Dorsal surface of each abdominal segment with 2 dark brown patches that form a pair of parallel bars extending from the posterior edge of the cephalothorax to the 5th abdominal segment when abdomen is fully extended. Dorsal surfaces of chela, carpus, and merus tan to light brown in color with dark brown patches. Dorsal surfaces of pereiopods with similar coloration and mottling pattern. Fingers of chelae with red tips. Ventral surfaces of chelae, cephalothorax, and abdomen cream to white.

Type locality.—Morris Creek at Tennessee Hwy. 424, 0.5 km W jct. W/Tennessee Hwy. 114, 1.6 km NE Yuma, Carroll County, Tennessee. Holotype was collected among woody debris in midchannel, 25 m downstream of Hwy. 424 bridge. At the time of collection, Morris Creek ranged in width from 5–8 m with an average depth of 0.4 m. Substrate at the type-locality was sand. Woody debris piles occurred commonly in the creek both upstream and downstream of the bridge.

Disposition of types.—The holotype, allotype, and morphotype are in the Illinois Natural History Survey Crustacean Collection (catalogue numbers INHS 5785, INHS 5772, and INHS 5777, respectively), as are the following paratypes: 14 form II males and 1 female (INHS 5764); paratypes consisting of 2 form I males, 2 form II males, and 2 females (USNM 130530), and one form I (USNM 284135) are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. The localities and dates of collection are provided in the following Range and specimens examined section.

Range and specimens examined.—*Orconectes pagei* is confined to streams draining the Cretaceous McNairy Sand and Coon Creek formations which occur as a

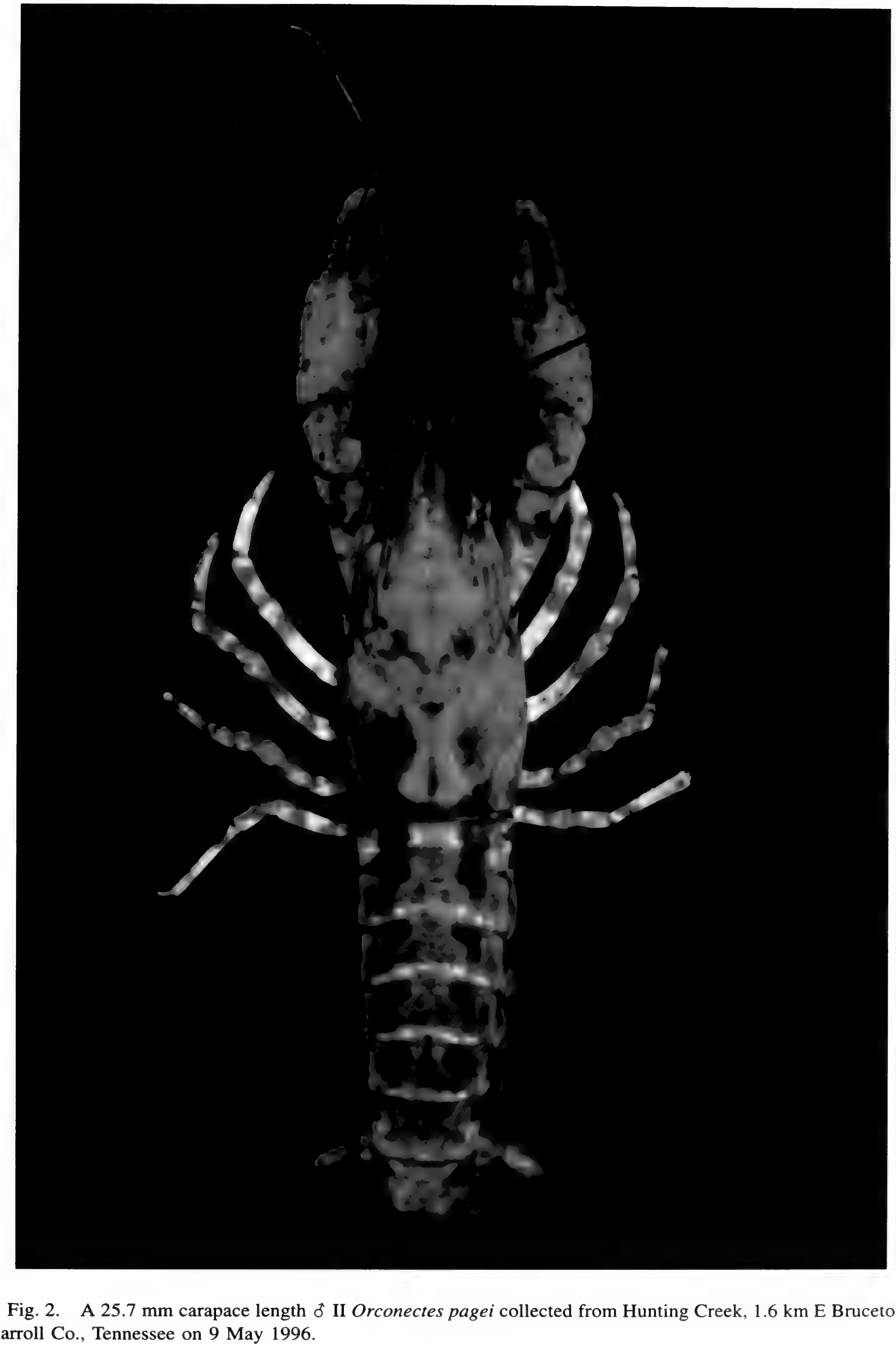

Fig. 2. A 25.7 mm carapace length ♂ II *Orconectes pagei* collected from Hunting Creek, 1.6 km E Bruceton, Carroll Co., Tennessee on 9 May 1996.

Table 1.—Measurements (mm) of *Orconectes pagei,* new species.

	Holotype	Allotype	Morphotype
Carapace:			
Total length	28.8	27.4	21.1
Postorbital length	26.1	20.7	15.5
Width	16.3	13.2	9.6
Height	14.4	13.1	8.9
Areola:			
Width	1.1	0.9	0.4
Length	10.7	7.8	5.9
Rostrum:			
Width	5.3	4.4	3.3
Length	9.2	7.6	6.0
Chela, left:			
Length, palm mesial margin	10.1	5.2	4.4
Palm width	11.0	5.9	4.6
Length, lateral margin	30.5	14.9	13.6
Dactyl length	16.9	7.5	7.2
Abdomen:			
Width	14.8	13.5	9.1
Length	40.5	33.8	25.0

narrow north-south band along the eastern edge of the crest of the Coastal Plain in Henry, Benton, Carroll, and Henderson counties, Tennessee (Fig. 3). The northernmost record for this species is Eagle Creek, a tributary of the Tennessee River in Henry County; the southernmost record being from Middleton Creek, a tributary of White Oak Creek in Henderson County. *Orconectes pagei* is most common in tributaries of the northern flowing Big Sandy River. Its propensity for streams with pure sand substrate of the McNairy Sand and Coon Creek formations most likely restricts its distribution to headwater streams of the Beech River and White Oak Creek drainages. Downstream portions of both of these drainages, and drainages south of White Oak Creek (e.g. Beason, Snake, Lick, and Chambers creeks), flow through high level alluvial deposits and are characterized by predominantly gravel substrates. In eastward flowing drainages of the Tennessee River south of White Oak Creek, *O. pagei* is replaced by *Orconectes* (*Faxonius*) *wrighti* Hobbs, 1948.

A total of 81 specimens from 14 localities have been examined from the following Tennessee counties: Benton County: 1) INHS 780, Big Sandy River at TN Hwy. 69, 3.2 km W Big Sandy, 26 Apr 1978 (2 ♂ II, 1 ♀); Carroll County: 2) USNM 148879, Hollow Rock Branch at Bruceton, 7 Jun 1978 (1 ♂ II); 3) INHS 5764, Morris Creek at TN Hwy. 424, 1.6 km NE Yuma (type locality), 9 May 1996 (14 ♂ II, 1 ♀, all paratypes); INHS 5785, INHS 5784, 15 Jul 1996 (holotype and 1 ♂ I, 8 ♂ II, 3 ♀,); 4) INHS 5772, INHS 5771, Hunting Creek at Old S.R. 1, 1.6 km E Bruceton, 9 May 1996 (allotype and 4 ♂ II,); Henderson County: 5) USNM 130530, Owl Creek at Rt. 20, 1 km E Lexington, 16 Apr 1969 (2 ♂ I, 2 ♂ II, 2 ♀, all paratypes); 6) INHS 5641, Haley Creek at Davis Rd., 8 km E Lexington, 11 Jun 1996 (1 ♂ I, 3 juvenile ♂, 2 ♀, 3 juvenile ♀); 7) INHS 5781, Middleton Creek at TN Hwy. 100, 3.4 km NNE Roby, 11 Jun 1996 (5 ♂ II, 5 ♀); Henry County: 8) INHS 5766, McGowen Branch at India Rd., 1.6 km NE Paris, 8 May 1996 (2 ♂ II); 9) INHS 5777, INHS 5776, Barnes Fork Creek at Reynoldsburg Rd., 7.2 km SSE Paris, 8 May 1996 (morphotype and 2 ♂ II, 2 ♀); 10) INHS 5778, USNM 284135, Gin Creek at Copper Springs Rd., 6 km WSW Big Sandy, 16 Apr 1996 (1 ♂ I, 1 ♂ I paratype to UNSM); 11) INHS 778, trib. Barnes Fork Creek 0.5 km downstream TN Hwy. 77, 1.6 km N Van Dyke, 4 May 1981 (1 ♂ II); 12) INHS 5634, West Sandy Creek at TN Hwy. 641/69, 4.2 km S Oakwood, 16 Oct 1996 (8 ♂ I, 4 ♂ I, 2 juvenile ♀); 13) INHS 5626, Holly Fork Creek at TN Hwy. 79, 1.2 km SW Nobles, 17 Oct 1996 (3 ♂ I, 3 ♂ II); 14) INHS 5637, Eagle Creek at TN Hwy. 79, 4 km SW Oak Hill, 17 Oct 1996 (1 ♂ I).

Etymology.—Named in honor of Dr. Lawrence M. Page, Principal Scientist and Curator of Fishes at the Illinois Natural History Survey. Dr. Page has contributed greatly to our knowledge of midwestern cray-

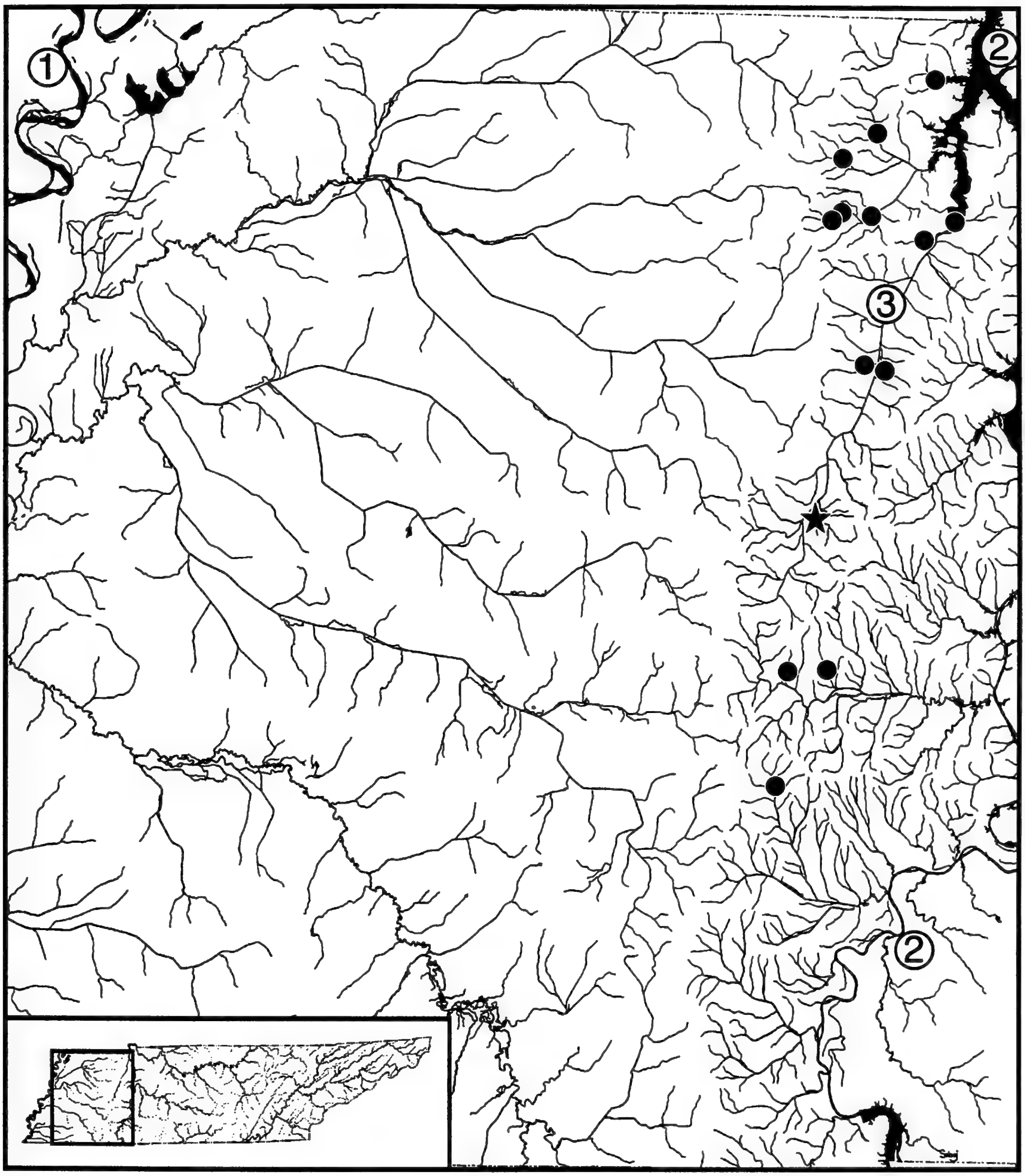

Fig. 3. Known range of *Orconectes pagei*. Type locality denoted by star. 1 = Mississippi River, 2 = Tennessee River, 3 = Big Sandy River.

fishes and continues to show an intense interest in the conservation and systematics of all aquatic organisms. This broad interest has been inherited by many of his co-workers and students.

Habitat and life-history notes.—During field sampling, all individuals were collected from small to medium-sized streams with sand substrate. Within these creeks, the species occurred exclusively in woody debris piles composed primarily of fallen tree limbs and bark in midchannel and along stream banks in areas with slow to moderate current. *Orconectes pagei* is strongly associated with sand substrate; the species was never collected from streams within its range with even the smallest amount of gravel or cobble substrate.

Form I males have been collected in the months of April, July, and October. Field collection efforts from April through July 1996 revealed form I males to be uncommon, accounting for only four of the 51 specimens collected. In October, form I males were much more common, accounting for 12 of the 21 specimens collected. Juveniles were observed in June and October. Ovigerous females were collected in the months of April and May. Two ovigerous females collected on 8 May 1996 measured 18.5 and 14.5 mm CL and carried 101 and 43 eggs, respectively. Eggs were spherical and ranged from 1.7 to 1.8 mm in diameter.

Crayfish associates.—The following species were collected from habitats containing *O. pagei: Cambarus* (*Depressicambarus*) *striatus* Hay, 1902, *Orconectes* (*Trisellescens*) *validus* (Faxon, 1914), *Procambarus* (*Ortmannicus*) *viaeviridis* (Faxon, 1914), and *P.* (*O.*) *acutus* (Girard, 1852).

Variation.—Size of spines on rostral margins appears to be inversely proportional to carapace length. Juveniles and small individuals (ca. <25 mm CL) have large, well developed spines while larger individuals, such as the holotype, have margins that terminate in rounded tubercles.

Comparisons.—*Orconectes pagei* differs from all other members of *Orconectes* in the shape of the form I male gonopod and by being pigmented. The gonopod of *O. pagei* is unique to pigmented members of the genus in possessing all of the following characteristics: terminal elements short, central projection comprising less than 12% of total length of gonopod; elements divergent; central projection laterally flattened, tapering rapidly to acute tip distally; mesial process flattened dorsoventrally and bladelike.

Relationships.—In his subgeneric reorganization of the genus *Orconectes,* Fitzpatrick (1987) stated that in crayfishes, most external morphological features are difficult to use for inferring intergroup relationships because they are readily modified to adapt to environmental conditions. While still variable, Fitzpatrick (1987) suggests that structures associated with amplexus are less susceptible to environmental modification and offer reliable characters for subgeneric classification. Since the form I male gonopod of *Orconectes pagei* is most similar to those of members of the subgenus *Orconectes,* we follow Fitzpatrick's contention and tenatively assign *O. pagei* to this subgenus. Within the subgenus *Orconectes* the form I gonopod of *O. pagei* is most similar to *Orconectes inermis testii,* a troglobitic species that occurs in south-central Indiana. *Orconectes pagei* presents somewhat of a dilemma in that it is pigmented, has developed eyes, possesses hooks on ischia of the third pereiopods only, and occurs in epigean habitats roughly 230 miles south of the known range of *O. inermis testii.* Future genetic analysis planned for *O. pagei* and other members of the genus will shed new light on interspecific and intersubgeneric relationships within *Orconectes* and possibly determine whether this unique species deserves its own subgeneric status.

Acknowledgments

We are grateful to J. W. Armbruster, T. J. Near, and J. M. Serb for field assistance. We are also indebted to K. Reed for graciously providing records from and access to the crustacean collections at the National Museum of Natural History, Smithsonian Institution. Special thanks to K. S. Cummings for photographic assistance with Fig. 2.

Literature Cited

Cope, E. D. 1872. On the Wyandotte Cave and its fauna.—American Naturalist 6(7):406–422.

Faxon, W. 1914. Notes on the crayfishes in the United States National Museum and the Museum of Comparative Zoölogy with descriptions of new species and subspecies to which is appended a catalogue of the known species and subspecies.—Memoirs of the Museum of Comparative Zoölogy at Harvard College 40(8):351–427.

Fitzpatrick, J. F., Jr. 1987. The subgenera of the crawfish genus *Orconectes* (Decapoda: Cambaridae).—Proceedings of the Biological Society of Washington 100:44–74.

Girard, C. 1852. A revision of the North American Astaci, with observations on their habits and geographical distribution.—Proceedings of the Academy of Natural Sciences of Philadelphia 6: 87–91.

Hay, W. P. 1891. The crustaceans of Indiana.—Proceedings of the Indiana Academy of Science 1891:147–150.

———. 1902. Observations on the crustacean fauna of Nickajack Cave, Tennessee, and vicinity.—Proceedings of the United States National Museum 25(1292):417–439.

Hobbs, H. H., Jr. 1948. A new crayfish of the genus *Orconectes* from southern Tennessee (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 61(15):85–91.

———, & T. C. Barr, Jr. 1972. Origins and affinities of the troglobitic crayfishes of North America (Decapoda: Astacidae), II: genus *Orconectes*.—Smithsonian Contributions to Zoology 105.

Rhoades, R. 1941. Notes on some crayfishes from Alabama caves, with the description of a new species and a new subspecies.—Proceedings of the United States National Museum 91(3129):141–148.

———. 1944. The crayfishes of Kentucky, with notes on variation, distribution and descriptions of new species and subspecies.—American Midland Naturalist 31:111–149.

Tellkampf, T. A. 1844. Ausflug nach der Mammuthhöhle in Kentucky.—Das Ausland. 168:671–672; 169:675–676; 170:679–680; 171:683–684; 172:687–688; 173:691–692; 174:695–696; 175:699–700.

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A new crawfish of the genus *Distocambarus*, subgenus *Fitzcambarus* (Crustacea: Decapoda: Cambaridae) from South Carolina

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Abstract.—A new crawfish, *Distocambarus* (*Fitzcambarus*) *hunteri,* is described from an apparently limited distribution in the Saluda River basin of South Carolina, U.S.A. The new species is distinguished by a large bladelike central projection and a mesial process that extends about half the length of the central projection; the mesial margin of the palm in males is shorter than the width of that structure and the postannular sternite of females is subequal in length to the annulus ventralis. The closest relative to the new species seems to be *D.* (*F.*) *youngineri* Hobbs & Carlson.

In the lengthy paper containing the description of *Procambarus* (*Distocambarus*) *devexus,* later to become the first member of the genus *Distocambarus,* Hobbs (1981: 308–309) commented on the serendipitous discovery of the initial specimens. Despite 40 years of intense collecting in Georgia, he had never encountered the species and was "reasonably certain" that the first juveniles collected were members of *Cambarus* (*Depressicambarus*) *latimanus* (LeConte 1856). Subsequent collecting, particularly by Dr. Paul Carlson in South Carolina, demonstrated sufficient diversity prompting Hobbs & Carlson (1983) to elevate the subgenus *Distocambarus* to a generic rank, which Hobbs (1983) then divided into two subgenera. By 1985 when Carlson had moved from South Carolina and Hobbs' advancing age had curtailed his field activities, the number of known species had risen to four (Hobbs 1989; Hobbs & Carlson 1985). All members of the genus are primary burrowers of somewhat limited distributions, which probably explains why so few records existed for a genus that not only displays unexpected diversity but also occurs in two different watersheds (Saluda and Savannah) in Georgia and South Carolina.

In 1994 the second author collected several burrowing crawfishes as part of a study of the rare crawfish species of South Carolina. He sent them to the first author for identification, and among them was a fifth member of *Distocambarus.*

In the text that follows, the following abbreviations are used: TCL, total carapace length; PCL, postorbital carapace length; TU, Tulane University Museum of Natural History, Belle Chasse, LA; USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UADC, University of Alabama Decapod Collections, Tuscaloosa, AL.

Distocambarus (*Fitzcambarus*) *hunteri,* new species

Fig. 1

Diagnosis.—Pigmented; eyes small, faceted. Rostrum subspatulate with tiny, beadlike acumen and lacking marginal spines. Carapace rarely with single cervical spine or tubercle on one or both sides, spine usually absent. Branchiostegal spines small but acute. Suborbital angle small to obtuse. Areola 37.1% to 47.9% (avg. 40.9%) of TCL, 43.5% to 54.1% (avg. 47.8%) of PCL; 10.5 to 14.8 (avg. 13.1) times longer than wide, with 1 or 2 punctations across narrowest part. Chela width less than length of mesial margin of palm, with row of 6 to 9 tubercles, flanked dorsolaterally by second row of 3 to 7 spiniform to squamiform tubercles; dactyl of Form I male about 1.3 times length of mesial of palm, and chela 68.8% to 74.5% (avg. 69.4%) of TCL; length of carpus greater than inner margin of palm. First pleopod of Form I male with small but distinct shoulder somewhat proximal to cephalic base of corneous, platelike, subquadrangular central projection, which projection oriented about 45° distolaterally to main axis of appendage; mesial process tapering from base to acute tip, noncorneous, extending distally about half distance of central projection; cephalic process only suggested by swelling near cephalomesial base of central projection; distal third of appendage inclined caudad; proximomesial base of pleopod usually with tiny spur.

Annulus ventralis of female with cephalomedian margin membraneous, allowing hingelike motion; annulus much elevated (ventrally) except for cephalomedian excavation; sinus originating near midline in cephalic third, then transcribing gentle arc to be lost just before reaching caudal margin. Postannular sclerite subtriangular, and subequal in length to annulus; first pleopods represented by tubercles at best. (Measurements of type specimens in Table 1.)

Description of holotypic male, form I.—Cephalothorax (Fig. 1*b, f*) subovate, compressed laterally; maximum width of carapace 1.1 times height at caudodorsal margin of cervical groove; abdomen slightly narrower than carapace. Areola 13.1 times longer than wide with only one punctation in narrowest part. Cephalic section of carapace 1.6 times length of areola, latter constituting 38.3% of TCL (46.7% of PCL). Carapace mostly punctate, except sparse granulose tuberculations in extreme cephalolateral region. Rostrum broadly spatulate, with apex produced into tiny, tuberculate acumen reaching distal margin of ultimate podomere of antennular peduncle; rostrum moderately depressed. Subrostral ridge moderately developed and evident in dorsal aspect to near midlength of rostrum. Suborbital angle obtuse but evident; branchiostegal spine small but acute. Fifth abdominal pleuron gently rounded distally with no evidence of acute caudo- or cephaloventral angles. Telson with single fixed acute spine in each caudolateral corner of cephalic portion. Epistome (Fig. 1*k*) with cephalic lobe broadly subtriangular, about as wide as long, with small cephalomedian projection; margins of lobe slightly elevated (ventrally)

Table 1.—Measurements (mm) of type specimens of *Distocambarus* (*Fitzcambarus*) *hunteri,* new species. The asterisk (*) indicates an estimation; left branchiostegite broken.

	Holotype	Allotype	Morphotype
Carapace			
Height	11.5	11.4	12.5
Width	12.4	12.1	13.0*
Entire length	27.4	25.9	27.6
Postorbital length	22.5	22.0	23.9
Areola			
Width	0.8	0.8	0.9
Length	10.5	10.4	10.4
Rostrum			
Width	7.5	6.1	6.3
Length	5.2	5.3	5.1
Chela			
Length of mesial margin of palm	7.9	5.7	7.0
Width of palm	6.9	6.0	6.5
Length of lateral margin	18.3	14.0	16.3
Length of dactyl	9.9	8.6	9.1
Carpus of cheliped			
Width	4.7	5.8	5.6
Length	8.9	7.1	7.3
Abdomen			
Width	10.4	11.2	10.2
Length	21.2	22.3	22.9

and obtuse submedian longitudinal fovea at caudal union of lobe with main body; epistomal zygoma broadly arched. Antennular peduncle lacking spine on ventral surface of proximal podomere; antennal peduncle with spine on ventral surface of basal podomere reduced to tubercle; tip of flagellum reaching nearly to caudal margin of carapace. Antennal scale (Fig. 1*g*) about 1.5 times longer than wide, widest slightly distal to midlength, lateral portion thickened and ending distally in small but stout spine; greatest width of lamellar area 1.8 times width of thickened lateral area.

Third maxilliped with palpus, when extended, reaching nearly to distal margin of antennal peduncle; ventromesial surface of ischium with dense mat of long stiff setae occurring in tufts, which mat completely obscuring dentate opposable margin.

Right chela (Fig. 1*i*) subelliptical in section, strongly depressed, palm somewhat narrower than length of mesial margin of palm; length of latter 44.5% of total length of chela; most of palm studded with squamous and subsquamous tubercles; mesial margin of palm with row of 8 tubercles, flanked dorsally by less developed row of 5 tubercles. Both fingers with well defined dorsomedian ridges flanked by setiferous punctations. Opposable margin of fixed finger with row of 4 subequal tubercles along proximal third of finger and single row of minute denticles lying between tubercles and reaching to base of corneous tip of finger; additional prominent tubercle ventral to denticle row just distal to midlength of finger; lateral margin weakly costate. Opposable margin of dactyl with 2 large tubercles in proximal third, distalmost distinctly larger, with single row of minute denticles extending from tubercles to base of corneous tip of finger; mesial margin with 2 weak squamous tubercles in basal portion, followed by indistinct row of setiferous punctations; setae of ventrolateral punctations of margin not conspicuously long or stiff.

Carpus of cheliped 1.1 times length of inner margin of palm; dorsal surface sparsely punctate, with slightly sinuous sulcus; mesial surface with 4 subacute spiniform tubercles in proximal half, flanked dorsally by 3, more rounded, tubercles; ventral margin with stout subspiniform distolateral tubercle, and weak squamous tubercles in mesial corner, lateral one articulating with condyle on propodus.

Merus with small dorsodistal subspiniform tubercle and tuberculate ventral margins, lateral row of 9 irregular tubercles and mesial row of 12, tubercles of both rows increasing in size distally. Ischium with row of 5 tubercles along mesial margin; sufflamen absent.

Chela of second pereiopod with conspicuous row of long stiff setae on lateral and mesial margins; carpus with similar row on mesial margin, lateral margin with few long setae; merus with only single tuft of about 10 long setae situated on dorsomedian margin. Hook on ischium of third pereiopod (Fig. 1*l*) stout but simple, slightly overreaching basioischial articulation and not opposed by strong tubercle on basis. Coxae of all pereiopods except first with conspicuous tufts of plumose setae masking sternal and coxal features; small rounded caudomesial eminence on fourth periopodal coxa.

First pleopods (Figs. 1*a, c, b*) symmetrical, bases not contiguous, tips reaching coxae of third pereiopods when abdomen flexed; prominent caudoproximal and proximomesial lobes present; pleopods flexed slightly distal to midlength and lacking subapical setae. Terminal elements as in "Diagnosis."

Mesial lobe of proximal podomere of uropod bearing acute spine, spine lacking on lateral lobe; mesial ramus with distomedian spine, spine small and not reaching distal margin.

Description of allotypic female.—Except for secondary sexual characters, differing from holotype in following respects: Branchiostegal spine more prominent; areola with 2 punctations in narrowest part; tuberculations of upper surface of chela more

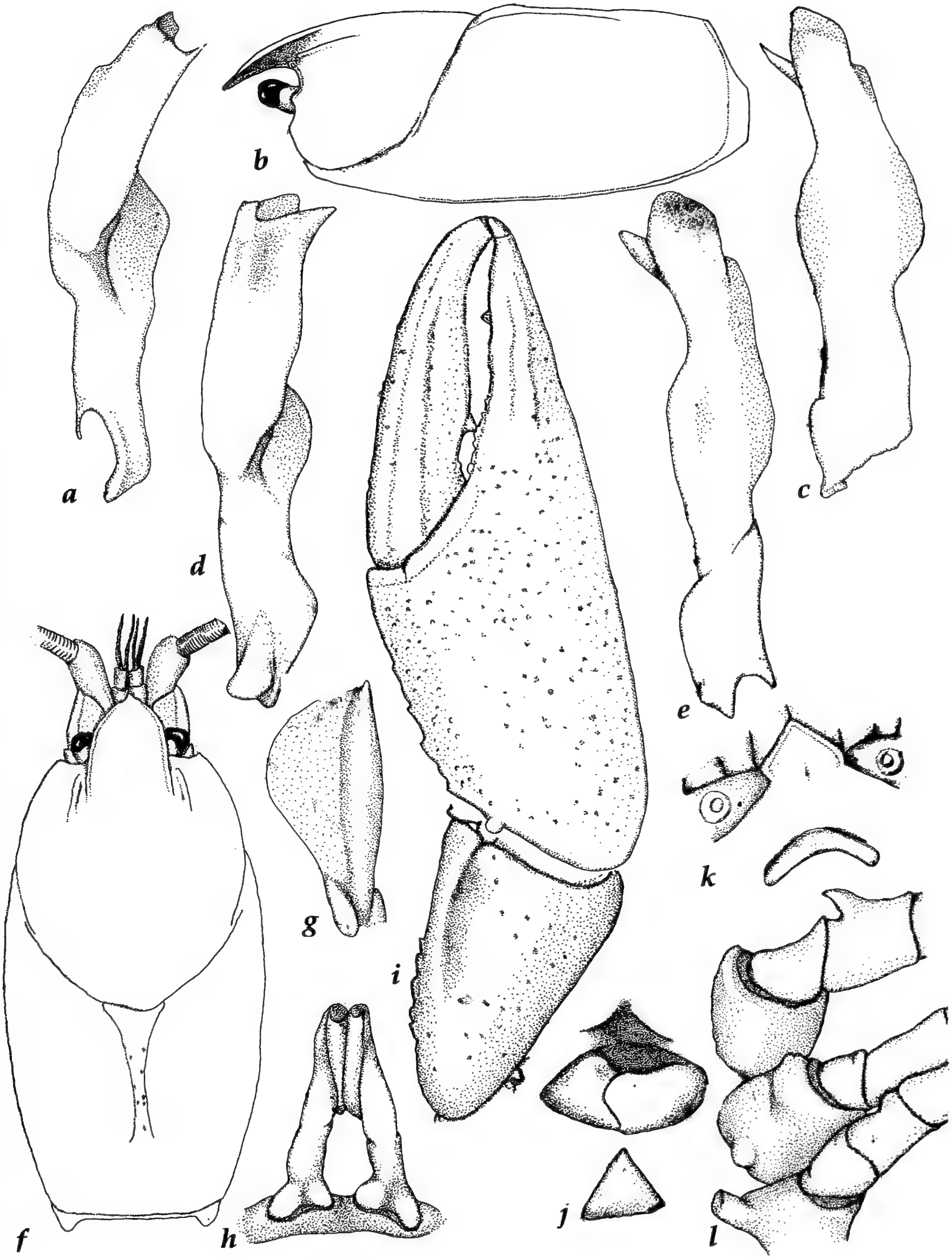

Fig. 1. *Distocambarus* (*F.*) *hunteri*, new species (all from holotypic male, Form I, except *d, e* from morphotypic male, Form II, and j from allotypic female): *a, d,* Mesial aspect of first pleopod; *b,* Lateral aspect of carapace; *c, e,* Lateral aspect of first pleopod; *f,* Dorsal aspect of carapace; *g,* Antennal scale; *h,* Caudal aspect of first pleopods; *i,* Dorsal aspect of distal podomeres of cheliped; *j,* Annulus ventralis and adjacent sternites; *k,* Epistome; *l,* Ventral aspect of proximal podomeres of left third through fifth pereiopods.

sparse. Sternal sclerites of third and fourth pereiopodal segments broadly excavate and densely setose laterally; setae of coxa and sternite of second segment shorter and less dense.

Annulus ventralis (Fig. 1*j*) broadly excavate cephalically and movable through arc of about 15 to 20°; 1.8 times wider than long; sinus arising in fossa. Postannular sclerite about 40% width of annulus; cephalic portion somewhat overreaching sternite of antecedent segment. First pleopods absent.

Description of morphotypic male, form II.—Except in secondary sexual characters, differing from holotype in following respects: Areola with 2 punctations in narrowest part; mesial margin of palm with row of 5 tubercles, flanked dorsally by second row of 5; both lobes of proximal podomere of uropod with acute spine, that of lateral lobe tiny; tuberculation of upper surface of chela intermediate between holotype and allotype.

Hook on ischium of third pereiopod represented by large but low tubercle and not overreaching more proximal segment. First pleopods (Figs. 1*d, e*) with incomplete juvenile suture delineating basal part; terminal elements much more blunt than those of form I male and noncorneous.

Color notes.—Ground color varies from lighter brown in recently molted individuals to darker brown in older intermolt ones. Staining from burrow soils and groundwater apparently masks exoskeleton colors. Cephalic sections of carapace more uniformly brown and less mottled than thoracic sections; mottling fading to reddish brown posteriorly in cephalic section and ventrally in thoracic section. Ground color of abdomen lighter than that of carapace; terga with paired, almost black, elongate spots, which become smaller and less obvious caudally; pleura with similarly colored markings giving appearance of stripe above lighter brown lateral margins; telson and uropods lacking distinct markings, and of lighter color than other abdominal segments. Distal portion of merus and carpus of cheliped ash brown and bearing dark brown tubercles; dorsal surface of palmar area of propodus paler brown; fingers of chela with reddish brown to red finger tips; movable finger darker of the two. Remaining pereiopods bluish to ash brown with more flesh-colored bases. Ventral surface of abdomen and pleopods brown to flesh-colored.

Specimens held in laboratory and fed artificial formulated diet retain the mottled appearance and abdominal markings. However, ground color of these animals has a distinctly blue hue, blue replaces brown in the chelipeds, and other pereiopods are pale blue. Ventral surfaces of the pereiopods are tan to bluish cream and the ventral abdomen is a pale blue. These observations are compatible with the suggestions put forth by Fitzpatrick (1987) concerning the effect of diet, and perhaps light, on coloration.

Disposition of types.—The holotypic male, Form I, the allotypic female, and the morphotypic male, Form II are in the collections of the National Museum of Natural History, USNM (282786, 282787, and 282788, respectively); paratypic series are in the Tulane Museum of Natural History (TU 6746, 1 ♂I, 1 ♀, 1 ♂imm; TU 6747, 2 ♀, 2 ♀imm) and the University of Alabama (UADC 450.01, 1 ♂II, 1 ♀; UADC 451.01, 1 ♂I, 1 ♀).

Type locality.—Burrows in runoff drainage just west of State Route 391 at junction of State Route 194; 34°05′26.8″N, 81°34′88.1″W; Saluda River drainage, Saluda Co., South Carolina. Here the sandy substrate was wet (water table <15 cm) from recent rains, but numerous chimneys were evident among the thick mat of roots from associated vegetation. Except for one female that was associated with recently released young, each burrow was occupied by a single animal, and the creatures were actively moving in the burrow. The overstory was composed of loblolly pine (*Pinus taeda*), red maple (*Acer rubrum*), willow oak (*Quercus phellos*), and American elm (*Ul-*

mus americana); the midstory was red maple and dogwood (*Cornus florida*); and the understory was red oak seedlings (*Q. falcata*), sumac (*Rhus glabra*), honeysuckle (*Lonicera* sp.), smilax (*Smilax* sp.), American holly (*Ilex americana*), and grapevine (*Vitis* sp.). At the type locality, one specimen of *Cambarus* (*Depressicambarus*) *latimanus* was collected from a burrow.

Range and specimens examined.—This species seems to be confined to a very limited portion of the Saluda drainage in Saluda County, South Carolina. This is not wholly surprising. It closest relative, *Distocambarus* (*Fitzcambarus*) *youngineri* Hobbs & Carlson 1985, likewise has a very limited distribution, being confined to Newberry County, just north of the Saluda River (Hobbs & Carlson 1985, Eversole 1995). The other members of the genus all have limited distributions. During the course of this study, the second author conducted extensive searches throughout the upper portions of the several drainages associated with the southern part of the state and no other collections of this species were found. Several other burrowing species, including other *Distocambarus* spp. were recorded, however.

Fourteen specimens from the type locality have been studied (counts below), plus four juveniles kept alive in the laboratory for collection of maturation data. The second site produced two adults.

Saluda County, South Carolina: (1) type locality, 1 ♂II, 1 ♀, 24 Sep 1994, A. G. Eversole, C. D. Baumann, colls.; 1 ♂II, 1 ♀, 1 ♂imm, 2 ♀imm, 18 Oct 1995, A. G. Eversole et al., colls.; 2 ♂I, 3 ♀, 1 ♂imm, 1 ♀imm, 20 Nov 1995, A. G. Eversole et al., colls.; (2) burrows on W side of Wyses Ferry Rd, about 0.6 mi N of St Rte 194, 1 ♂I, 1 ♀, 4 Oct 1994, C. J. Kempton and C. D. Baumann, colls.

Variations.—The small sample, almost all from the same locality, gave little information on variation beyond that encompassed by the descriptions of the primary types. Most conspicuous, as is usual, was the varying numbers and types of tuberculation associated with the podomeres of the pereiopods; additional collections from other sites may indicate a wider range of expression of other characters.

Size and life history notes.—The largest specimen was a form I male of 29.4 mm TCL (25.6 mm PCL); the smallest mature animal, a female, was 18.0 TCL (14.0 mm PCL). No ovigerous females or females bearing young were collected, although a female collected on 18 October 1995 and another on 20 November 1995 each had recently released young in its burrow, the only recorded instances, save one noted below, of an adult animal sharing its burrow. Form I males were collected in October and November.

Ecological notes.—*Distocambarus* (*Fitzcambarus*) *hunteri* is a primary burrower and as characteristic of other members of the genus, the burrows extend to the water table. Under some circumstances, vertical shafts of the burrows may reach more than a meter in depth and the main burrow may have an array of side shafts connecting with the surface at capped openings. Many of the burrow shafts were adjacent to tree and shrub roots, making excavation difficult. Freshly capped burrows appeared as if the crawfish individually stacked uniformly made balls (approximately 5 to 6 mm diam) of excavation material into a chimney shaped mound. The chimneys reached 10 mm in height in some cases, but both the architecture and chimney height were subject to weathering. Although weathered chimneys appeared as only a clod of excavated soil, their different color was noticeable against the forest floor. The species seems to be a solitary animal because on only one occasion (Oct) was more than one adult (1 ♂I, 1 ♀) excavated from a burrow. On two occasions, however, a female was collected from a burrow that contained free-ranging juveniles, eight in one burrow and six in the other. Unfortunately, all of our collections come from September through November, and it is not possible to say that recruitment occurs solely in the fall of the year. The exoskeleton on the specimen collected on 10 October 1995 appeared soft, a sign that crawfish were rapidly growing and molting at that time of year. The preferred habitat seems to be a mixed pine-hardwood woodland, with a comparatively high water table.

Relationships.—This crawfish is most closely related to *D.* (*F.*) *youngineri,* the nearest populations of which occur about 9.5 airmi (15.3 air km) northwest of the sites where *D. hunteri* is found. The pleopods of the Form I males are quite similar, both having a large subquadrangular central projection that is bladelike and oriented somewhat oblique to the cephalocaudal axis of the appendage. In *D. hunteri,* the central projection is disposed mesially almost 45° to this axis, whereas in *D. youngineri* it is disposed about 30°. The cephalic process of *D. hunteri* is scarcely recognizable, but is usually visible, albeit as a vestigial structure, in *D. youngineri.* The mesial process of the new species extends only half as far distally as does the central projection, while in *D. youngineri* the process extends at least two-thirds as far. The areola of *D. hunteri* is wider and, accordingly, frequently has an extra punctation in its narrowest part. In *D. hunteri* the areola is 10.5 to 14.8 (avg. 13.1) times longer than wide and it constitutes 37.1% to 47.9% (avg. 40.9%) of TCL. The comparable numbers in *D. youngineri* are 13.0 to 24.0 (avg. 17.6) and 37.6% to 41.9% (avg. 38.9%) of TCL. The branchiostegal spine, usually absent or extremely obtuse in *D. youngineri,* is small but evident in *D. hunteri.* In Form I males of the latter, the second tubercle of the opposable margin of the dactyl is distinctly larger than the more proximal one, and the mesial margin of the palm is longer than the palm is wide. In *D. youngineri,* the primary tubercles of the opposable margin of the dactyl are subequal in size, and the mesial margin of the palm is shorter than the palm width. The ventral surface of the ischium of the third maxilliped of *D. hunteri* is provided with so dense a mat of long stiff setae that the denticulate opposable margin is completely obscured. In the female, the cephalomedian margin of the annulus ventralis is less deeply and widely excavate, and a less extensive membranous area permits a movement through an arc of 15° to 20°, as opposed to 30° to 45° in *D. youngineri.* In the new species, too, the sternite between the fourth pereiopods is broadly excavate, rather than having a fissure-like configuration. Females of *D. hunteri* can also be distinguished by the much longer postannular sclerite that is subequal in length to the annulus and is subtriangular in outline. The large, bladelike central projection of the first pleopod of the first form male, coupled with the comparative length of the mesial process, will serve to separate *D. hunteri* from the other members of the genus. Several features of the new species (e.g., the ratio of palm width to mesial margin length, areola width, and postannular sclerite of females) may require a redefinition of the subgenus, but we deem it prudent to defer such until more specimens of the several species are available to permit a greater appreciation of the limits and extent of variation.

Etymology.—This crawfish is named in honor of Dr. W. D. Russell-Hunter, formerly of the Department of Biology, Syracuse University, Syracuse, New York, and the Marine Biology Laboratory, Woods Hole, Massachusetts, for his friendship, support and guidance during the formative years of the second author's education. We are pleased to propose this taxon honoring Dr. Russell-Hunter for all his contributions to invertebrate zoology.

Acknowledgments

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Literature Cited

Eversole, A. G. 1995. Distribution of three rare crayfish species in South Carolina, USA.—Freshwater Crayfish 8:113–120.

Fitzpatrick, J. F., Jr. 1987. Notes on the so-called "blue color phase" in North American cambarid crawfishes (Decapoda, Astacoidea).—Crustaceana 52:316–319.

Hobbs, H. H., Jr. 1981. The crayfishes of Georgia.—Smithsonian Contributions to Zoology 318:1–549.

———. 1983. *Distocambarus* (*Fitzcambarus*) *carlsoni,* a new subgenus and species of crayfish (Decapoda: Cambaridae) from South Carolina.—Proceedings of the Biological Society of Washington 96:429–439.

———. 1989. An illustrated checklist of the American crayfishes (Decapoda: Astacidae, Cambaridae, and Parastacidae).—Smithsonian Contributions to Zoology 480:1–236.

———, & P. H. Carlson. 1983. *Distocambarus* (Decapoda: Cambaridae) elevated to generic rank, with an account of *D. crockeri,* new species from South Carolina.—Proceedings of the Biological Society of Washington 96:420–428.

———, & ———. 1985. A new member of the genus *Distocambarus* (Decapoda: Cambaridae) from the Saluda Basin, South Carolina.—Proceedings of the Biological Society of Washington 98:81–89.

LeConte, J. 1856. Description of new species of *Astacus* from Georgia.—Proceedings of the Academy of Natural Sciences of Philadelphia 7:400–402.

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Neogonodactylus campi, a new species of stomatopod crustacean from the Caribbean Sea, with additional records for *N. caribbaeus* (Schotte & Manning)

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Abstract.—*Neogonodactylus campi*, a sublittoral species, is described from two localities in the Caribbean Sea. It is the second western Atlantic species to be recognized that has both dorsal spinules on the telson and a spined posterolateral angle on the fifth abdominal somite. It differs from *N. caribbaeus* (Schotte & Manning) in having much shorter anterior submedian carinae on the telson and a longer basal portion on the rostral plate. The first records for *N. caribbaeus* from Florida and the Bahamas are provided.

Recognition of a new species of *Gonodactylus* from Tobago (Schotte & Manning 1993) that resembled *G. spinulosus* Schmitt in having some of the carinae of the telson armed with dorsal spinules prompted me to reexamine all of the material in the crustacean collections of the National Museum of Natural History identified as *G. spinulosus*. The new species described below was found among that material, as were the additional specimens of *Neogonodactylus caribbaeus* listed below, most of which had been identified as *G. spinulosus* in Manning (1969).

All of the American species formerly referred to *Gonodactylus* were transferred to the genus *Neogonodactylus*, type species *Gonodactylus oerstedii* Hansen, 1895, by Manning (1995).

Abbreviations used in the account below include: AWCLI, abdominal width-carapace length index (abdominal width divided by carapace length × 100), fm (fathoms), ft (feet), leg. (collector), m (meters), mm (millimeters), n (number), sta (station).

All of the specimens are in the crustacean collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The number following the number of specimens is total length, measured on the midline.

Neogonodactylus campi, new species
Figs. 1, 2

Material.—Dominican Republic: Navidad Bank, 20°11′N, 68°52′W, depth 14–15 fm (26–27 m), 8 ft tumbler dredge, M/V *Oregon* sta 5474, 12 Jun 1965: 1 ♀, 36 mm (holotype, USNM 126013).—Off Navidad Bank, 20°04′N, 68°53′W, depth 20–24 fm (37–44 m), 8 ft tumbler dredge, M/V *Oregon* sta 5471, 12 Jun 1965: 1 ♀, 28 mm (paratype, USNM 126014).

St. Lucia: West of Pointe du Cap, 14°06′N, 61°05′W, depth 16 fm (29 m), tumbler dredge, M/V *Oregon* sta 5946, 8 Mar 1966: 1 ♂, 26 mm (paratype, USNM 126034).

Diagnosis.—Size relatively small, total length of adults less than 40 mm. Rostral plate slightly longer than broad, basal part obtusely rounded anterolaterally, anterior margins sloping to slender median spine, latter more than 1.5 times as long as basal part of plate. Ocular scales relatively broad, flattened, separate. Thoracic somites lacking dark pigment dorsally. Ab-

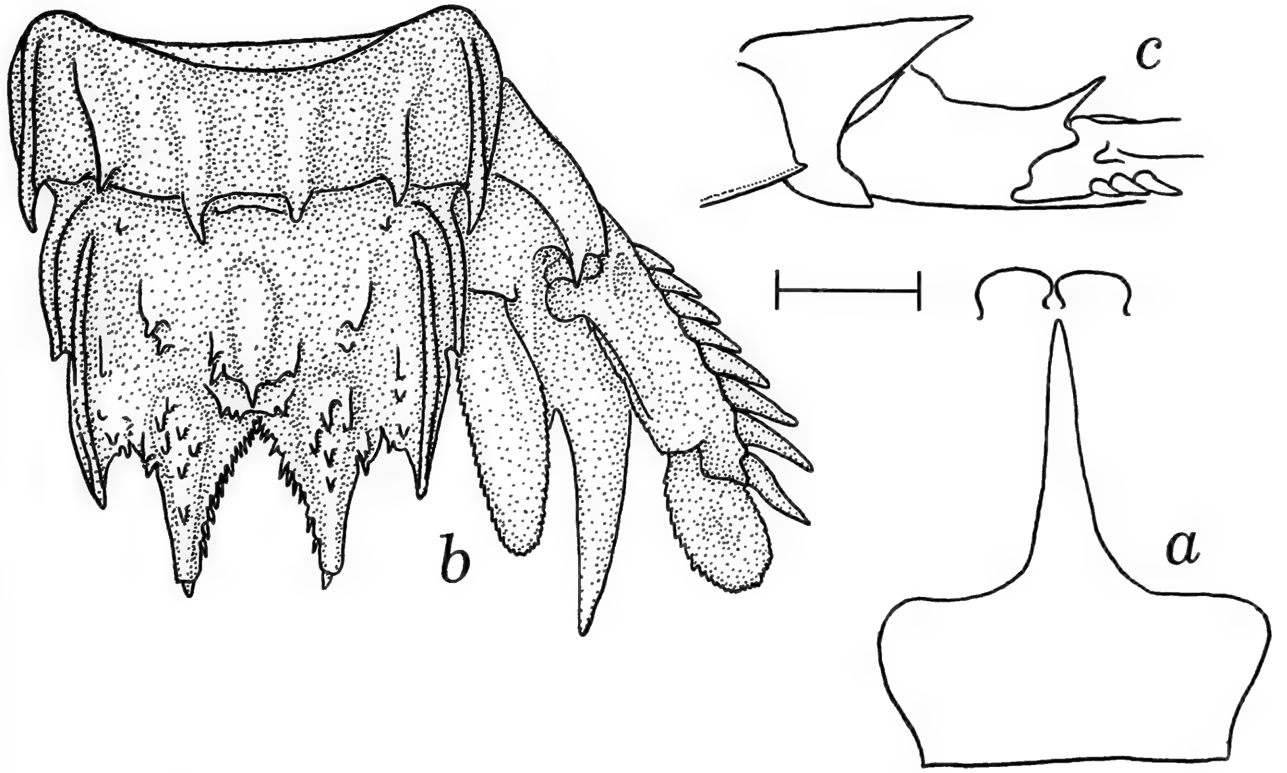

Fig. 1. *Neogonodactylus campi,* new species, female holotype, 36 mm. *a,* Rostral plate and ocular scales; *b,* Sixth abdominal somite, telson and right uropod, dorsal view (distalmost uropod spine hidden by distal segment of exopod); *c,* Fifth abdominal somite, lateral view. Scale = 1 mm (*a*), 2 mm (*b, c*).

domen lacking distinctive dark pigment dorsally; anterior 4 somites unarmed posterolaterally, fifth somite with sharp posterolateral spines; sixth somite with 6 carinae, each with sharp posterior spine; AWCLI of male 852, of females 857. Telson of oerstedii-type, with dorsal tubercles on carinae, latter sharp, intermediates cristate in female; anterior tubercles of telson each produced into erect spinule; median carina ending in sharp spine; accessory median carinae forming anchor posteriorly, extending anteriorly about ⅓ length of median carina, with 1–3 dorsal and no posterior tubercles; knob evenly rounded, with 4–5 tubercles; anterior submedian carinae short, not extending posteriorly beyond bases of accessory medians, with terminal spine followed posteriorly by single sharp, erect tubercle; submedian marginal teeth slender, movable apices present, with 3–7 sharp dorsal tubercles, inner margin lined with spiniform denticles; carina of intermediate tooth cristate, usually unarmed (with 5–6 spinules in 1 specimen only); accessory intermediate carinae cristate, with 1–5 spines dorsally, 1 usually terminal; inner intermediate denticle with short dorsal carina, spined posteriorly, both intermediate denticles with sharp apical spinule; lateral teeth sharp, unarmed dorsally. Uropod with 9–11 graded, movable spines laterally.

Size.—Total lengths of male (n = 1), 26 mm; of females (n = 2), 28 and 36 mm. Other measurements of female holotype, total length 36 mm: carapace length 7.7 mm; rostral plate length 2.8 mm, width 2.5 mm; fifth abdominal somite width 6.6 mm; telson length 5.5 mm, width 5.3 mm.

Remarks.—*Neogonodactylus campi* is the second species to be recognized from localities in the western Atlantic in which: (a) the fifth abdominal somite is armed posterolaterally; (b) some dorsal carinae of the telson are armed with sharp spinules or tubercles; and (c) there are no patches of dark pigment on the sixth thoracic somite and abdomen. In these features it resembles *N.*

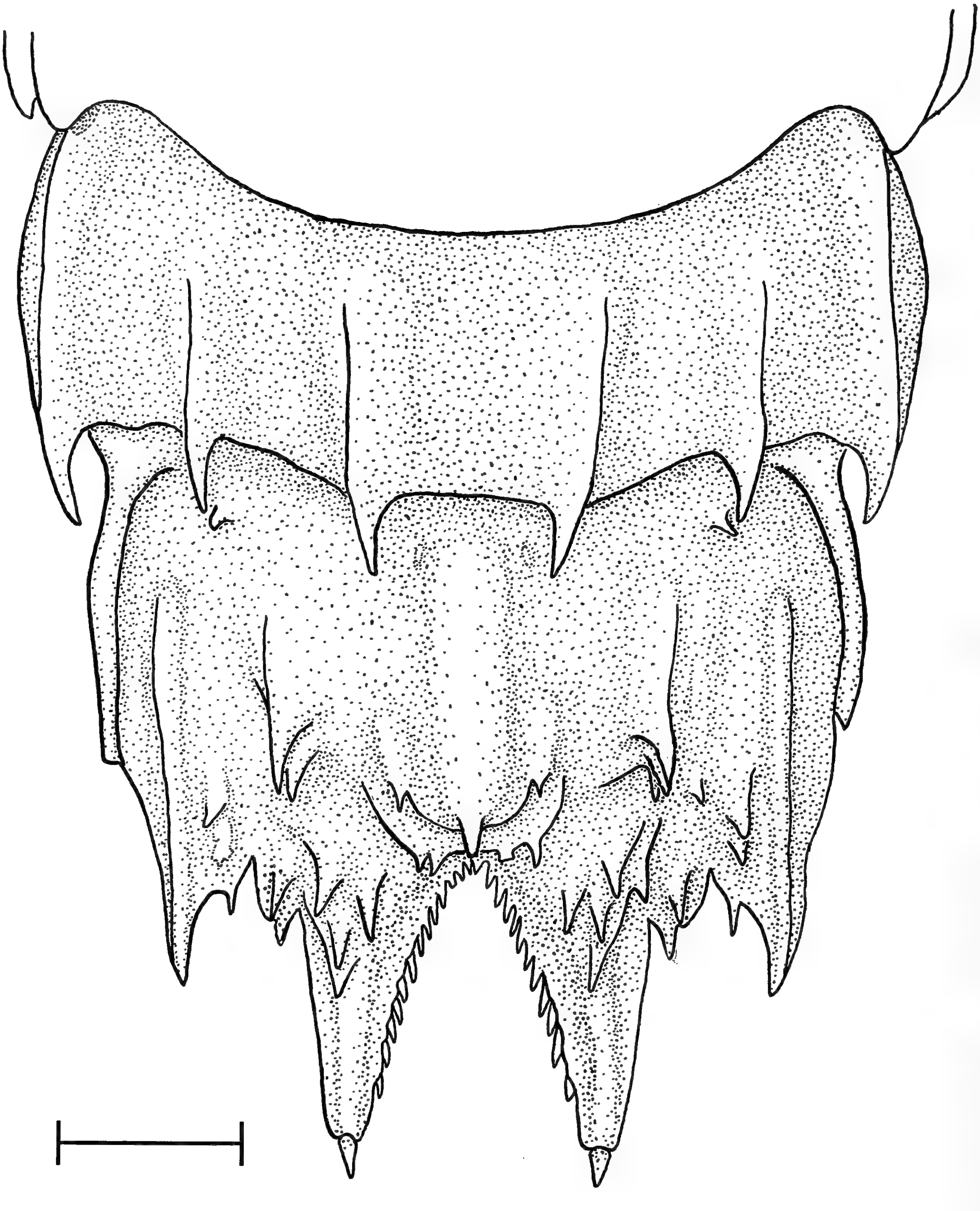

Fig. 2. *Neogonodactylus campi,* new species, female paratype, 28 mm. Telson, dorsal view. Scale = 2 mm.

caribbaeus (Schotte & Manning, 1993) and differs from *N. spinulosus* (Schmitt, 1924). It differs from *N. caribbaeus* in having shorter anterior submedian carinae on the telson armed with a posterior spine, followed posteriorly by a sharp tubercle, as well as a longer basal part of the rostral plate. *Neogonodactylus campi* differs from *N. minutus* (Manning, 1969), the only other species in the western Atlantic with spinules or tubercles on the dorsal carinae of the telson, in having many more dorsal tubercles on those carinae.

Variation in size and distribution of dorsal tubercles on the telson of two different females is shown in Figs. 1b and 2.

Etymology.—Named for my colleague and friend David K. Camp, Florida Depart-

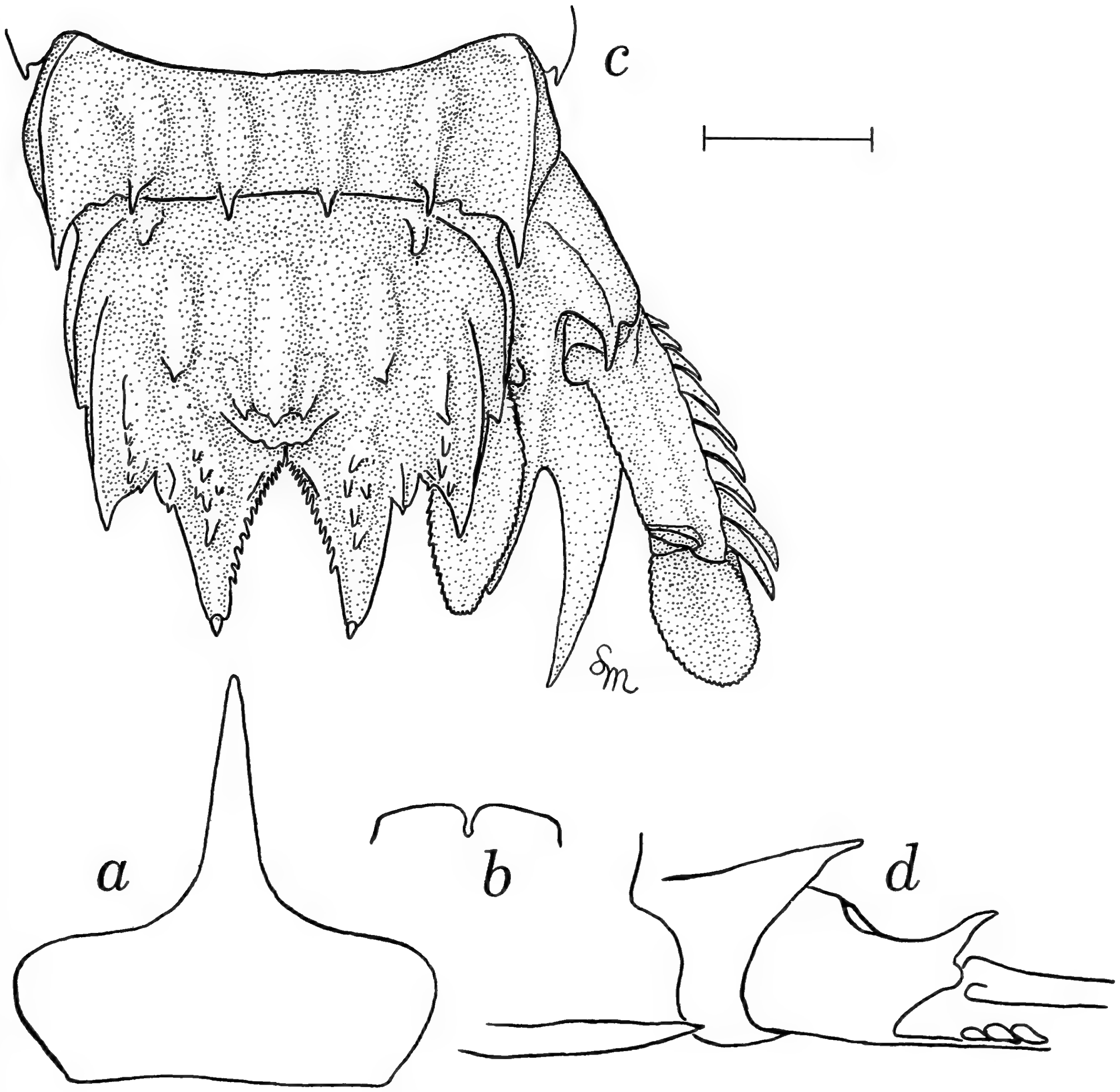

Fig. 3. *Neogonodactylus caribbaeus* (Schotte & Manning), Florida, female, 36 mm. *a,* Rostral plate; *b,* ocular scales; *c,* sixth abdominal somite, telson, and uropod; *d,* posterolateral angle of fifth abdominal somite, sixth abdominal somite, and base of uropod, lateral view. Scale = 1 mm (*a, b*), 2 mm (*c, d*).

ment of Environmental Protection, Florida Marine Research Institute, St. Petersburg, Florida. David has added much to our knowledge of the diverse and important marine invertebrate fauna of Florida through his own research on stomatopods and other groups, and through his efforts to have the extensive Hourglass collections of invertebrates studied by others and published by the Institute under his guidance. Recognition of his contributions to our knowledge of systematics of marine crustaceans is long overdue.

Neogonodactylus caribbaeus
(Schotte & Manning, 1993)
Fig. 3

Gonodactylus spinulosus.—Manning, 1969: 299 [part, all specimens listed below except for those from the Bahamas; not *G. spinulosus* Schmitt, 1924].

Gonodactylus caribbaeus Schotte & Manning, 1993:568, fig. 1.

Material.—Florida: Monroe County, ¼ mile (ca 400 m) south–southwest of Alligator Reef Light [24°51′N, 80°38′W], depth

15 ft (about 5 m), leg. W. A. Starck, II, 26 Aug 1961: 1 ♀, 36 mm (USNM 124639).—200 yards (ca 183 m) southwest of Alligator Reef Light, depth 15–20 ft (4.6–6 m), leg W. A. Starck, II, 7 Jan 1962: 1 ♂, 25 mm (USNM 119320).

Bahama Islands: Providence Channel, off Abaco Island, 25°50′N, 77°10′W, depth 12 fm (22 m), R/V *Silver Bay* sta 5133, 1 Oct 1963: 1 ♂, 30 mm, 1 ♀, 21 mm (USNM 126033).

U.S. Virgin Islands: St. John, Coral Harbor, base of Coral Bay (18°21′N, 64°43′W), leg. L. P. Thomas, 20 Dec 1958: 1 ♂, 25 mm (USNM 124636).

Barbuda: Martello Tower (13°53′N, 60°53′W), reefs off south coast, Smithsonian-Bredin Expedition sta 92-56, leg. D. V. Nicholson, 7 Apr 1956: 2 ♀♀, 17 and 20 mm (USNM 124633).

Mexico: Quintana Roo, Ascension Bay (19°40′N, 87°30′W), behind central part of Nicchehabin Reef, Smithsonian-Bredin Expedition sta 67–60, 13 Apr 1960: 1 juvenile ♀, 14 mm (USNM 124634).—Same locality, depth 4–6 ft (1–2 m), Smithsonian-Bredin Expedition sta 72-60, 14 Apr 1960: 1 juvenile ♀, 12 mm (USNM 124635).

Size.—Total lengths of males ($n = 3$), 25–30 mm; of females ($n = 6$), 12–36 mm. The specimens studied by Schotte & Manning (1993) were up to 33 mm long.

Remarks.—The material reported here extends the range of this species from Tobago in the southern Caribbean to other localities in the Caribbean, and provide the first records for the species from Florida, the Bahamas, the U.S. Virgin Islands, Barbuda, and Mexico.

In addition to differing from *N. campi* in having longer anterior submedian carinae on the telson, extending posteriorly beyond the bases of the accessory median carinae and less produced posterior spines on the anterior submedian carinae, *N. caribbaeus* has a rostral plate with a markedly different shape. In *N. caribbaeus* (Fig. 3a) the basal part of the plate is quite short and broadly rounded laterally, whereas in *N. campi* (Fig. 1a) the basal part of the plate is longer and has a distinct angle anterolaterally.

Acknowledgments

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Literature Cited

Hansen, H. J. 1895. Isopoden, Cumaceen und Stomatopoden der Plankton-Expedition.—Ergebnisse der Plankton-Expedition der Humboldt-Stiftung 2(Gc):1–105, pls. 1–8.

Manning, R. B. 1969. Stomatopod Crustacea of the western Atlantic.—Studies in Tropical Oceanography, Miami 8:380 pp.

———. 1995. Stomatopod Crustacea of Vietnam: The legacy of Raoul Serène.—Crustacean Research, Carcinological Society of Japan, Special Number 4:339 pp., 38 colored plates.

Schmitt, W. L. 1924. Report on the Macrura, Anomura and Stomatopoda collected by the Barbados–Antigua Expedition from the University of Iowa in 1918.—University of Iowa Studies in Natural History 10(4):65–99, pls. 1–5.

Schotte, M., & R. B. Manning. 1993. Stomatopod Crustacea from Tobago, West Indies.—Proceedings of the Biological Society of Washington 106:566–581.

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A new subgenus and four new species of *Gliricola* (Phthiraptera: Gyropidae) from Caribbean hutias (Rodentia: Capromyidae)

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Abstract.—A new subgenus, *Hutiaphilus* (Phthiraptera: Gyropidae), is described for five previously named species of *Gliricola* (*G. armatus, G. capromydis, G. cubanus, G. ewingi,* and *G. omahonyi*) and four new species (*G. rabbi,* with the type host *Geocapromys ingrahami*; and *G. pinei, G. schwartzi,* and *G. wernecki,* all with the type host *Mysateles melanurus melanurus*). We redescribe and illustrate the previously described species, and provide a key for the identification of these nine species. The nine species of *Hutiaphilus* are restricted to the caviomorph rodent family Capromyidae, the West Indian hutias. This chewing louse-host association is parallel to other louse-host associations we have documented for caviomorph rodents in that there are two (and in one case, three) species of lice on each host species and typically two even on single host individuals. *Hutiaphilus* is a derived clade well supported by several synapomorphic features. Its position within the genus *Gliricola* suggests that the family Capromyidae may be nested within what is now recognized as the Neotropical family Echimyidae.

Resumen.—Se describe *Hutiaphilus,* un nuevo subgénero de *Gliricola* (Phthiraptera: Gyropidae). Se incluyen en *Hutiaphilus* cinco especies de *Gliricola* ya descritas (*G. armatus, G. capromydis, G. cubanis, G. ewingi y G. omahonyi*) y quatro especies nuevas (*G. rabbi,* con el hospedero típico *Geocapromys ingrahami*; y *G. pinei, G. schwartzi* y *G. wernecki,* las tres con el hospedador típico *Mysateles melanurus melanurus*). Se redescriben las especies anteriormente descritas, incluyendo ilustraciones. Además se presenta una clave de identificación de las nueve especies, que se restringen a la familia de roedores caviomorfos Capromyidae, las jutías antillanas. Las relaciones piojo/hospededor de estas especies se aproximan a las que hemos documentado de otros roedores caviomorfos, por tener dos (y en un caso hasta tes) especies de piojos en cada especie hospededor, incluso en un solo individuo hospededor. *Hutiaphilus* es un clado derivido bien apoyado por varios caracteres sinapomórficos. Su posición dentro del género *Gliricola* sugiere que la familia Capromyidae posiblemente se encuentre filogenéticamente dentro de lo que actualmente se reconoce como la familia neotropical Echimyidae.

The chewing louse genus *Gliricola* Mjöberg (Phthiraptera: Gyropidae) is restricted in its distribution to the New World rodent families Capromyidae, Caviidae, and Echimyidae—caviomorph rodents of the Caribbean islands and Central and South

America. Thirty-five species of *Gliricola* are now recognized (Price & Timm 1993). Emerson & Price (1975) and Price & Timm (1993) provide species descriptions, illustrations, brief reviews of species, host distributions, and literature citations for a number of these taxa. Of the 35 species of *Gliricola,* 5 are from 3 species of West Indian hutias (Rodentia: Capromyidae). Werneck (1944) described *Gliricola capromydis* and *G. cubanus* from the Cuban hutia, *Capromys pilorides* (Say). In the same paper, *G. ewingi* and a second subspecies of *G. capromydis, G. c. armatus* [herein considered a full species], were described from a second species of Cuban hutia, *Capromys prehensilis* [now *Mysateles prehensilis* (Poeppig)]. Werneck (1951) subsequently described the fifth and final species, *G. omahonyi* from the Bahamian hutia, *Geocapromys ingrahami* (J. A. Allen).

The hutias are a Caribbean radiation of mid-sized, terrestrial caviomorph rodents that occupied many of the larger and smaller islands of the Greater and Lesser Antilles and the Bahamas in the West Indies. The capromyids are a complex and poorly understood radiation of rodents that are in need of revision. Modern authors recognize from 20 to 40 Recent species in the family, grouped in 6 to 8 genera in 4 subfamilies (Hall 1981, Nowak 1991, Woods 1989, 1993). The majority of these species are now extinct, with many of the extinctions having taken place since the arrival of Europeans on these islands in the 16th century (Woods 1989).

We recently obtained a number of *Gliricola* lice from specimens of hutias collected in the 1950's by the late Albert Schwartz and his colleagues. These hutia specimens have only recently become available for study. This collection is extremely significant in that it contains a host, *Mysateles melanurus* (Poey), from which lice were unknown previously, and it provides additional collections of *Gliricola* from poorly represented hosts. This prompted us to re-examine as many specimens of *Gliricola* from capromyids that we could locate in collections and to collect additional material from specimens of hutias in the collections of the Field Museum and University of Kansas Natural History Museum.

The purposes of this paper are to: describe a new subgenus for the nine species of *Gliricola* we now recognize from West Indian capromyids; redescribe the five previously named species; describe four new species of *Gliricola*; provide a key for the identification of the nine species in the new subgenus; and discuss the host relationships and geographic distribution of the louse genus *Gliricola* on capromyids.

In the following descriptions, all measurements are in millimeters. The scientific names of the hosts follow Hall (1981), with updates by Woods (1993). The deposition of the holotypes is given in each new species description; as numbers allow, paratypes will be placed in the collections of the National Museum of Natural History (Washington, DC), the Field Museum (Chicago, IL), University of Minnesota (St. Paul, MN), and Oklahoma State University (Stillwater, OK). Acronyms designating museum collections where the hosts are deposited are: FMNH = Field Museum of Natural History; KU = University of Kansas Natural History Museum (Lawrence, KS); USNM = National Museum of Natural History.

Genus *Gliricola* Mjöberg

Micropus Denny, 1842:247 (nec Meyer & Wolf 1810:280). Type species: *Gyropus gracilis* Nitzsch.

Gliricola Mjöberg, 1910:292. Type species: *Gyropus gracilis* Nitzsch.

Paragliricola Ewing, 1924:29. Type species: *Paragliricola guadrisetosa* Ewing.

Clay (1970), in discussing supraspecific relationships within the suborder Amblycera, placed *Gliricola* as the principal component of the subfamily Gliricolinae (family Gyropidae). The only other members of this subfamily are two species of *Mono-*

thoracius Werneck described, respectively, from *Myoprocta acouchy* (Erxleben) and *Kerodon rupestris* (Wied) from Brazil and one species of *Pitrufguenia* Marelli from *Myocastor coypus* (Molina) from Chile (Werneck 1948). Werneck (1948) and Clay (1970) discuss these louse taxa and the characters distinguishing them.

Morphologically, members of *Gliricola* may be characterized by the following combination of features: grossly much as in Fig. 29, except for terminalia; antennae clubbed, mostly concealed beneath head, with third segment pedunculate; with two-segmented maxillary palps; without ventral spinous head processes; with only five pairs of abdominal spiracles, those on segment VIII absent; with single thin tarsal claw on each leg; prothorax distinctly separated from fused meso/metathorax; and little sexual dimorphism except that associated with terminalia and dimensions.

Hutiaphilus, new subgenus

Type species.—*Gliricola capromydis* Werneck

Description.—The features that uniquely characterize species of *Hutiaphilus* are the male dorsal terminalia with a conspicuous bilobed plate (Fig. 4), and the male genitalia with variably complicated mesosomal features and large parameres each bearing two conspicuous subapical setae (Fig. 5). This separation is reinforced by the geographical distribution of the hosts, all of which are hutia species on the West Indies islands.

The remaining 30 *Gliricola* species, all herein considered to be in the nominate subgenus *Gliricola,* are found on the mainland of Central and South America, on a considerably different array of hosts. No males of these louse taxa have any suggestion of the bilobed plate on the dorsal terminalia. Their male genitalia are quite different, with the single exception of those of *G. mirandai* described by Werneck (1935) from *Isothrix bistriatus* Wagner in Bolivia. This genitalic similarity led Werneck (1951) to include his five taxa from hutias with *G. mirandai* as forming a well-defined group within *Gliricola.* We have studied specimens of *G. mirandai* and have concluded, in spite of this genitalic similarity, that this species is a member of the nominate subgenus. Both sexes of *G. mirandai* have a markedly different sternum II and sternal and pleural chaetotaxy; the male lacks the bilobed dorsal plate on the last segment; and the female terminalia are of a grossly different configuration.

Etymology.—The new subgenus proposed herein, *Hutiaphilus,* derives its name from the common name of the hosts, hutias, in combination with the substantive suffix *phila,* derivable from *philos* (φιλος), "loving." The gender is masculine.

In the following species descriptions, setal counts are provided only for selected abdominal terga and sterna, as the compromised quality of many of the available specimens and the large number of setae involved made quantification difficult; the counts are given only to reflect the overall pattern of abundance. The principal features for separation of males involve details of the genitalia and the dorsal and ventral terminalia; for females, the chaetotaxy associated with the terminalia, especially that of the subgenital plate and anus; and for both sexes, the shape and chaetotaxy of sternum II, the size of spiracles, and dimensions.

Abbreviations for dimensions are: POW, preocular width; TW, temple width; HL, head length; PW, prothorax width; MW, metathorax width; AWIV, abdomen width at segment IV; TL, total length; GW, male genitalia width at paramere base; GPL, male genitalia paramere length; GL, male genitalia length measured from anterior end of outer demarcated portion of basal apodeme to tip of paramere (see Fig. 5). Bracketed information under material examined are additions that we have made to the original data. For split drawings with a median vertical line, dorsal is to the left and ventral to the right.

Gliricola (*Hutiaphilus*) *capromydis* Werneck
Figs. 1–5

Gliricola capromydis Werneck, 1944:394.
Type host: *Capromys pilorides* (Say).

Male.—Sternum II shaped as in Fig. 2, constricted and weakly pigmented medially. Setae on tergum IV, 45–73. Setae on sternum II, 4–7; IV, 10–15; V, 14–20; VII, 22–35. Spiracle diameter, 0.010–0.015. Dorsal terminalia as in Fig. 4; dorsal sclerite with prominent widely spaced lobes; short spiniform setae on each lobe, other setae fine. Ventral terminalia as in Fig. 3, with terminal portion bearing scattered small projections. Genitalia as in Fig. 5; prominent apically pointed triangular mesosome. Dimensions: POW, 0.18–0.20; TW, 0.23–0.26; HL, 0.23–0.27; PW, 0.17–0.19; MW, 0.22–0.24; AWIV, 0.35–0.40; TL, 0.96–1.12; GW, 0.13–0.16; GPL, 0.15–0.17; GL, 0.31–0.33.

Female.—Sternum II as for male. Setae on tergum V, 55. Setae on sternum II, 7; IV, 19; V, 25. Spiracle diameter, 0.020–0.025. Terminalia as in Fig. 1; dorsal anterior setae distributed across segments; subgenital plate with total of 32 setae, none of these very long; setae around anus as shown. Dimensions: POW, 0.21; TW, 0.28; HL, 0.28; PW, 0.20; MW, 0.28; AWIV, 0.52; TL, 1.42.

Type material.—Holotype male, allotype female, ex *Capromys pilorides*: Cuba: [Pinar del Río], San Diego de los Baños, coll. W. M. Mann #2202; in collection of the National Museum of Natural History (Washington, DC).

Other material examined.—3 males, ex *Capromys pilorides* [*pilorides*]: Cuba: Las Tunas, 29 km W of Victoria de las Tunas, Samalloa Farm, 15 Jun 1952, coll. E. T. Willis, Albert Schwartz #2327 ♀ (KU 147702); 1 male, same data, except Albert Schwartz #2328 ♀ (KU 147703); 1 male, same data, except Albert Schwartz #2329 ♀ (KU 147704). 1 male, ex *Capromys pilorides* [*pilorides*]: Cuba: [Camagüey], Camagüey, 10 Mar 1913, coll. C. Sheldon #10154X ♂ (USNM 181232).

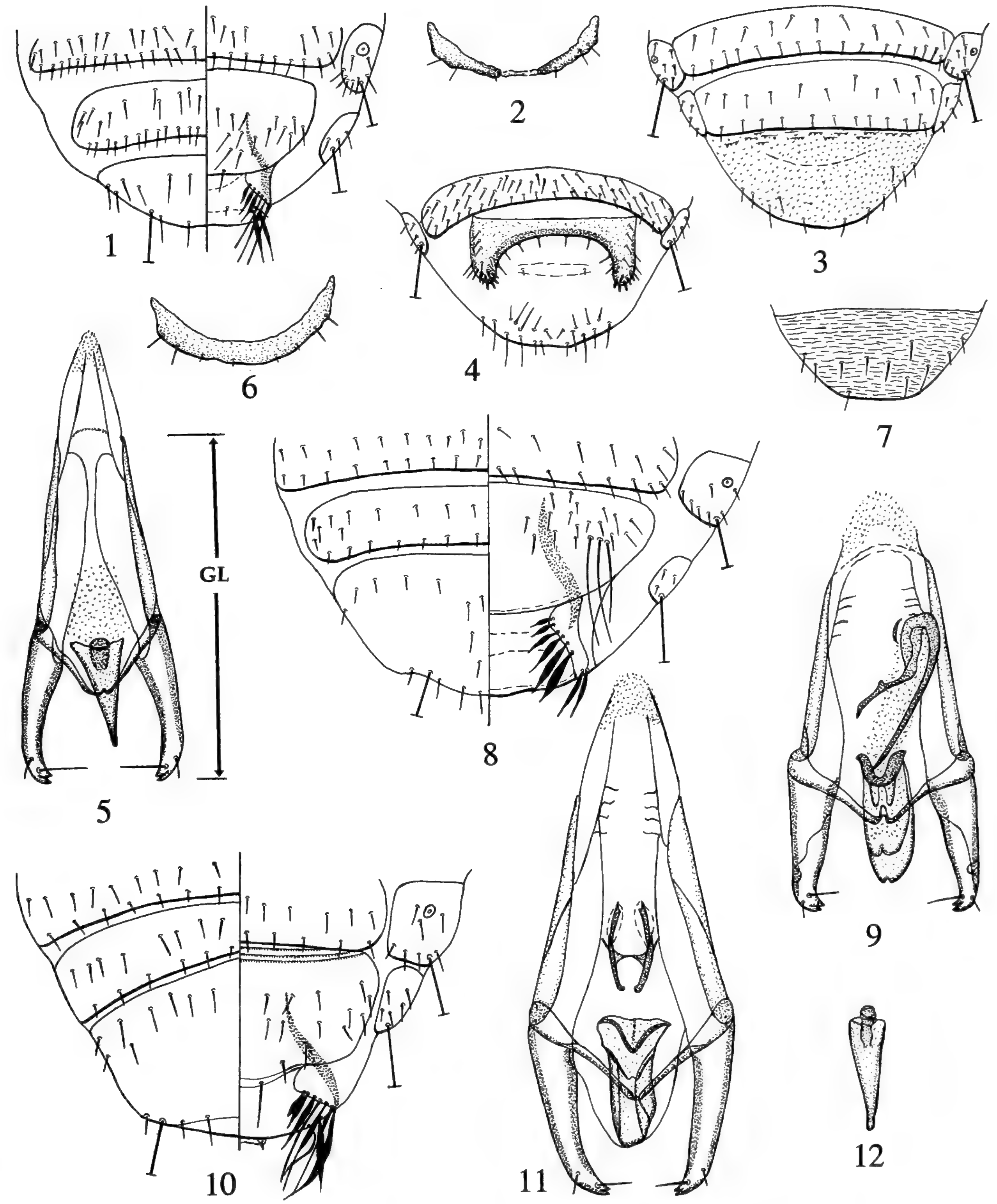
Remarks.—The male of this species is readily distinguished from all others of the subgenus by the details of the genitalia, especially the shape of the mesosome, in conjunction with the type of dorsal terminal plate, the sculpturing of the ventral terminal segment, and the structure of sternum II. The female is recognizable by the chaetotaxy of the terminalia and the chaetotaxy and shape of sternum II.

Gliricola (*Hutiaphilus*) *cubanus* Werneck
Figs. 6–9

Gliricola cubanus Werneck, 1944:397.
Type host: *Capromys pilorides* (Say).

Male.—Sternum II shaped as in Fig. 6, of fairly equal width throughout. Setae on tergum IV, 57–75. Setae on sternum II, 7–8, much shorter medially; IV, 16–24; V, 25–31; VII, 32–40. Spiracle diameter, 0.010–0.015. Dorsal terminalia near to Fig. 18; dorsal sclerite with prominent close-set lobes; short spiniform setae on each lobe, other setae fine. Ventral terminal segment as in Fig. 7, with terminal portion bearing weak transverse lines. Genitalia as in Fig. 9; with complex mesosomal structures, broad and rounded apically, with prominent elongate often convoluted sclerite anterior to these. Dimensions: POW, 0.17–0.19; TW, 0.23–0.25; HL, 0.22–0.24; PW, 0.17–0.19; MW, 0.20–0.22; AWIV, 0.36–0.40; TL, 0.96–1.10; GW, 0.15–0.18; GPL, 0.15–0.16; GL, 0.29–0.31.

Female.—Sternum II as for male. Setae on tergum V, 44–48. Setae on sternum II, 7–9; IV, 19–21; V, 25–26. Spiracle diameter, 0.013. Terminalia as in Fig. 8; dorsal anterior setae distributed across segments; subgenital plate with total of 27–32 short, 5–6 very long setae; broad setae around anus, as shown. Dimensions: POW, 0.19–0.20; TW, 0.24–0.26; HL, 0.23–0.25; PW,



Figs. 1–12. 1–5, *Gliricola capromydis:* (1) female terminalia; (2) sternum II; (3) male ventral terminalia; (4) male dorsal terminalia; (5) male genitalia (GL = genitalia length). 6–9, *Gliricola cubanus:* (6) sternum II; (7) male ventral terminalia; (8) female terminalia; (9) male genitalia. 10–11, *Gliricola ewingi:* (10) female terminalia; (11) male genitalia. 12, *Gliricola armatus:* male genitalic mesosome.

0.19–0.20; MW, 0.23–0.25; AWIV, 0.44–0.49; TL, 1.18–1.22.

Type material.—Paratype male, ex *Capromys pilorides* [*pilorides*]: Cuba: [Camagüey], Camagüey, 10 Mar 1913, coll. C. Sheldon #10154X ♂ (USNM 181232); in collection of University of California (Berkeley).

Other material examined.—1 male, 1 female, ex *Capromys pilorides* [*pilorides*]:

Cuba: Las Tunas, 29 km W of Victoria de las Tunas, Samalloa Farm, 15 Jun 1952, coll. E. T. Willis, Albert Schwartz #2327 ♀ (KU 147702); 4 males, 1 female, same data, except Albert Schwartz #2328 ♀ (KU 147703); 4 males, 2 females, same data, except Albert Schwartz #2329 ♀ (KU 147704).

Remarks.—There are considerable differences between this taxon and *Gliricola capromydis,* which co-occurs on individuals of *Capromys pilorides.* The male mesosomal sclerites are profoundly different, as well as the shape of sternum II, the close-set lobes of the dorsal terminal plate, and the sculpturing of the ventral male terminalia; the female, with 2–3 very long setae on each side of the subgenital plate, is easily separated from *G. capromydis.*

Gliricola (*Hutiaphilus*) *ewingi* Werneck
Figs. 10, 11

Gliricola ewingi Werneck, 1944:399. Type host: *Capromys* [=*Mysateles*] *prehensilis* [*prehensilis*] (Poeppig).

Male.—Sternum II as in Fig. 2, constricted and weakly pigmented medially. Setae on tergum IV, 83–86. Setae on sternum II, 7; IV, 22–24; V, 27; VII, 35–36. Spiracle diameter, 0.015. Dorsal terminalia near to Fig. 18; dorsal sclerite with prominent close-set lobes; short spiniform setae on each lobe, other setae fine. Ventral terminalia as in Fig. 7, with terminal portion bearing weak transverse lines. Genitalia as in Fig. 11; complex of mesosomal structures as shown, broadly rounded, with H-shaped anterior sclerite. Dimensions: POW, 0.17–0.18; TW, 0.23–0.24; HL, 0.22; PW, 0.19–0.20; MW, 0.21–0.23; AWIV, 0.43–0.44; TL, 1.14; GW, 0.20; GPL, 0.17–0.19; GL, 0.38–0.41.

Female.—Sternum II as for male. Setae on tergum V, 42–45. Setae on sternum II, 8; IV, 17–18; V, 20–23. Spiracle diameter, 0.018–0.025. Terminalia as in Fig. 10; dorsal anterior setae distributed across segments; subgenital plate with total of 28–32 setae, none of these very long; several uninterrupted transverse rows of projections across base of subgenital plate; setae around anus as shown. Dimensions: POW, 0.17–0.19; TW, 0.23–0.25; HL, 0.22–0.24; PW, 0.20; MW, 0.23; AWIV, 0.44; TL, 1.21.

Type material.—Paratypes 2 males, 1 female, ex *Mysateles prehensilis* [*prehensilis*]: Cuba: [Pinar del Río], San Diego de los Baños, 8 Apr 1900, Palmer and Riley #137 ♂ (USNM 103887); in collection of University of California (Berkeley).

Other material examined.—1 male, ex *Mysateles prehensilis* [*prehensilis*]: Cuba: Pinar del Río, 4 December 1940, coll. I. Perez Viqueras. 1 female, ex *M. p. prehensilis*: Cuba: Havana, Feb 1886, coll. C. B. Cory (FMNH 15021).

Remarks.—The male genitalia of *Gliricola ewingi* are unique in possessing the H-shaped anterior mesosomal sclerite and in being larger in all dimensions than for any of the other species of the subgenus. The female is separable on the basis of the structure and chaetotaxy of its terminalia; the rows of projections at the base of the subgenital plate are much as those of the first new species described below, but with much smaller spiracles and a different shape of sternum II.

Gliricola (*Hutiaphilus*) *armatus* Werneck
Figs. 12–15

Gliricola capromydis armatus Werneck, 1944:397. Type host: *Capromys* [=*Mysateles*] *prehensilis* [*prehensilis*] (Poeppig).

Male.—Sternum II apparently near Fig. 2, constricted and weakly pigmented medially, but difficult to discern. Setae on tergum IV, 54. Setae on sternum II, 8; IV, 19; V, 24; VII, 27. Spiracle diameter, 0.015. Dorsal terminalia as in Fig. 14; dorsal sclerite with prominent widely spaced lobes; short spiniform setae on each lobe and along medioposterior border. Ventral terminalia as in Fig. 15, with terminal portion bearing weak groups of projections basally, transverse lines of fine projections apically. Genitalia close to Fig. 5; mesosomal structure as in Fig. 12, more slender and apically blunt. Dimensions: POW, 0.17; TW, 0.23; HL, 0.23; PW, distorted; MW, 0.23; AWIV, 0.38; TL, distorted; GW, 0.15; GPL, 0.14; GL, 0.28.

Female.—Sternum II as for male. Setae on tergum V, 43–51. Setae on sternum II, 8; IV, 22–24; V, 25–27. Spiracle diameter, 0.015. Terminalia as in Fig. 13; only lateral dorsal anterior setae on terminal segments; subgenital plate with total of 36–41 setae, none of these very long; setae around anus as shown. Dimensions: POW, 0.18–0.20; TW, 0.24–0.26; HL, 0.23–0.25; PW, 0.21; MW, 0.23–0.24; AWIV, 0.48–0.50; TL, 1.28–1.29.

Type material.—Holotype male, allotype female, ex *Mysateles prehensilis* [*prehensilis*]: Cuba: [Pinar del Río], San Diego de los Baños, 8 Apr 1900, coll. Palmer and Riley #137 ♂ (USNM 103887); in collection of University of California (Berkeley).

Other material examined.—1 female, ex *Mysateles prehensilis* [*prehensilis*]: Cuba: Pinar del Río, 4 December 1940, coll. I. Perez Viqueras. 1 female, ex *M. p. prehensilis*: Cuba: Havana, Feb 1886, coll. C. B. Cory (FMNH 15021).

Remarks.—This species co-occurs with *Gliricola ewingi* on individuals of *Mysateles prehensilis.* While the male genitalia are close to those of *G. capromydis,* the unique chaetotaxy of the dorsal terminal plate and the sculpturing of the ventral terminal segment will separate males of these species. The female, with the virtual absence of any median anterior setae on the last 2 abdominal terga, is unique; this is further supported by differences in the ventral terminalia chaetotaxy.

Gliricola (*Hutiaphilus*) *omahonyi* Werneck
Figs. 16–20

Gliricola o'mahonyi Werneck, 1951:309. Type host: *Geocapromys ingrahami* (J. A. Allen).

Male.—Sternum II as in Fig. 17, of equal width throughout, curve relatively flattened. Setae on tergum IV, 55–62. Setae on sternum II, 0–2; IV, 10–11; V, 15–16; VII, 21. Spiracle diameter, 0.010. Dorsal terminalia as in Fig. 18; dorsal sclerite with prominent closely-set lobes; short spiniform setae on each lobe, sparse fine setae elsewhere. Ventral terminalia as in Fig. 19, with terminal portion bearing weak transverse lines basally, weak transverse lines of fine projections apically. Genitalia as in Fig. 20; with ovoid mesosomal structure as shown, only small slender sclerite anterior to this; parameres with sharp barb on outer margin. Dimensions: POW, 0.16–0.17; TW, 0.22; HL, 0.19–0.20; PW, 0.15–0.16; MW, 0.18–0.19; AWIV, 0.32; TL, 0.84; GW, 0.11; GPL, 0.12; GL, 0.25–0.26.

Female.—Sternum II as for male. Setae on tergum V, 31–38. Setae on sternum II, 2; IV, 10–11; V, 15–17. Spiracle diameter, 0.010–0.013. Terminalia as in Fig. 16; dorsal anterior setae distributed across segments; subgenital plate with total of 24–30 setae, none of these very long; setae around anus as shown. Dimensions: POW, 0.15–0.18; TW, 0.21–0.24; HL, 0.19–0.21; PW, 0.16–0.18; MW, 0.19–0.22; AWIV, 0.37–0.40; TL, 0.91–0.99.

Material examined.—1 male, 3 females, ex *Geocapromys ingrahami*: Bahamas: Little Way Cay, 12 Dec 1985, coll. K. C. Jordan. 1 male, 1 female ex *Geocapromys ingrahami ingrahami*: Bahamas: [Plana Keys], East Plana Cay, 22°27′N, 73°32′W, 4 Mar 1953, coll. George B. Rabb and E. B. Hayden, Jr. #136 ♂ (KU 60655). 3 females, *G. i. ingrahami*: Bahamas: Plana Keys, East Plana Cay, Feb 1891, coll. D. P. Ingraham (FMNH 5624); 1 female, same data, except (FMNH 15022).

Remarks.—The reduced chaetotaxy of sternum II and the unique male genitalia, in conjunction with the close-set lobes of the male terminal dorsal plate and the chaetotaxy of the female terminalia, easily distinguish *Gliricola omahonyi* from the other species of *Hutiaphilus.* Even though we were unable to study any type material of *G. omahonyi,* the description and illustrations furnished by Werneck (1951) left no doubt as to the correct identity of our material.

In his initial description, Werneck (1951) used the spelling *o'mahonyi* for this species. Under articles 27, 32(c)(vi), and 32(d) of the International Code of Zoological Nomenclature, no apostrophes are to be used in scientific names. Names containing apostrophes are now considered to be spelled incorrectly, and as such are to be changed to omit the apostrophe (ICZN 1985). We herein correct the spelling of the specific epithet to *omahonyi.*

Gliricola (*Hutiaphilus*) *rabbi,* new species
Figs. 21–23

Type host.—*Geocapromys ingrahami* (J. A. Allen)

Male.—Sternum II much as in Fig. 6. Setae on tergum IV, 63–64. Setae on sternum II, 6–8; IV, 13–14; V, 17–19; VII, 21–22. Spiracle diameter, 0.010. Dorsal terminalia as in Fig. 21; dorsal sclerite with prominent widely spaced lobes; short spiniform setae on each lobe, fine setae elsewhere. Ventral terminalia as in Fig. 22, with terminal portion bearing conspicuous uninterrupted transverse lines of projections basally, weak scattered heavier projections apically. Genitalia as in Fig. 23; with tapered blunt mesosomal structure as shown only small slender sclerites anterior to this. Dimensions: POW, 0.18–0.19; TW, 0.24–0.25; HL, 0.23; PW, 0.19; MW, 0.22; AWIV, 0.38; TL, 0.99–1.01; GW, 0.12; GPL, 0.12–0.13; GL, 0.27–0.28.

Female.—Sternum II as for male. Setae on tergum V, 51. Setae on sternum II, 7; IV, 12; V, 13. Spiracle diameter, 0.010. Terminalia distorted preventing adequate illustration, but grossly near Fig. 16; dorsal anterior setae extending across segments; subgenital plate with total of 25 setae, none of these very long, and basally with 4 uninterrupted transverse rows of projections, much as for male. Dimensions: POW, 0.18; TW, 0.25; HL, 0.23; PW & MW, distorted; AWIV, 0.47; TL, 1.20.

Type material.—Holotype male, ex *Geocapromys ingrahami*: Bahamas: Little Way Cay, 12 Dec 1985, coll. K. C. Jordan; in collection of Oklahoma State University (Stillwater, OK). Paratypes: 1 male, same data as holotype; 1 female, ex *Geocapromys ingrahami ingrahami*: Bahamas: [Plana Keys], East Plana Cay, 22°27′N, 73°32′W, 4 Mar 1953, coll. George B. Rabb and E. B. Hayden, Jr. #136 ♂ (KU 60655).

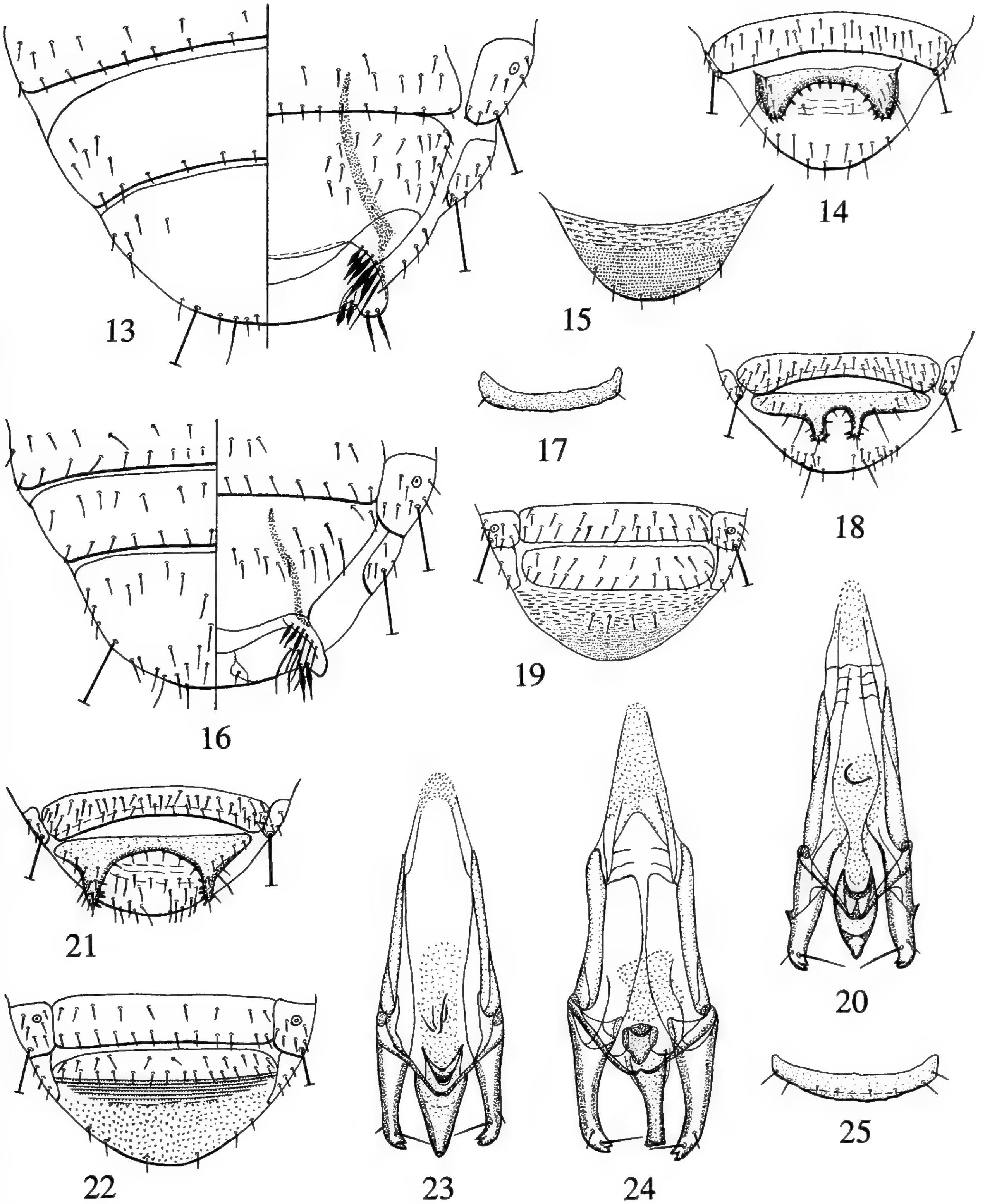
Etymology.—This species is named in honor of George B. Rabb, Director of the Chicago Zoological Society (Brookfield Zoo), and collector of the original host from which we recovered this species of louse over four decades later and in recognition of his long commitment to conservation and public education.

Remarks.—The presence in both sexes of *Gliricola rabbi* of uninterrupted transverse rows of small projections near the base of the ventral terminal segment sets this species apart from all other *Hutiaphilus* except the female of *G. ewingi.* Separation is further supported by the unique male genitalia. It is interesting that our entire series of lice from *Geocapromys ingrahami* bore the identification of *Gliricola omahonyi.* The fact that there were two easily separated species involved had escaped the identifier's attention. This represents the third instance of a pairing of species of *Hutiaphilus* on the same host individual.

Gliricola (*Hutiaphilus*) *schwartzi,* new species
Figs. 24–29

Type host.—*Mysateles melanurus melanurus* (Poey)

Male.—As in Fig. 29. Sternum II as in Fig. 25. Setae on tergum IV, 53–62. Setae on sternum II, 7–8, shorter median setae recessed from posterior margin; IV, 15–17; V, 16–18; VII, 20–25. Spiracle diameter, 0.013–0.015. Dorsal terminalia as in Fig.



Figs. 13–25. 13–15, *Gliricola armatus:* (13) female terminalia; (14) male dorsal terminalia (15) male ventral terminalia. 16–20, *Gliricola omahonyi:* (16) female terminalia; (17) sternum II; (18) male dorsal terminalia; (19) male ventral terminalia; (20) male genitalia. 21–23, *Gliricola rabbi:* (21) male dorsal terminalia; (22) male ventral terminalia; (23) male genitalia. 24–25, *Gliricola schwartzi:* (24) male genitalia; (25) sternum II.

28; dorsal sclerite with prominent widely spaced lobes; short spiniform setae on each lobe, sparse fine setae elsewhere. Ventral terminalia as in Fig. 27, with terminal portion bearing weak short transverse lines basally, weak short transverse lines of fine projections apically. Genitalia as in Fig. 24; with slender, apically truncate mesosomal structure as shown. Dimensions: POW, 0.17–0.18; TW, 0.24–0.25; HL, 0.19–0.20;

PW, 0.17–0.18; MW, 0.19–0.21; AWIV, 0.36–0.37; TL, 0.92–0.96; GW, 0.13–0.14; GPL, 0.14; GL, 0.28–0.30.

Female.—Sternum II as for male. Setae on tergum V, 44–57. Setae on sternum II, 7–9; IV, 12–16; V, 16–20. Spiracle diameter, 0.015–0.025. Terminalia as in Fig. 26; dorsal anterior setae extending across segments; subgenital plate with total of 28–35 setae, none of these very long, but with short row of 5–8 longer submarginal setae associated with U-shaped pigmentation; setae around anus as shown. Dimensions: POW, 0.18–0.21; TW, 0.26–0.28; HL, 0.21–0.24; PW, 0.19–0.22; MW, 0.23–0.26; AWIV, 0.44–0.52; TL, 1.13–1.34.

Type material.—Holotype male, ex *Mysateles melanurus melanurus*: Cuba: Holguín; Santa María, Gibara, 24 August 1951, coll. M. Díaz-Piferrer, Albert Schwartz #3500 ♂ (KU 147709); in collection of the National Museum of Natural History (Washington, DC). Paratypes: 4 males, 3 females, same data as holotype; 3 females, Cuba: [Santiago de Cuba], 22 km S of Bueycito, 26 Dec 1954, coll. Ventura, Albert Schwartz #3026 ♂ (KU 147707); 4 females, Cuba: Holguín, Cueto, Guira River, 11 Jul 1949, coll. M. Díaz-Piferrer, Albert Schwartz #3499 ♂ (KU 147708).

Etymology.—This species is named after the late Albert Schwartz in honor of his career in documenting the fauna of the Caribbean islands and in recognition of his assembling the exceedingly valuable collection of hutias, which made this study possible. Schwartz's efforts in training and supporting students, his foresight in assembling zoological collections, and his written works are an irreplaceable contribution to our knowledge of the evolution of this fauna and its conservation.

Remarks.—The unique male genitalic mesosome, with its slender shape and truncate apical margin, the female ventral terminalia with the longer submarginal setae, and the anal setae as shown, along with details of the shape and chaetotaxy of sternum II and the male terminalia, afford separation from the other taxa. This species represents the first of three new species reported here from the host taxon *Mysateles melanurus.*

Gliricola (*Hutiaphilus*) *pinei,* new species

Fig. 35

Type host.—*Mysateles melanurus melanurus* (Poey)

Male.—Unknown.

Female.—Sternum II close to Fig. 2. Setae on tergum V, 38–44. Setae on sternum II, 7–8; IV, 20–27; V, 26–29. Spiracle diameter, 0.010. Terminalia as in Fig. 35; dorsal anterior setae extending across segments; subgenital plate with total of 25–28 short, 6 very long setae; setae around anus as shown. Dimensions: POW, 0.16; TW, 0.21–0.22; HL, 0.19–0.20; PW, 0.18–0.19; MW, 0.20–0.21; AWIV, 0.41–0.42; TL, 0.97–1.06.

Type material.—Holotype female, ex *Mysateles melanurus melanurus*: Cuba: Holguín; Sarta María, Gibara, 24 Aug 1951, coll. M. Díaz-Piferrer, Albert Schwartz #3500 ♂ (KU 147709); in collection of the National Museum of Natural History (Washington, DC). Paratypes: 2 females, same data as holotype.

Etymology.—This species is named for Ronald H. Pine in honor of his long commitment to the study of biodiversity through both field collections and published works. His efforts have greatly increased our understanding of Central and South American mammals.

Remarks.—Although the male is unknown for *Gliricola pinei,* the female is sufficiently different with its three very long setae on each side of the subgenital plate and the unusual anal chaetotaxy to justify its recognition as a distinct species. Its dimensions also are consistently smaller than either of the other two species of *Mysateles melanurus.* This species co-occurred with *G. schwartzi* on the same host individual.

Gliricola (*Hutiaphilus*) *wernecki*, new species
Figs. 30–34

Type host.—*Mysateles melanurus melanurus* (Poey)

Male.—Sternum II as in Fig. 30, of equal width throughout, but with fainter median area. Setae on tergum IV, 65. Setae on sternum II, 8, all prominent; IV, 19; V, 23; VII, 29. Spiracle diameter, 0.023. Dorsal terminalia as in Fig. 32; dorsal sclerite with prominent slender widely spaced lobes; short spiniform setae on each lobe, sparse fine setae elsewhere. Ventral terminalia as in Fig. 31, with terminal portion bearing weak interrupted transverse lines basally, weak short transverse lines of fine projections apically. Genitalia as in Fig. 34; with broad, parallel-sided mesosomal structure as shown, apically rounded with median indentation. Dimensions: POW, 0.18; TW, 0.24; HL, 0.23; PW, 0.18; MW, 0.19; AWIV, 0.37; TL, 1.09; GW, 0.14; GPL, 0.15; GL, 0.31.

Female.—Sternum II as for male. Setae on tergum V, 43–47. Setae on sternum II, 8, lengths as for male; IV, 15–16; V, 22–24. Spiracle diameter, 0.025–0.028. Terminalia as in Fig. 33; dorsal anterior setae extending across segments; subgenital plate with total of 29–32 short, 9–11 very long setae; setae around anus as shown. Dimensions: POW, 0.20–0.21; TW, 0.27–0.28; HL, 0.26–0.28; PW, 0.22–0.23; MW, 0.24–0.26; AWIV, 0.48–0.50; TL, 1.35–1.36.

Type material.—Holotype male, ex *Mysateles melanurus melanurus*: Cuba: [Santiago de Cuba], 22 km S of Bueycito, 26 December 1954, coll. Ventura, Albert Schwartz #3026 ♂ (KU 147707); in collection of the National Museum of Natural History (Washington, DC). Paratypes: 3 females, same data as holotype.

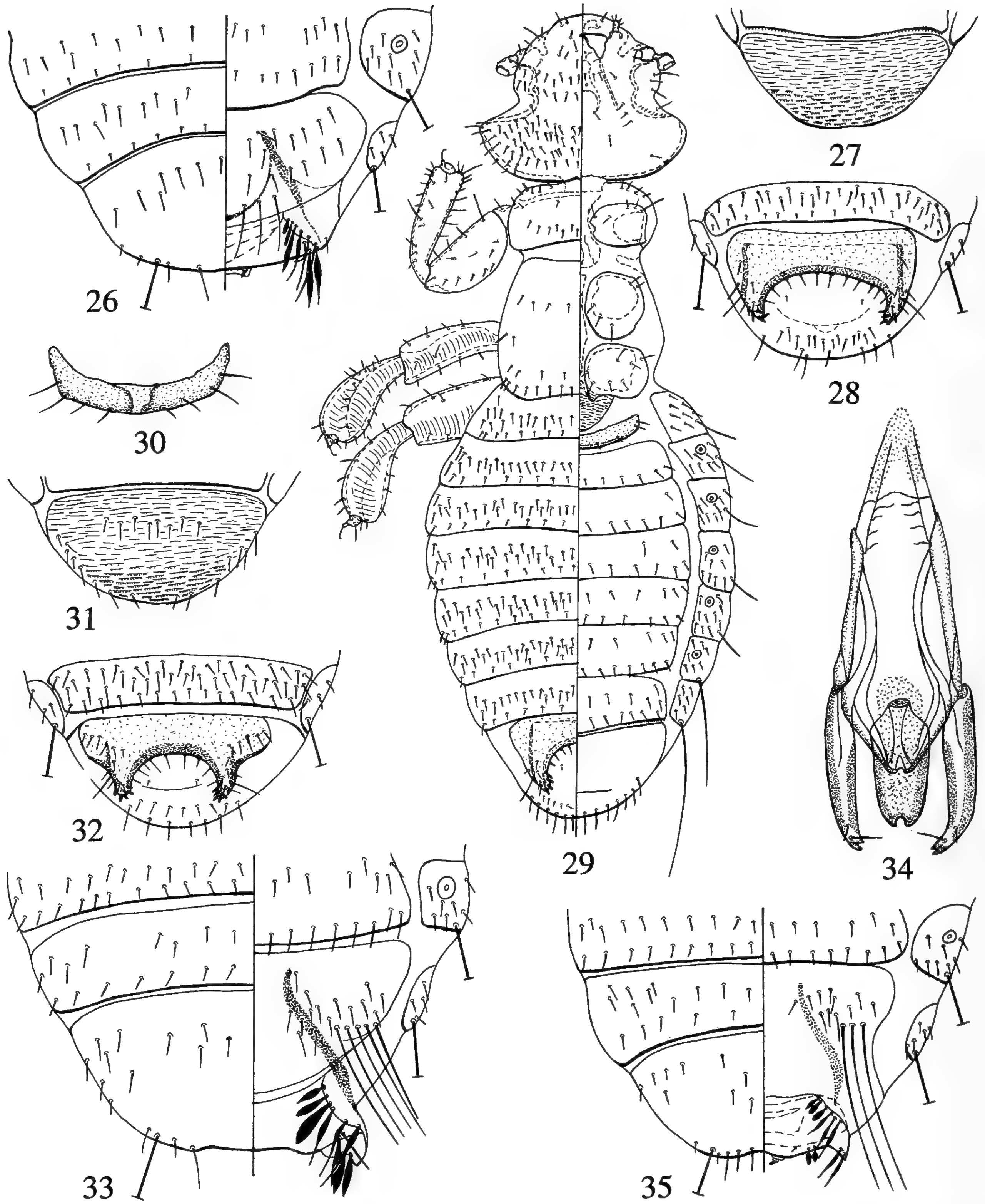
Etymology.—This species is named in honor of Fabio Leoni Werneck in recognition of his pioneering work on the taxonomy of chewing lice of mammals, including extensive studies on the taxa of *Gliricola.*

Remarks.—The female of *Gliricola wernecki,* with its 4–6 very long setae on each side of the subgenital plate, its anal chaetotaxy, its large dimensions, and other minor features, is separable from that of *G. pinei* and others of the subgenus. As has proven to be the case with all species for which male genitalia are known, the genitalic details of *G. wernecki* are unique. This louse species also co-occurred with *G. schwartzi* on the same individual of *Mysateles melanurus,* but from a different locality than that with the pairing of *G. schwartzi* and *G. pinei.* We cannot comment further on this now, but it may be an indication of a potential problem with contamination or host identifications.

Discussion

The amblyceran family Gyropidae is restricted to the Neotropics and contains eight genera, which are found on an array of rodents (primarily caviomorphs), as well as on night monkeys (Primates: Cebidae) (Price & Timm 1995). Clay (1970) recognized three subfamilies within the Gyropidae: Gyropinae, Protogyropinae, and Gliricolinae. The Gliricolinae contains the currently known 39 species of *Gliricola,* including 30 in the nominate subgenus and 9 in the new subgenus *Hutiaphilus.* The *Hutiaphilus* are found only on the Caribbean hutias of the family Capromyidae; they are absent from all other families of New World caviomorph rodents.

Where accurate records are available, gyropids appear to be extremely host specific (Price & Timm 1993, 1995). The older literature, especially for South American rodents, provides numerous examples where several species of lice have been described from a single host species. Most of these have been difficult for us to evaluate when host individuals were collected in different parts of a species range, hosts have not been preserved for confirmation of identifications, and workers in different time periods and in different countries had different no-



Figs. 26–35. 26–29, *Gliricola schwartzi:* (26) female terminalia; (27) male ventral terminalia; (28) male dorsal terminalia; (29) male. 30–34, *Gliricola wernecki:* (30) sternum II; (31) male ventral terminalia; (32) male dorsal terminalia; (33) female terminalia; (34) male genitalia. 35, *Gliricola pinei:* female terminalia.

tions as to species limits. An extreme example of this is the complex array of names for *Gliricola* found on the spiny rats of the genus *Proechimys* (Emerson & Price 1981). There is little doubt that some of the named species of *Gliricola* are associated with hosts whose names have been applied erroneously.

Recently, however, we have shown that two, and even three, species of chewing lice co-occur on two other groups of caviomorph rodents. Individuals of the spiny tree rat, *Mesomys hispidus* (Desmarest), in Peru have two species of *Gliricola,* a situation parallel to our findings on hutias presented herein (Price & Timm 1993). In the New World porcupines (Erethizontidae), we documented that two, and on occasion three, species of chewing lice of the genus *Eutrichophilus* Mjöberg occur on several of the South American porcupine species (Timm & Price 1994). These parallel findings are remarkable in that *Gliricola* and *Eutrichophilus* are not closely related, with the former belonging to the suborder Amblycera and the latter to the suborder Ischnocera. Historically, it was considered rare to find multiple species of chewing lice on a single mammal host species (Hopkins 1957), whereas on birds it is typical to find chewing lice of several species belonging to two, three, or more genera on a single host species.

We herein confirm that each species of *Gliricola* (subgenus *Hutiaphilus*) is restricted to a single host species (high host specificity). Additionally, each host species has two (and in one case, three) species of lice, and two species of *Hutiaphilus* are typically found on single host individuals, confirming that these chewing lice can be truly sympatric.

Four subfamilies are recognized in the West Indian rodent family Capromyidae. We now have lice from only one of the four subfamilies, the Capromyinae, which includes three extant genera: *Capromys, Geocapromys,* and *Mysateles.* Woods (1989) hypothesized that the Capromyidae almost certainly evolved from South American echimyid rodents in the central Antilles (Hispaniola) and that the subfamily Capromyinae is a derived clade that originated on Cuba and secondarily dispersed to other islands in the Greater Antilles as well as to islands in the Bahamas. Although the fossil record for the capromyids goes back only to the Pleistocene, Woods dates the origin of the Capromyinae as "after the early Miocene" or "as late as the Pliocene" (Woods 1989:760).

Our discovery of lice of the subgenus *Hutiaphilus* on all species of capromyines that we have studied to date (four species, representing the three extant genera of the Capromyinae) suggests that these lice are broadly distributed on these rodents and differentiated as their hosts dispersed and speciated on the various islands of the western Antilles. We herein recognize the subgenera *Gliricola* and *Hutiaphilus* as sister clades within the genus *Gliricola.* Lice of the subgenus *Gliricola* are broadly distributed on the Central and South American rodents of the family Echimyidae, and as we now recognize the subgenus, it is restricted to the echimyids. Thus, the relationships of the lice fully support Woods's hypothesis that capromyids evolved from echimyids. Although at present we are recognizing the subgenera *Gliricola* and *Hutiaphilus* as sister clades, further resolution of the relationships of these species within the genus *Gliricola* may suggest that the family Capromyidae is nested within what is now recognized as the Neotropical family Echimyidae.

The South American nutria or coypu, *Myocastor coypus,* has been included as a member of the family Capromyidae (see Hall 1981, Nowak 1991). To date only a single species of chewing louse, *Pitrufguenia coypus* Marelli, is known to parasitize *M. coypus.* Based upon the morphology and relationships of this louse in the distinctive genus *Pitrufguenia,* we concur with recent classifications that treat nutria as a separate lineage (family Myocastoridae) of caviomorph rodents.

The host family Capromyidae is a Caribbean endemic, being found throughout many of the islands of the Lesser and Greater Antilles, as well as the Bahamas. The family contains 20 to 40 Recent species, although at least 70% of these are extinct. The causes of extinctions are complex and certainly involve overhunting by the Amerindian civilizations, who utilized hutias as a major portion of their diet (Wing 1989). The introduction of feral cats to the islands by Europeans also contributed significantly to the extinction of hutias (Morgan 1985).

Although we have much to learn about the chewing louse genus *Gliricola,* our recognition of one clade, *Hutiaphilus,* restricted to the rodent family Capromyidae (subfamily Capromyinae), is an important step towards clarifying host-distributional relationships. Given that chewing lice have now been found on only 4 of the 20 to 40 capromyid species, we strongly suspect that numerous new species of *Gliricola* await discovery. Unfortunately, a number of the species of capromyids are now extinct. Although teeth and/or skeletal remains for all of the species of extinct hutias are known from the fossil record, we will never be able to reconstruct the true diversity of the parasitic chewing lice from these interesting Caribbean endemic rodents.

Key to the Species of *Gliricola* (*Hutiaphiluxs*)

Males
(excluding *G. pinei*)

1\. Dorsal plate of terminalia with close-set lobes (Fig. 18) 2
– Dorsal plate of terminalia with widely spaced lobes (Figs. 4, 14, 21, 28, 32) 4
2\. Genitalia (Fig. 20) without conspicuous anterior mesomeral sclerites, with barb on outer margin of each paramere. Ex *Geocapromys ingrahami* .... *G.* (*H.*) *omahonyi* Werneck
– Genitalia otherwise (Figs. 9, 11) 3
3\. Genitalia with long slender often convoluted anterior mesosomal sclerite (Fig. 9). Ex *Capromys pilorides* .... *G.* (*H.*) *cubanus* Werneck
– Genitalia with H-shaped anterior mesosomal sclerite (Fig. 11). Ex *Mysateles prehensilis.* ...... *G.* (*H.*) *ewingi* Werneck
4\. Dorsal plate of terminalia with short spiniform setae along medioposterior margin (Fig. 14). Ex *Mysateles prehensilis* .... *G.* (*H.*) *armatus* Werneck
– Dorsal plate of terminalia with fine setae along medioposterior margin (Figs. 4, 21, 28, 32) 5
5\. Genitalia with mesosome triangular, either pointed (Fig. 5) or blunt (Fig. 23) 6
– Genitalia with mesosome either slender and apically truncate (Fig. 24) or broad and apically rounded (Figs. 34) 7
6\. Genitalia as in Fig. 23; ventral terminal segment basally with uninterrupted rows of close-set projections (Fig. 22). Ex *Geocapromys ingrahami* .... *G.* (*H.*) *rabbi* n. sp.
– Genitalia as in Fig. 5; ventral terminal segment without such rows of projections (Fig. 3). Ex *Capromys pilorides* .... *G.* (*H.*) *capromydis* Werneck
7\. Genitalia with mesosome slender, apically truncate (Fig. 24). Ex *Mysateles melanurus* ...... *G.* (*H.*) *schwartzi* n. sp.
– Genitalia with mesosome broad, apically rounded, with indentation (Fig. 34). Ex *Mysateles melanurus* .... *G.* (*H.*) *wernecki* n. sp.

Females

1\. Subgenital plate laterally with 2–6 very long prominent setae (Figs. 8, 33, 35) .. 2
– Subgenital plate without such setae .. 4
2\. Subgenital plate laterally with 4–6 very long setae (Fig. 33); spiracle diameter greater than 0.020. Ex *Mysateles melanurus* .... *G.* (*H.*) *wernecki* n. sp.
– Subgenital plate laterally with only 2–3 very long setae (Figs. 8, 35); spiracle diameter less than 0.015 3
3\. Anterior anal setae (Fig. 8) long, prominent; temple width more than 0.23; total length greater than 1.15. Ex *Capromys pilorides* .... *G.* (*H.*) *cubanus* Werneck
– Anterior anal setae (Fig. 35) short, less conspicuous; temple width less than 0.23; total length less than 1.10. Ex *Mysateles melanurus* .... *G.* (*H.*) *pinei* n. sp.
4\. Without median anterior setae on last 2 terga (Fig. 13). Ex *Mysateles prehensilis.* ..... *G.* (*H.*) *armatus* Werneck
– With median anterior setae on last 2 terga 5
5\. Basal portion of subgenital plate with several uninterrupted rows of small projections (Fig. 10) 6

- Without such rows of small projections 7
6. Sternum II as in Fig. 2; spiracle diameter greater than 0.015. Ex *Mysateles prehensilis* . . . . *G.* (*H.*) *ewingi* Werneck
- Sternum II as in Fig. 6; spiracle diameter less than 0.015. Ex *Geocapromys ingrahami* . . . . *G.* (*H.*) *rabbi* n. sp.
7. Sternum II (Fig. 17) with total of 2 or less setae. Ex *Geocapromys ingrahami* . . . . *G.* (*H.*) *omahonyi* Werneck
- Sternum II (Figs. 2, 25) with at least 6 setae 8
8. Subgenital plate with medioposterior row of 5–8 longer submarginal setae associated with U-shaped pigmentation (Fig. 26); sternum II as in Fig. 25. Ex *Mysateles melanurus* . . . . *G.* (*H.*) *schwartzi* n. sp.
- Subgenital plate without such row of longer setae (Fig. 1); sternum II much as in Fig 2. Ex *Capromys pilorides* . . . . *G.* (*H.*) *capromydis* Werneck

Acknowledgments

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Literature Cited

Clay, T. 1970. The Amblycera (Phthiraptera: Insecta).—Bulletin of the British Museum (Natural History), Entomology 25:73–98.

Denny, H. 1842. Monographia anoplurorum Britanniae. Henry G. Bohn, London, xxvi + 262 pp. [+xxvi plates].

Emerson, K. C., & R. D. Price. 1975. Mallophaga of Venezuelan mammals.—Brigham Young University Science Bulletin, Biological Series 20(3):1–77.

———. 1981. A host-parasite list of the Mallophaga on mammals.—Miscellaneous Publications of the Entomological Society of America 12:1–72.

Ewing, H. E. 1924. On the taxonomy, biology, and distribution of the biting lice of the family Gyropidae.—Proceedings of the United States National Museum 63(20):1–42.

Hall, E. R. 1981. The mammals of North America. Vol. 2. 2nd Edition. John Wiley & Sons, New York, xv + 601-1181 + 90 pp.

Hopkins, G. H. E. 1957. The distribution of Phthiraptera on mammals. Pp. 88–119, *in* First symposium on host specificity among parasites of vertebrates. Institut de Zoologie, Université de Neuchâtel, Neuchâtel, 324 pp.

ICZN. 1985. International Code of Zoological Nomenclature, 3rd ed. International Trust for Zoological Nomenclature in association with the British Museum (Natural History), London, 338 pp.

Meyer, B., & J. Wolf. 1810. Taschenbuch der deutschen Vögelkunde, oder Kurze beschreibung aller vögel Deutschlands. Frankfurt am Main, Friedrich Wilmans.

Mjöberg, E. 1910. Studien über Pediculiden und Mallophagen.—Zoologischer Anzeiger 35:287–293.

Morgan, G. S. 1985. Taxonomic status and relationships of the Swan Island hutia, *Geocapromys thoracatus* (Mammalia: Rodentia: Capromyidae), and the zoogeography of the Swan Islands vertebrate fauna.—Proceedings of the Biological Society of Washington 98:29–46.

Nowak, R. M. 1991. Walker's mammals of the world. Vol. II. 5th ed. Johns Hopkins University Press, Baltimore, pp. 643–1629.

Price, R. D., & R. M. Timm. 1993. Two new species of *Gliricola* (Phthiraptera: Gyropidae) from the spiny tree rat, *Mesomys hispidus,* in Peru.—Proceedings of the Biological Society of Washington 106:353–358.

———. 1995. The chewing louse genus *Aotiella* (Phthiraptera: Gyropidae) from South American night monkeys, *Aotus* (Primates: Cebidae).—

Proceedings of the Entomological Society of Washington 97:659–665.

Timm, R. M., & R. D. Price. 1994. Revision of the chewing louse genus *Eutrichophilus* (Phthiraptera: Trichodectidae) from the New World porcupines (Rodentia: Erethizontidae).—Fieldiana: Zoology (New Series) 76:1–35.

Werneck, F. L. 1935. Notas para o estudo da ordem Mallophaga.—Memorias do Instituto Oswaldo Cruz 30:417–435.

———. 1944. Cinco espécies novas do gênero "Gliricola" (Mallophaga, Gyropidae).—Revista Brasileira de Biologia 4:391–399.

———. 1948. Os malófagos de mamíferos. Parte I: Amblycera e Ischnocera (Philopteridae e parte de Trichodectidae).—Revista Brasileira de Biologia 8:1–243.

———. 1951. Notas sôbre malófagos (Gyropidae).—Revista Brasileira de Biologia 11:303–313.

Wing, E. S. 1989. Human exploitation of animal resources in the Caribbean. Pp. 137–152, *in* C. A. Woods, ed., Biogeography of the West Indies: past, present, and future. Sandhill Crane Press, Inc., Gainesville, 878 pp.

Woods, C. A. 1989. The biogeography of West Indian rodents. Pp. 741–798, *in* C. A. Woods, ed., Biogeography of the West Indies: past, present, and future. Sandhill Crane Press, Inc., Gainesville, 878 pp.

———. 1993. Suborder Hystricognathi. Pp. 771–806, *in* D. E. Wilson & D. M. Reeder, eds., Mammal species of the world: A taxonomic and geographic reference. 2nd ed. Smithsonian Institution Press, Washington, 1206 pp.

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Morphology, systematics, and distribution of *Meoma ventricosa grandis* and *M. ventricosa ventricosa* (Echinodermata: Echinoidea: Brissidae) along Mexican coasts

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Abstract.—Two subspecies of the genus *Meoma* are known from the coasts of México, *Meoma ventricosa grandis* and *M. ventricosa* s.s. These conspicuous spatangoids, easily recognized by their incomplete subanal fasciole, are confined to the tropical region of the American seas and are thus characteristic of this region. The systematics of *M. ventricosa grandis* and *M. ventricosa* s.s. are reviewed. A new northern distribution limit is now recognized for *M. ventricosa grandis,* extending its range to Magdalena Bay, Baja California Sur, México.

Resumen.—En las costas de México, existen dos subespecies del género *Meoma: Meoma ventricosa grandis* y *M. ventricosa ventricosa.* Estos conspícuos espatangoides que se reconocen fácilmente por su fasciola subanal incompleta, están confinados a la región tropical de los mares americanos siendo eminentemente característicos de la misma. En este trabajo se revisa la sistemática de las dos subespecies. Por otra parte, se amplia el rango de distribución de *Meoma ventricosa grandis* hasta Bahía Magdalena, Baja California Sur, México, que es el límite norte de su distribución.

Species of the order Spatangoida live on muddy and sandy bottoms in all oceans, exhibiting wide bathymetric distributions, from the intertidal zone down to 5000 m (Chesher 1970). The family Brissidae Gray, 1855, is represented along the Mexican coasts by 15 species, most of which have wide bathymetric distributions and are abundant in deep waters, they are *Brissopsis alta, B. columbaris, B. pacifica, B. atlantica*; *Plethotaenia spatangoides*; *Brissus latecarinatus, B. obesus, B. unicolor, B. elongata*; *Plagiobrissus grandis, P. pacificus*; *Meoma ventricosa grandis, M. ventricosa ventricosa*; *Metalia maculosa, M. nobilis* and *M. pectoralis.*

Meoma ventricosa is the most widely distributed species of brissid in Mexican waters: *M. ventricosa grandis* Gray, 1851 is distributed along the Mexican Pacific coast and *M. ventricosa* s.s. (Lamarck, 1816) in the south east of the Gulf of Mexico and the Caribbean Sea. *M. ventricosa* s.s. is abundant in the Mexican Caribbean Sea, while *M. ventricosa grandis* is scarce within Mexican waters (Caso 1949, 1961, 1983). Their thin test and digging habits make them difficult to collect and preserve with conventional sampling methods.

There are few published works referring to the taxonomy of the genus *Meoma* Gray. Mortensen (1951) mentioned the existence of two recent species of the genus for the American coasts: *Meoma ventricosa* (Lamarck) and *M. grandis* Gray. Chesher (1970) expanded the genus *Meoma* by including a new species. He also considered the previously known recent species as two subspecies of *M. ventricosa: Meoma ventricosa* s.s. and *M. ventricosa grandis.* Although the taxonomic status of these subspecies has been reviewed by Chesher (1970), some aspects of the classification at this level have not yet been completely resolved.

The purpose of this work is to clarify as much as possible the taxonomic status of the subspecies of *Meoma ventricosa* and to document a new distribution range for *M. ventricosa grandis* along the Pacific Coast.

Material and Methods

Measurements of the test of *Meoma ventricosa* were taken using some of the standard measurements suggested by Chesher (1969, 1970). All measurements were made with vernier calipers to the nearest 0.1 mm. A total of 39 specimens was used in this work and data from 18 specimens were assembled for the statistical analysis (nine of each subspecies). To ameliorate the effects of growth and allometry, specimens of similar sizes of both subspecies were chosen. The range in the test length of *M. ventricosa* s.s. is from 94.84 to 145.41 mm ($\bar{X}$ 122.06 mm) and *M. ventricosa grandis* is from 110.25 to 130.81 mm ($\bar{X}$ 119.92 mm). Variations between subspecies were analized by simple and multiple regression analyses. Throughout the study, statistical significance is set at the 95 per cent level using Student's *t* test values.

A total of 33 measurements was chosen to assess variation in test shape and the characteristics of some important structures. The variables and their abbreviations are defined as follows: test length (TL); test width (TW); test height (H); height of the periproct (AH); width of the periproct (AW); distance from the adoral median section of the subanal fasciole to the periproct (SAFT); width of the base of 5 tubercles for each ambulacra zone (I, II, III, IV, V) located in a perimeter of 20 mm around the apical system (T), and width of the peristome (PW).

Material used in this study is housed in the Laboratorio de Sistemática y Ecología de Equinodermos of the Instituto de Ciencias del Mar y Limnología at the Universidad Nacional Autónoma de México (ICMyL-UNAM).

Results and Discussion

Taxonomy

Family Brassidae Gray, 1855

Genus *Meoma* Gray, 1851

Diagnosis.—Large echinoids, with peripetalous fasciole markedly indented between the paired petaloids, forming an acute angle in interambulacra 2 and 3. Test oval, broad, with a moderate frontal depression, high, thick-walled, regularly arched, with highest point almost central. Oral surface flat. Posterior end obliquely directed downwards, truncated. Frontal ambulacrum slightly depressed, with podial pores arranged in 2 regular rows distally. Paired ambulacra sunken, narrow, straight; only the anterior ones are slightly curved backwards at their distal ends. Interporiferous zones narrow, densely covered by small tubercles. Apical system slightly anterior, of the ethmolytic type with 4 genital pores; madreporite prolonged backwards so as to separate the posterior genital and ocular plates. Peristome situated anteriorly, wide, semilunar, slightly sunken. Labrum anteriorly extended, densely covered with tubercles. Large periproct, located at the truncated posterior end of the test and overhung. Sternum short and narrow, densely covered with large tubercles. Long episternum (nearly half the length of sternum). Anal fasciole absent. Subanal fasciole bilobed in *Meoma frangibilis* and *M. cadenati,* aborally degenerate in adults of *M. ventricosa* s.s. and *M. ventricosa grandis* (only the adoral transverse branch remains differentiated). Five types of pedicellariae: globiferous, tridentate, ophicephalous, triphyllous and rostrate.

Type species:—*Meoma grandis* = (*M. ventricosa grandis* Gray, 1851).

In Mexico, this genus is represented by two subspecies: *Meoma ventricosa grandis* (West Coast) and *M. ventricosa ventricosa* (East Coast).

Meoma ventricosa ventricosa (Lamarck, 1816)
Figs. 1–3, Table 1

Spatangus ventricosus.—Lamarck 1816: 29; Blainville 1827: 89.

Brissus ventricosus.—Gray 1825: 431.

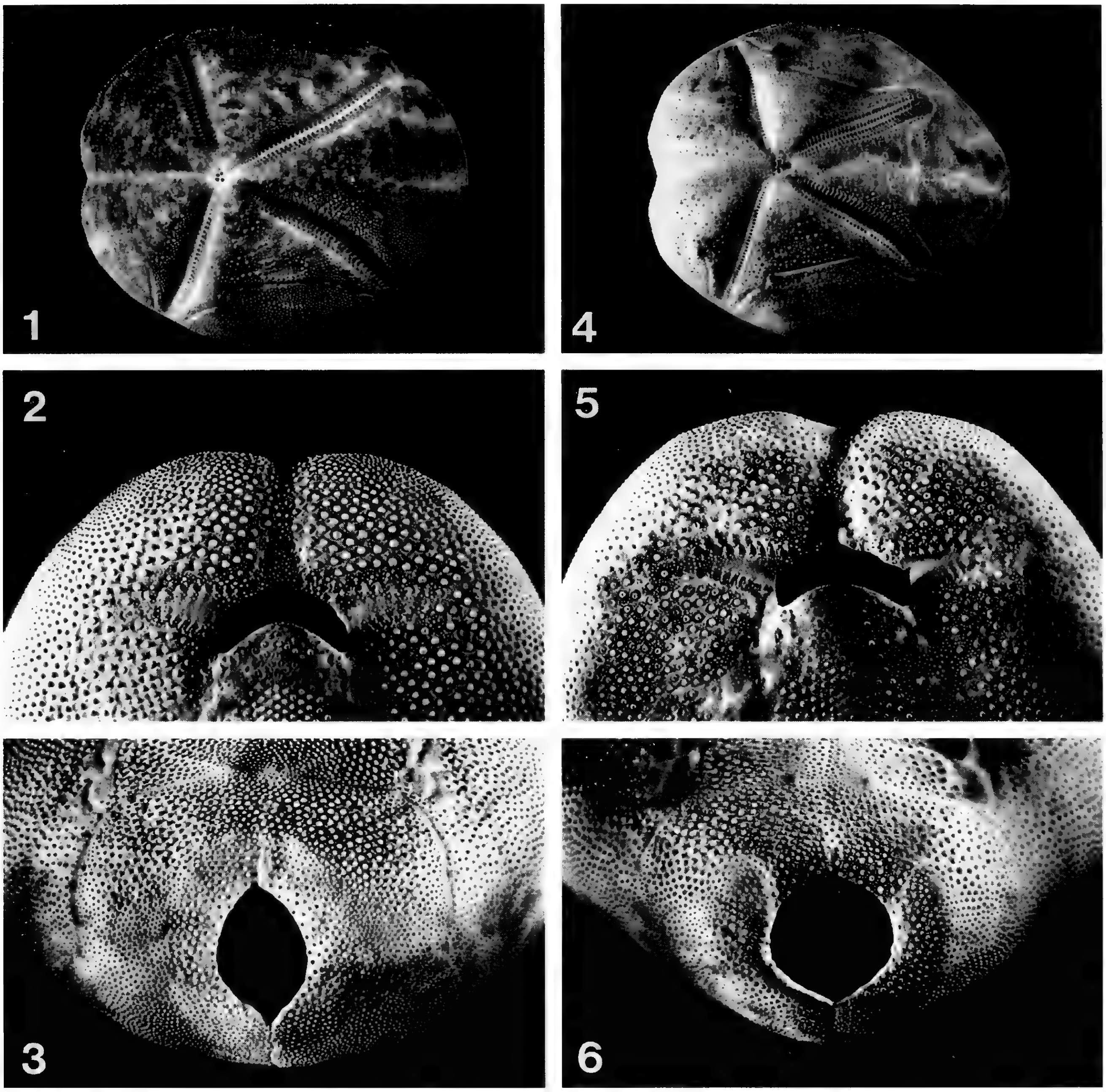
Meoma ventricosa.—Mortensen 1951: 529; Fontaine 1953: 8; Mayr 1954: 6; Hyman 1955: 548, 556; Madsen 1957: 476; Caso 1961: 309; Kier & Grant 1965: 38; Fischer 1966: U592; Chesher 1969: 72-110.

Meoma ventricosa ventricosa.—Chesher 1970: 737–745; Serafy 1979: 94–98; Pawson 1986: 537; Hendler et al. 1995: 243–245.

Material examined.—2 specimens, Puerto Morelos, Quintana Roo, México (20°54′07″N, 86°52′05″W), ICMyL-UNAM 4.95.0; 1 specimen, Puerto Morelos, Quintana Roo, México (20°51′03″N, 86°51′07″W), ICMyL-UNAM 4.95.1; 1 specimen, Puerto Morelos, Quintana Roo, México (20°50′06″N, 86°52′03″W), ICMyL-UNAM 4.95.2; 3 specimens, north of Cabo Catoche, Quintana Roo, México (22°32′08″N, 87°06′09″W), ICMyL-UNAM 4.95.3; 3 specimens, north of Cabo Catoche, Quintana Roo, México (22°56′11″N, 87°16′01″W), ICMyL-UNAM 4.95.4; 3 specimens, north of Cabo Catoche, Quintana Roo, México (22°33′01″N, 87°05′9″W), ICMyL-UNAM 4.95.5; 4 specimens, north of Cabo Catoche, Quintana Roo, México (22°32′08″N, 87°06′09″W), ICMyL-UNAM 4.95.6; 1 specimen, northwest of Cabo Catoche, Quintana Roo, México (22°48′06″N, 87°13′07″W), ICMyL-UNAM 4.95.7; 1 specimen, north of Cabo Catoche, Quintana Roo, México (22°56′01″N, 87°16′01″W), ICMyL-UNAM 4.95.8; 4 specimens, northwest of Cabo Catoche, Quintana Roo, México (23°14′09″N, 87°28′02″W), ICMyL-UNAM 4.95.9; 3 specimens, northwest of Cabo Catoche, Quintana Roo, México (23°14′09″N, 87°28′02″W), ICMyL-UNAM 4.95.10; 2 specimens, northwest Isla Contoy, Quintana Roo, México (22°07′08″N, 86°52′03″W), ICMyL-UNAM 4.95.11; 1 specimen, Puerto Morelos, Quintana Roo, México (20°51′08″N, 86°51′06″W), ICMyL-UNAM 4.95.12.

Diagnosis.—Test broad, with elongate outline. Peristome broad (14 to 18% of TL). Periproct vertically elongated; distance from lower portion of periproct to adoral portion of subanal fasciole usually equal to, or greater than, the vertical diameter of the periproct.

Description.—Test broad anteriorly emarginated; the posterior contour is almost truncated and oblique in its end. Reddish brown test, covered with short and striated spines. Naked test brownish, brown or earth brown color. Apical system anterior, ethmolytic, each of the four genital plates bears a gonopore; two posterior plates are larger and more widely separated. Large tubercles on aboral surface scant, widely dispersed, distributed within the peripetalous fasciole. Small tubercles numerous, distributed over entire surface. Tubercles of the oral surface relatively enlarged, irregularly distributed. Anterior and posterior ambulacral grooves deep and narrow. Length of ambulacral grooves variable: some specimens with ones on right side longer, others with those of left side longer. Anterior ambulacral grooves curved backward. Posterior ambulacral grooves slightly longer than anterior ones. Scarce miliar granules occur on external edge of poriferous zone, between pairs of pores. Peristome anterior, sunken, narrow (14.4 to 17.6% of TL); anterior edge semicircular, keeled labrum. Periproct vertically elongated (17.75 mm mean height, 11.73 mm mean width). Peripetalous fasciole narrow, angular in course around petals. Subanal fasciole incomplete



Figs. 1–6. Comparison of denuded tests of both subspecies. 1. *Meoma ventricosa ventricosa,* dorsal view; 2, peristome; 3, periproct. (Test length 134.56 mm), Puerto Morelos, Quintana Roo, México (20°51′03″N, 86°51′07″W), (ICMyL-UNAM 4.95.1). 4. *Meoma ventricosa grandis,* dorsal view; 5, peristome; 6, periproct., (test length 122.19 mm), Playa Las Gatas, Zihuatanejo, Guerrero, México, (ICMyL-UNAM 4.57.0).

in adults, enclosing a small area compared with *M. ventriocosa grandis.*

Distribution.—Fort Lauderdale, Florida, and the Bahamas Islands, southward through the Greater and Lesser Antilles; in the Gulf of México from southern Florida westward to Central America; the Orinoco River is the southern limit of this subspecies (Hendler et al. 1995). In Mexican waters it has been collected in Mérida, Yucatán (Serafy 1979); Cabo Catoche, Isla Contoy and Puerto Morelos, Quintana Roo.

Bathymetric distribution.—From the intertidal to 200 m.

Holotype.—Unknown.

Type locality.—"Antilles" (Lamarck 1816).

Meoma ventricosa grandis Gray, 1851
Figs. 4–6, Table 1

Meoma grandis.—Gray 185: 132; Verrill 1867: 302; Agassiz 1872-74: 142; H. L. Clark 1917: 220; L. Boone 1928: 12; Zie-

Table 1.—Statistical summary. Coefficients of simple and multiple regression analysis of *M. ventricosa* s.s. ($n = 9$) and *Meoma ventricosa grandis* ($n = 9$). (Abbreviations in section of methods). Statistical significance level 95%.

	Meoma ventricosa ventricosa		*Meoma ventricosa grandis*	
Variables	Correlation coeff.	r^2	Correlation coeff.	r^2
TL-TW	0.991	0.983	0.605	0.366
TL-H	0.957	0.917	0.511	0.261
TW-H	0.937	0.878	0.596	0.355
TL-PW	0.987	0.974	−0.078	0.006
TL-TW-H	*t*-values	r^2	*t*-values	r^2
TL-TW	4.501	0.999	2.856	0.998
TL-H	1.188		0.647	

senhenne 1937: 236; U. S. Grant & L. G. Hertlein 1938: 130; H. L. Clark 1940: 344; J. Steinbeck & E. F. Ricketts 1941: 401; H. L. Clark 1948: 344; Caso 1949: 354; Mortensen 1951: 526; Madsen 1957: 476; Caso 1961: 300–303; Fischer 1966: U592; Caso 1983: 66.

Kleinia nigra.—Agassiz 1863-1869: 27.

Meoma nigra.—Verrill 1867: 251; 1870: 93.

Macropneustes grandis.—Cooke C. W. 1959: 83.

Meoma ventricosa grandis.—Chesher 1970: 745.

Material examined.—2 specimens, Acapulco, Guerrero, México, ICMyL-UNAM 4.57.1; 7 specimens, Playa Las Gatas, Zihuatanejo, Guerrero, México, ICMyL-UNAM 4.57.0; 1 specimen, outside of the Laguna de Yavaros, Sonora, México, ICMyL-UNAM 4.57.2, and 2 specimens from Magdalena Bay, Baja California Sur, México, not in catalogue.

Diagnosis.—Test with broad outline; peristome broad (19 to 22% of TL). Periproct almost circular. Distance from lower portion of periproct to adoral portior of subanal fasciole usually less than the vertical diameter of the periproct.

Description.—Dark brown test, covered with short, striated spines. Test wide and oval, anteriorly emarginated; posterior test contour almost truncated and oblique in its end. Some specimens somewhat flattened, but majority arched at apex. Naked test light brown, dark brown or earth gray color. Apical system anterior, ethmolytic, each of the four genital plates possesses a gonopore; two posterior plates larger and more widely separated. Large tubercles on aboral surface scant and widely dispersed, distributed within the peripetalous fasciole. Small tubercles numerous, distributed over entire surface. Tubercles of the oral surface relatively enlarged, irregularly distributed, more tightly packed towards the anterior. Anterior and posterior ambulacral grooves wide (compared to those of *Meoma ventricosa ventricosa*). Anterior ambulacral grooves curved backward; in some specimens, length varies less than those of the posterior region (minimal variation 30 mm). Posterior ambulacral grooves slightly longer than anterior ones. Scarce, small miliary granules occur on the external edge of the poriferous zone, between pairs of pores. Peristome broad (19.1 to 21.1% of TL), anterior, sunken. Anterior edge formed by two lines converging on its anterior end, forming an obtuse angle, with lateral parts formed by small vertical lines. Labrum prominent, semicircular, not keeled; the posterior prolongation short. Periproct almost circular (16.8 mm mean high, 14.2 mm mean width).

Remarks.—Contour of peripetalous fasciole is highly variable in the observed specimens. The portion across the anterior interambulacral region varies less than other parts; nevertheless, in some specimens, the middle transverse portion is almost straight and in others it is slightly curved. Also, in some specimens it is folded at the level of the ambulacral groove; it generally folds over a small distance, forming a right angle on each side. In other specimens there are two bends, the second one larger than the first, near the anterior lateral grooves. As in *M. ventricosa ventricosa,* some of spines in the interambulacral zones are slightly curved. Large, primary spines are dark brown. In adult specimens, the average between the anterior genital pores is 1 mm, and between the posterior pores 2 mm.

Distribution.—Northern part of the Gulf of California (Angeles Channel, 29°01′05″N and 113°29′05″W) to Punta Choco, Puerto Utria, Colombia; Galapagos and Revillagigedo Islands. In the Gulf of Panama, outside Tortolita and Taboguilla Islands, at depths of 0.5-10 m (Mortensen 1951). In Mexican waters it has been collected in Punta Arena, Punta Gorda, Cabo San Lucas, Baja California; on the seaward side of Laguna de Yavaros, Sonora; Bahía Tenacatita, Jalisco; Playa Las Gatas, Zihuatanejo, Acapulco, Guerrero; Bahía Tangola Tangola, Bahía Santa Cruz, Oaxaca (Caso 1949, 1961, 1983). Chesher (1970) reports it from Bahía Santa Inés, Bahía Concepción, Gulf of California; Manzanillo, Colima; Acapulco, Guerrero; Puerto Huatulco, Oaxaca.

Geographic range extension.—Bahía Magdalena, Baja California Sur (24°35′00″N and 112°03′15″W); two adult specimens collected in the spring of 1991, on sandy bottoms, with an Ekman–Birge dredge at 26 m.

Bathymetric distribution.—From the intertidal to 100 m.

Holotype.—*Meoma grandis* (=*M. ventricosa grandis* Gray, 1851), The Natural History Museum, London, Catalogue number 1949.10.24.6.

Type locality.—Australia (locality which was taken from original label, the label no longer exists). The species is western Mexican and the locality Australia is therefore wrong (S. Halsey pers. comm. 1996). The original material was not labeled "Acapulco, México" as pointed out by Chesher (1970).

Statistical Analysis

Simple regression and correlation analysis showed that between the variables LT–TW, TW–H, TW–H (Table 1) in the case of *Meoma ventricosa* s.s. the correlation coefficients and the r^2 were highly significant. Otherwise, in the case of *M. ventricosa grandis* this correlation was relatively weak (Table 1). The above results were confirmed by multiple regression analysis of TL with respect to TW and H, which indicated that in the case of *Meoma ventricosa* s.s. fit of the regression line in the plot was more significant (Fig. 7) than in the case of *M. ventricosa grandis* (Fig. 8). The shape of the test in *M. ventricosa* s.s. tended to be more broad and anteriorly emarginated than in *M. ventricosa grandis,* which bears a wide and oval shape. The simple regression analysis between TL and PW for *M. ventricosa* s.s. showed a highly significant correlation, while that of *M. ventricosa grandis* was not significant (Table 1). The simple regression analysis of AH with AW for *M. ventricosa* s.s. showed a correlation coefficient (0.713) and r^2 (0.508) that indicated AH was significantly higher than AW. This is easy to recognize by simple observation of the specimens (Fig. 3). The simple regression analysis of AH with AW for *M. ventricosa grandis* showed a correlation coefficient (0.311) and r^2 (0.097) that indicated lack of

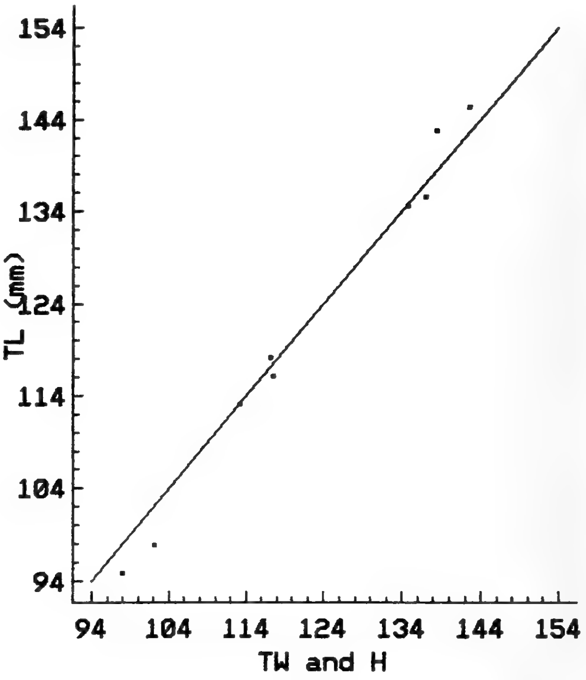


Fig. 7. Multiple regression analysis of the test length (TL), test width (TW) and test high (H) of *Meoma ventricosa ventricosa.* (r^2 = 0.999, n = 9).

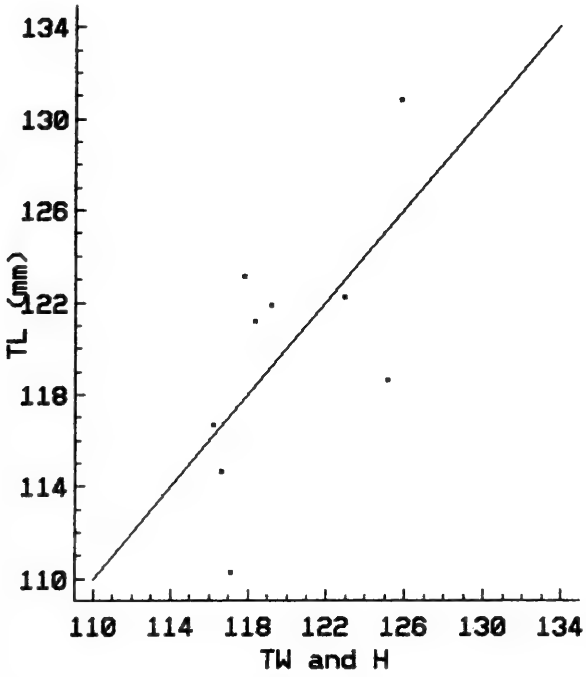


Fig. 8. Multiple regression analysis of the test length (TL), test width (TW) and test high (H) of *Meoma ventricosa grandis*. (r^2 = 998, n = 9).

significance: the periproct is almost circular (Fig. 6). For the correlation analysis between AH and SAFT, the r^2 (*M. ventricosa* s.s. = 0.227 and *M. ventricosa grandis* = 0.181) didn't show a significant difference.

Descriptive statistics showed no significant difference between the two subspecies in analysis of TL versus width of the base of the tubercles for each ambulacral zone. r^2 was 0.99 in all cases. This character overlaps in both subspecies: *M. ventricosa* s.s., $\bar{X}$ = 1.03, max = 1.4, min = 0.7 and *SD* = 0.152; *M. ventricosa grandis*, $\bar{X}$ = 1.02, max = 1.4 min = 0.7 and *SD* = 0.114.

Discussion

Mortensen (1951) state that "only the characters of the primary tubercles of the aboral side, the frontal ambulacrum, and the peripetalous fasciole seem to afford reliable distinction between the two species". Chesher (1970) state that the differences between *M. ventricosa* s.s. and *M. ventricosa grandis* are the distance from the periproct to the adoral portion of the subanal fasciole compared with the vertical diameter of the periproct, and the distance from the apical system to the lateral portion of the peripetalous fasciole.

In the present work, the statistical analyses showed following characters to be important in separating the two subspecies: 1) the shape of the test—in *M. ventricosa* s.s. it is broad and anteriorly emarginated, whereas in *M. ventricosa grandis* it is wide and oval; 2) the shape and size of the peristome—in *M. ventricosa* s.s. it is narrow, with the anterior edge semicircular and a keeled labrum, whereas in *M. ventricosa grandis* it is broad, with anterior edge formed by two lines converging on its anterior end and forming an obtuse angle, with lateral parts formed by small vertical lines, prominent labrum, that is semicircular and not keeled; 3) the shape of the periproct—vertically elongated in *M. ventricosa* s.s. and almost circular in *M. ventricosa grandis*.

We agree with Chesher (1970) that the distance from the periproct to the adoral portion of the subanal fasciole compared with the height of the periproct is important to separate the two subspecies.

Statistical analysis showed that the size of the aboral tubercles is not useful in distinguishing the two subspecies, as was also pointed out by Chesher (1970). It was shown by the same author that "this character is subject to ecological variation".

A new distribution range is now recognized for *M. ventricosa grandis*, extending to Magdalena Bay, Baja California Sur, México. This may be the northern limit of its distribution. This locality shows a special "faunistic conglomerate" that is transitional sub-tropical, with mingling of tropical and temperate faunas (Solís-Marín 1991). This transitional fauna does not prevail along the entire Baja California coast; in Magdalena Bay, a qualitative faunistic change is evident (Williams 1974). This change is explained by the influence of the California current (Loeb et al. 1983).

Acknowledgments

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Literature Cited

Agassiz, A. 1863–1869. Preliminary report on the echini and starfishes dredged in deep water between Cuba and the Florida Reef.—Bulletin of the Museum of Comparative Zoology 1(1–13): 253–308.

———. 1872–74. Revision of the Echini.—Illustrated Catalogue of the Museum of Comparative Zoology at Harvard University 7(1):1–242; (3): 381–629.

Blainville, H. M. 1827. Oursins.—Dictionnaire des Sciences Naturelles 37:59–245.

Boone, L. 1928. Echinoderms from the Gulf of California and the Perlas Islands.—Bulletin of the Bingham Oceanographic Collection, Yale University 2(6):1–14.

Caso, M. E. 1949. Contribución al conocimiento de los equinodermos litorales de México.—Anales del Instituto de Biología. México (20):351–354.

———. 1961. Los equinodermos de México. Unpublished Doctoral Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, 388 pp.

———. 1983. Los equinoideos del Pacífico de México. Parte cuarta, ordenes Cassiduloida y Spatangoida.—Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Publicación especial 6:66–71.

Chesher, R. H. 1969. Contribution to the biology of *Meoma ventricosa* (Echinoidea: Spatangoida).—Bulletin of Marine Science 19(1):72–110.

———. 1970. Evolution in the genus *Meoma* (Echinoidea: Spatangoida) and a description of a new species from Panama.—Biological Results of the University of Miami Deep-Sea Expedition 68:731–761.

Clark, H. L. 1917. Hawaiian and other Pacific Echini. The Echinoneidae, Nucleolitidae, Urechinidae, Echinocorythidae, Calymnidae, Pourtalesiidae, Palaeostomatidae, Aeropsidae, Palaeopneustidae, Hemiasteridae and Spatangidae.—Memoirs of the Museum of Comparative Zoology at Harvard College 46(2):85–283.

———. 1940. Notes on echinoderms from the west coast of Central America.—Eastern Pacific Expeditions of the New York Zoological Society, No. 21, Zoologica (New York) 25:331–352.

———. 1948. A report of the echini of the warmer eastern Pacific, based on the collections of the "Velero" III.—Allan Hancock Pacific Expedition 8(5):225–351.

Cooke, C. W. 1959. Cenozoic echinoids of eastern United States.—United States Geology Survey, Professional Papers 321:1–106.

Fischer, A. G. 1966. Spatangoids. Pp. U543-U628 *in* R. C. Moore. ed. Treatise on invertebrate paleontology. Part U, Echinodermata 3, 2:695 pp.

Fontaine, A. 1953. The shallow-water echinoderms of Jamaica, part. 3. The sea urchins (class Echinoidea).—Natural History Notes Jamaica 61:3–9.

Grant, U. S. IV, & L. G. Hertlein. 1938. The west American Cenozoic Echinoidea.—University of California Publications in Mathematical and Physical Sciences 2:1–225.

Gray, J. E. 1825. Attempt to divide the Echinida or sea-eggs into natural families.—Annals of Philosophy 26:423–431.

———. 1851. Description of some new genera and species of Spatangidae in the British Museum.—Annals and Magazine of Natural History Ser. 2, 7:130–134.

———. 1855. An arrangement of the families of Echinida, with descriptions of some new genera and species.—Proceedings of the Zoological Society of London 1855:35–39.

Hendler, G., J. E. Miller, D. L. Pawson, & P. M. Kier. 1995. Sea stars, sea urchins & allies: Echinoderms of Florida & the Caribbean. Smithsonian Institution Press, Washington, D.C., 390 pp.

Hyman, L. H. 1955. The Invertebrates, vol. 4: Echinodermata, the Coelomate Bilateria. New York, Mc. Graw Hill, 763 pp.

Kier, P. M. & R. E. Grant. 1965. Echinoid distribution and habits, Key Largo Coral Reef Preserve, Florida.—Smithsonian Miscellaneous Collections 149(6):68 pp.

Lamarck, J. B. P. A. de M. de. 1816. Histoire naturelle des animaux sans vertèbres. Volumen 3. Baillière, Paris, 1–59 pp.

Loeb, V. J., P. E. Smith, & H. G. Moser. 1983. Icthyoplankton and zooplankton abundance patterns in the California Current areas. CalCOFI, Report 24:109–131.

Madsen, F. J. 1957. On a new species of *Meoma*, and on a few other echinoids from tropical West Africa.—Bulletin de Institute fra Africa Noire, Serie A 19(2):474–481.

Mayr, E. 1954. Geographic speciation in tropical echinoids.—Evolution 8(1):1–18.

Mortensen, Th. 1951. A monograph of the Echinoidea. V. 2. Spatangoida 2, Reitzel, Copenhagen, 593 pp.

Solís-Marín, F. A. 1991. Composición y distribución espacio-temporal de los macroinvertebrados bentónicos del complejo lagunar Magdalena-Almejas, de la costa occidental de Baja California Sur. Unpublished Professional Thesis, Universidad Michoacana de San Nicolás de Hidalgo, 95 pp.

Serafy, D. K. 1979. Memoirs of the Hourglass Cruises. V (III): Echinoids (Echinodermata: Echinoidea). St. Petesburg, Florida: Florida Departament of Natural Resources, 120 pp.

Steinbeck, J., & E. F. Ricketts. 1941. Sea of Cortez. A leisurely journal of travel and research. New York: The Viking Press, 598 pp.

Verrill, A. E. 1867. The echinoderms of Panama and West coast of America.—Transactions of the Connecticut Academy of Arts and Sciences 1(2):251–322.

———. 1870. Descriptions of echinoderms and corals from the Gulf of California.—American Journal of Science 49(2):93–100.

Williams, A. B. 1974. The swimming crabs of the genus *Callinectes* (Decapoda, Portunidae).—United States Natural Marine Fisheries Services. Bulletin (3):685–798.

Ziesenhenne, F. C. 1937. Echinoderms from the west coast of Lower California. Zoologica, New York, Zoological Society (22):236 pp.

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110(2):310–313. 1997.

New species of *Paratriacanthodes* spikefish (Triacanthodidae: Tetraodontiformes) from the South China Sea

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Abstract.—A new species of deep-water triacanthodid spikefish from the MacClesfield Bank in the South China Sea between the Philippines and Vietnam is described in the subfamily Triacanthodinae as *Paratriacanthodes abei.* It differs from the other two species of that western Pacific and Indian Ocean genus in several meristic and proportional characteristics and in coloration.

Among fishes received from the Fisheries Research Station of Hong Kong in 1972 for deposit in the Smithsonian Institution's National Museum of Natural History (USNM) is the single specimen of a new species of the genus *Paratriacanthodes* described below. It had been identified for shelving purposes when received as the more common of the two species then known.

Methods.—Descriptive data are in conformity with those of the revision of the family by Tyler (1968).

Paratriacanthodes abei, new species
Fig. 1

Holotype.—USNM 342571, 49.9 mm SL, mature male, MacClesfield Bank, South China Sea, 16°19.3′–16°22.2′N, 114°29′–114°24.5′E, 200–210 fathoms (366–384 m), 20 Jun 1964, RV *Cape St. Mary,* cruise 3/64, station 55, Agassiz trawl.

Diagnosis.—A member of the Triacanthodinae (posterior process of pelvis flattened and tapering posteriorly; supraoccipital flattened, as determined from a radiograph) referable to *Paratriacanthodes* by the unique combination in that genus of: short snout; conical teeth in a single series; short pseudobranch with few lamellae; dorsal-fin spines decreasing gradually in length posteriorly; and gill opening moderate. Differs from the two previously known species of the genus, *P. retrospinis* Fowler and *P. herrei* Myers, by having: 16 dorsal-fin rays (versus usually 15 in the other two species); 14 anal-fin rays (versus usually 13); 13 pectoral-fin rays (versus usually 14); 7–8 olfactory lamellae (versus 10–14); greater body depth (54% SL versus about 40–47% SL); longer first dorsal-fin spine (38% SL versus about 28–32% SL); and color pattern with wavy reticulate stripes (versus alternating dark and light horizontal lines).

Description.—See Table 1 for meristics of the fins, teeth, gill rakers, and olfactory and pseudobranch lamellae of the new species in comparison to those of related species. The intact right side (left side has a large cut) is shown in Fig. 1.

Body depth 54.3% SL. Head length 38.9% SL, with a slightly concave profile. Snout short, 12.4% SL. Distance between tip of snout and base of first dorsal-fin spine 47.7% SL. Orbit 15.6% SL; width of relatively flat interorbital 7.0% SL. Postorbital length of head 9.4% SL. Gill opening relatively short, reaching ventrally only to a level about one-fifth down pectoral-fin base, 4.8% SL. Lamellae of pseudobranch reaching ventrally to a level just above top of pectoral-fin base. Width of slightly supraterminal mouth 7.0% SL. A single series of strong, bluntly conical teeth in each jaw. Vertebrae 8 + 12 = 20.

Length of pelvic-fin spine 34.3% SL;

Table 1.—Meristics of the species of *Paratriacanthodes* and *Mephisto.*

	P. retrospinis			*P. herrei*			*P. abei*	*M. fraserbrunneri*	
	No. Spec.	Range	Average	No. Spec.	Range	Average	Holotype	No. Spec.	Range
Dorsal rays	65	14–16	15.0	3	15	—	16	5	16
Anal rays	65	12–14	13.0	3	13	—	14	5	14
Pectoral rays*	128	13–15	13.9	6	14–15	14.2	13	9	14
Pelvic rays*	130	1	—	6	1–2	1.7	1	10	1
Olfactory lamellae	38	10–13	11.8	2	13–14	—	7–8	2	9–10
Pseudobranch lamellae	36	12–16	13.5	3	21–24	22.3	12	2	18–19
Gill rakers	37	17–23	20.3	3	19–21	20.0	18	2	19
Teeth, upper jaw	45	10–18	14.7	3	13–17	15.0	15	2	17
Teeth, lower jaw	45	15–24	19.2	3	16–19	17.3	23	2	19–20

* Usually two fins from the same specimen.

length of unbranched rudimentary ray 1.0% SL. Basal flange of pelvic-fin spine only slightly grooved, apparently with a single position of spine erection against pelvis (fully erect, at a right angle to pelvis). External surface of posterior process of pelvis flattened, with upturned lateral edges and tapering to a blunt point posteriorly. Length

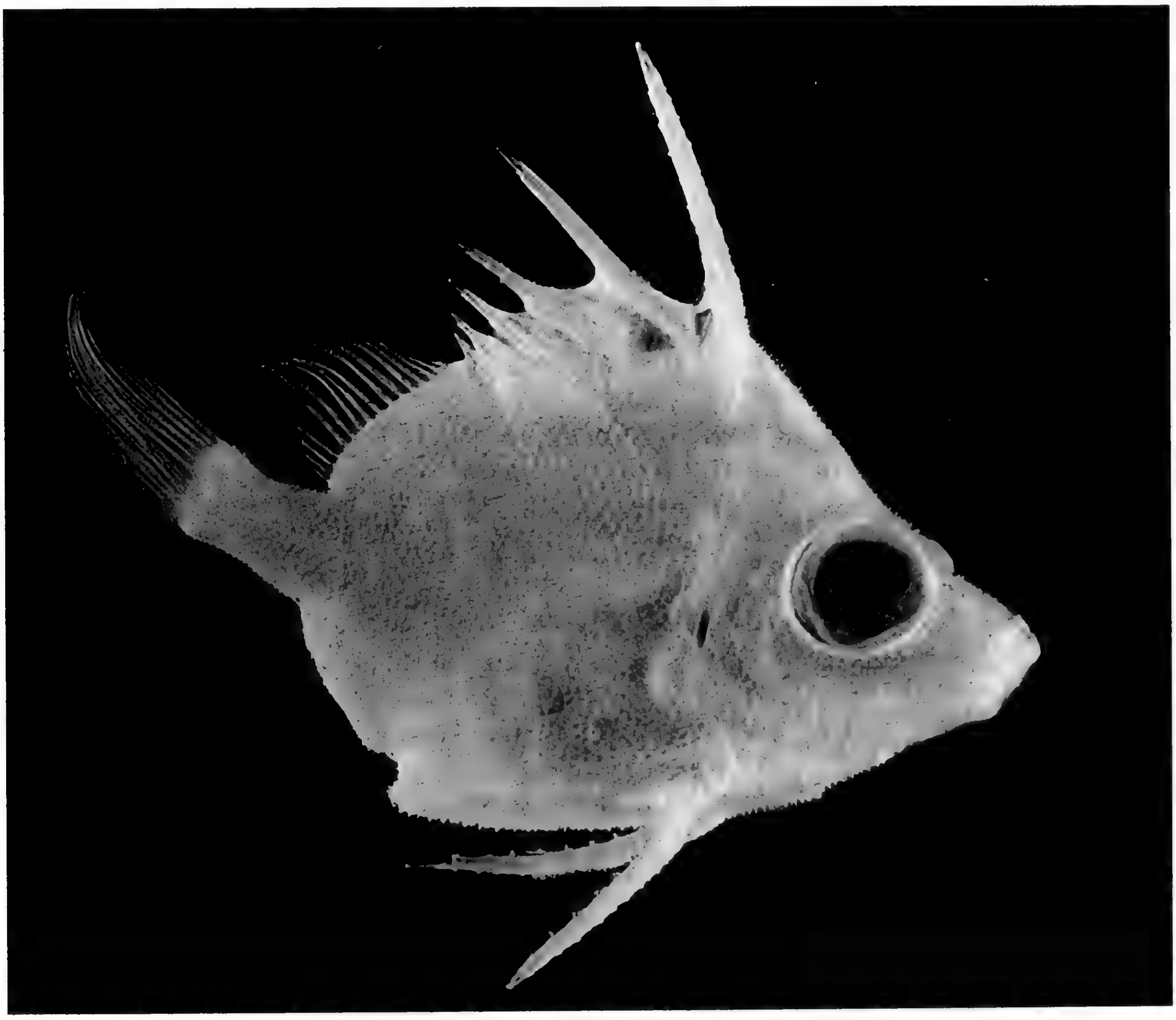

Fig. 1. *Paratriacanthodes abei,* new species, holotype, USNM 342571, 49.9 mm SL, South China Sea: the anal fin is folded up against the side of the body; the pelvic-fin spines from both sides of the body are visible, that of the left side less fully erected than the other.

of posterior pelvic process 36.3% SL; its width between pelvic-fin spines 8.8% SL. Pectoral-fin length 17.2% SL; length of uppermost ray 5.1% SL. Lengths of dorsal-fin spines, from first to last, 38.0, 33.3, 24.4, 16.8, 9.4, and 4.0% SL. Soft dorsal-fin base 20.0% SL; longest ray 21.0% SL. Anal-fin base 17.6% SL; longest ray 17.4% SL. Anal-fin origin at level of about third dorsal-fin ray. Caudal-peduncle depth 10.0% SL; its length 17.0% SL. Caudal-fin length 30.5% SL. Caudal-fin rays 12, with 10 unbranched.

Most of the scales of the body have a row of three upright spinules, the center one the longest, but some scales have only a single central spinule, and the lateral-line scales have a pair of spinules surrounding the pore; the spinules are all simple. There is a broad patch of spinulose scales on the upper lip but none on the lower lip. Spinulose scales extend out most of the length of the soft dorsal-fin rays and along all but the distal one-tenth of the length of the dorsal-fin spines. Some of the spinulose scales are slightly enlarged laterally on the first dorsal-fin spine, but none of them is retrorse.

The color pattern is faded, but melanophores indicate a pattern of wavy reticular stripes, one below the spiny and soft dorsal fins and another with very irregular outlines from the eye, over the pectoral-fin base, and onto the top of the abdomen, with an irregular pattern in the region between these two wavy stripes. There are no well-defined horizontal lines or spots in the pattern. The peritoneum is tan, lightly speckled with darker color.

The color in life is unknown, but if the new species is like other triacanthodins for which living color is known, the wavy reticulate stripes are probably pale blue and the background color pinkish red.

Etymology.—The patronym is given in honor of the late Dr. Tokiharu Abe (3 Apr 1911–9 Aug 1996), of the Museum of Tokyo University and of the Fish Museum at Tsukiji Fish Market, an authority on the fishes of Japan, and especially on the tetraodontiform fugus; he always shared his enthusiasm, knowledge, and specimens with other researchers having similar interests.

Remarks.—One of the two previously described species of *Paratriacanthodes, P. herrei* Myers, is known from only the three type specimens from the Philippines, and until recently the other species, *P. retrospinis* Fowler, was known from only twelve specimens, the four type specimens from the South China Sea and eight others from Japan and east Africa (Tyler 1968, Amaoka 1982). However, a large series of 65 specimens of *P. retrospinis* has recently been collected by ORSTOM expeditions around New Caledonia in the South Pacific, and the species has been redescribed by Matsuura & Tyler (1997) on the basis of these 65 specimens. Therefore, the degree of variability in meristics of *P. retrospinis* can be compared with the meristics of the new species.

The dorsal-, anal-, and pectoral-fin rays of *P. abei* are, respectively, 16, 14, and 13, whereas in *P. retrospinis* only 3 of 65 specimens (7 from Tyler 1968, and 58 from Matsuura & Tyler 1997) have 16 dorsal-fin rays, only 2 of 65 have 14 anal-fin rays, and only 6 of 128 pectoral fins counted have 13 rays; all three specimens of *P. herrei* have 15 dorsal-, 13 anal-, and 14 pectoral-fin rays, like the large majority of specimens of *P. retrospinis*. There is no overlap in the number of olfactory lamellae between *P. abei* (7–8) and the other two species (10–14) of the genus.

There also is no overlap in the proportional measurements of body depth and dorsal-spine length between *P. abei* and the other two species of the genus. Relative body depth decreases somewhat with increasing body length from juveniles to adults in triacanthodids. The average body depth in *P. retrospinis* is 46% SL at sizes between 22–40 mm SL and 40% SL at sizes between 51–110 mm SL. Thus, *P. retrospinis* at all sizes has a more slender body than *P. abei* (54% SL), as do the three specimens of *P. herrei,* with an average depth of 47% SL for the 66–71 mm SL specimens. The length of the first dorsal-fin spine in *P. retrospinis* ranges from 28–33% SL ($\bar{X}$ 31% SL) and in *P. herrei* from 31–33% SL ($\bar{X}$ 32% SL), whereas it is 38% SL in *P. abei.*

There are some similarities between *P. abei* and one or the other previously described species of the genus. The number of pseudobranch lamellae is relatively low in both *P. abei* (12) and *P. retrospinis* (12–16), versus *P. herrei* (21–24). The gill opening is relatively shorter in both *P. abei* (4.8% SL) and *P. retrospinis* (3.7–6.6% SL, $\bar{X}$ 5.3), versus *P. herrei* (7.0–7.6% SL, $\bar{X}$ 7.3). The postorbital portion of the head is relatively shorter in *P. abei* (9.4% SL) and *P. retrospinis* (8.0–10.5% SL, $\bar{X}$ 9.2), versus *P. herrei* (10.8–11.7% SL, $\bar{X}$ 11.2). The pelvic-fin ray is relatively shorter in *P. abei* (1.0% SL) and *P. retrospinis* (1.5–3.8% SL, $\bar{X}$ 2.4), versus *P. herrei* (5.1–7.2% SL, $\bar{X}$ 6.3). Conversely, both *P. abei* and *P. herrei* lack retrorse barbs on the first dorsal- and pelvic-fin spines, whereas these are well developed in *P. retrospinis. Paratriacanthodes abei* and *P. herrei* have only slightly grooved flanges at the base of the pelvic-fin spine and only a single position of erection, whereas this flange is well grooved in *P. retrospinis,* allowing for multiple positions of erection.

Paratriacanthodes abei shares several features with the single species of *Mephisto, M. fraserbrunneri* Tyler, including numbers of dorsal- and anal-fin rays (respectively 16 and 14 in both species) and low numbers of olfactory lamellae (7–8 in *P. abei* and 9–10 in *M. fraserbrunneri*). Both *P. abei* and *M. fraserbrunneri* have relatively irregular wavy stripes or blotches on the body versus more regular horizontal lines in *P. retrospinis* and *P. herrei.* These similarities between *P. abei* and *M. fraserbrunneri* presumably are either primitive or independently derived. The two species can most easily be distinguished by the much greater depth of the gill opening in *M. fraserbrunneri* (12–14% SL, reaching to a level slightly below the pectoral-fin base, versus 5% SL and reaching only to the upper region of the pectoral-fin base in *P. abei*).

All three species of *Paratriacanthodes* are known to occur in either the South China Sea (*P. abei* and *P. retrospinis*) or the adjacent Philippines (*P. herrei*). Only *P. retrospinis* is known to have a wider distribution outside of this area, with records from Japan and China to South Africa and into the western Pacific as far as New Caledonia (Matsuura & Tyler 1997). A specimen of *P. retrospinis* from Fiji examined for this paper extends the range even further to the east (University of the South Pacific cat. no. 4393, 33.7 mm SL, from 485 m depth on the Suva Barrier Reef, 30 September 1981, R/V *Nautilus*).

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Literature Cited

Amaoka, K. 1982. Tetraodontiformes. Pp. 302–306, 409–410 *in* O. Okamura, K. Amaoka, & F. Mitani, eds., Fishes of the Kyushu–Palau Ridge and Tosa Bay. Japan Fisheries Resource Conservation Association, Tokyo.

Matsuura, K., & J. C. Tyler. 1997. Tetraodontiform fishes of New Caledonia (south-western Pacific) collected by ORSTOM, mostly in deep water (100–650 m). Pp. 1–35 *in* B. Séret, ed., Résultats des campagnes MUSORSTOM.—Mémoires du Muséum National d'Histoire Naturelle (in press).

Tyler, J. C. 1968. A monograph on plectognath fishes of the Superfamily Triacanthoidea.—Academy of Natural Sciences of Philadelphia, Monograph 16:1–364.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(2):314–319. 1997.

Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 3. Parentage of *Lesbia ortoni* Lawrence

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Abstract.—*Lesbia ortoni* Lawrence, 1869, collected in the Quito Valley, Ecuador, is shown to be a hybrid between *Lesbia victoriae* and *Ramphomicron microrhynchum,* sympatric inhabitants of Andean forest edge and shrublands from Colombia to Peru. The hybrid exhibits a blended mosaic of plumage characters of the parental species. Although the parental species differ significantly in size, the external measurements of the hybrid approximate those predicted by least squares regression.

Ornithological literature of the 19th century is littered with the descriptions of dozens of enigmatic trochiline taxa from South America (Gould 1861, Salvin 1892, Boucard 1893) that now are treated as plumage mutations or hybrids (e.g., Berlioz & Jouanin 1944, Greenway 1978, Graves 1990). Unfortunately, these taxonomic disposals were often too brief and insufficiently documented to permit considered rejection of alternate hypotheses. Consequently, the status of a significant number of nominal taxa, now all but forgotten, in fact is unresolved.

The spectacular holotype of *Lesbia ortoni* Lawrence, 1869, was sent to Professor Orton of Vassar College from the Quito Valley of Ecuador (see Greenway 1978). It was deposited in the American Museum of Natural History (AMNH) on loan, 21 October 1921; ownership was finally transferred to the AMNH in March 1965 (fide M. LeCroy, pers. comm.). *Lesbia ortoni* was considered a valid species for more than 50 years (Elliot 1879, Salvin 1892, Boucard 1893, Oberholser 1902, Cory 1918, Chapman 1926). Mulsant & Verreaux (1876) erected the genus *Zodalia,* with *ortoni* as the type species. Simon (1921) treated *ortoni* as a junior synonym of *Zodalia glyceria,* believing it to represent the adult male plumage of that taxon (Peters 1945). Finally, in a terse appraisal of several puzzling taxa, Meyer de Schauensee (1947) pronounced as hybrids both *ortoni* and *Z. glyceria* (*Lesbia victoriae* × *Ramphomicron microrhynchum*). This opinion was followed implicitly by subsequent authors (e.g., Morony et al. 1975, Greenway 1978, Fjeldså & Krabbe 1990, Sibley & Monroe 1990, Collar et al. 1992). Meyer de Schauensee's proposal could be correct, but rigorous documentation of *Lesbia ortoni* is a critical and necessary first step in unraveling the parentage of other enigmatic Andean taxa believed to represent hybrids (Graves, unpubl.). Here I provide a detailed hybrid diagnosis of *Lesbia ortoni* employing the methods and assumptions outlined in Graves (1990).

Materials and Methods

The unsexed holotype of *L. ortoni* (AMNH 156651), a relaxed taxidermy mount with glass eyes, lacks the left wing (at the time of my first examination of the specimen in March 1986). The greatly elongated rectrices, large brilliant gorget, purple dorsal plumage, and unstriated maxillary ramphothecum indicate that the specimen is an adult male in definitive plumage (Figs. 1, 2). The unique appearance of *Lesbia or-*

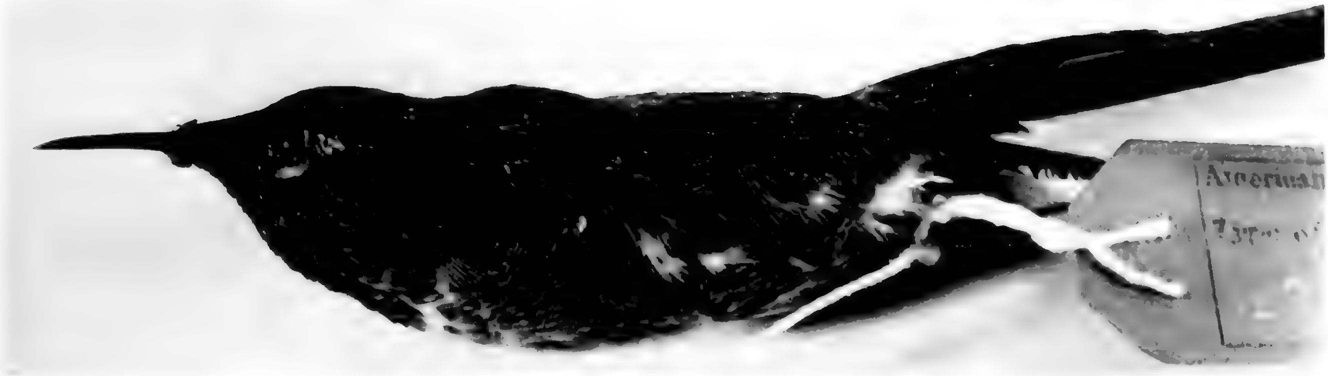

Fig. 1. Lateral view of the type of *Lesbia ortoni* Lawrence (AMNH 156651).

toni cannot be attributed to mutation or developmental variation of any known taxon. It must then represent a hybrid or a valid taxon. As hybrids have no standing in zoological nomenclature, the burden of proof lies with the taxonomist to reject conclusively the hybrid origin of *L. ortoni* before bestowing species status on it. As the results will show, I was unable to reject the hypothesis of hybridity.

Assuming a hybrid origin of *L. ortoni,* the pool of potential parental species (=geographic pool) includes the species of hummingbirds ($n = 48$; see Appendix 1 in Graves 1996b) known to occur regularly above 2000 m elevation in the Ecuadorian Andes (Chapman 1926, Fjeldså & Krabbe 1990). I compared *L. ortoni* directly with males of the potential parental species and the holotype of *Chalcostigma purpureicauda* at the American Museum of Natural History (AMNH 483931). Notes, photographs, and videotape of *L. ortoni* were compared with the holotypes of *Zodalia glyceria* (The Natural History Museum, BM[NH] 1888.7.25.184), *Zodalia thaumasta* (National Museum of Natural History, Smithsonian Institution, USNM 173911), and *Heliangelus zusii* (Academy of Natural Sciences of Philadelphia, ANSP 159261; see Graves 1993a). The taxonomic status of *C. purpureicauda, Z. glyceria,* and *Z. thaumasta* will be addressed in future papers.

Color descriptions were made under natural light. Measurements of 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) were taken with digital calipers and rounded to the nearest 0.1 mm (Table 1). Measurements and least squares regression lines were projected on bivariate plots to illustrate size differences (Wilkinson 1989).

The hybrid diagnosis was approached in a hierarchical manner. The presumed parental species of *L. ortoni* were hypothesized through the comparative analysis of plumage pattern and color and feather shape. As a second step, the restrictive hypothesis was tested with the quantitative analysis of size and external proportions. Concordance of results is regarded as strong support for the hypothesis (Graves 1990, 1993b, 1996a; Graves & Zusi 1990).

Results and Discussion

Characters of *Lesbia ortoni* (hereafter hybrid) that permit its parental species to be identified include: large brilliant gorget; forked tail (depth = 59.7 mm); tips of outermost rectrices "bowed" in cross section; purple feather tips on dorsal body plumage; lack of brilliant frontlet or crown; and short tibial plumes. None of the potential parental species alone exhibits this character combination.

Four species (*Ocreatus underwoodii, Lesbia victoriae, L. nuna, Aglaiocercus kingi*) in the geographic source pool have deeply forked tails. *Ocreatus* can be eliminated from consideration because the hy-

Fig. 2. Ventral view of the type of *Lesbia ortoni* Lawrence (AMNH 156651).

brid shows no evidence of racket-tipped rectrices or elongated tibial plumes. The hybrid also lacks evidence of the awl-shaped bill (dorsal profile) and brilliant crown of *Aglaiocercus kingi.* Thus, by the process of elimination, one of the "trainbearers" (*Lesbia victoriae* or *L. nuna*) is implicated in the parentage of *L. ortoni.* Plumage characters of the hybrid are consistent with this hypothesis, but it is doubtful that the specific identity of the *Lesbia* parent can be determined from plumage color or pattern alone.

Determination of the other parent seems straightforward. Only one species in the geographic pool, *Ramphomicron microrhynchum,* has the rich purple dorsal plumage (including crown) exhibited by the hybrid. In fact, the hybrid appears to exhibit a blend of definitive male plumage characters of *R. microrhynchum* and the trainbearers (*Lesbia* sp.). No other combination ($\binom{48}{2} = 1128$ possible pairs of species) of species in the geographic pool could have produced the phenotype of the hybrid (Appendix).

External measurements.—Examination of external measurements enables identifi-

Table 1.—Ranges and means (± one standard deviation) of measurements (mm) of adult male *Lesbia victoriae, Ramphomicron microrhynchum,* and the hybrid, *Lesbia victoriae* × *Ramphomicron microrhynchum* (= *Lesbia ortoni* Lawrence, 1869; AMNH 156651). Measurements of *L. nuna* are included for comparison.

	victoriae[a] (*n* = 12)	*nuna*[a] (*n* = 12)	*microrhynchum*[a] (*n* = 12)	Hybrid
Wing chord	58.7–62.2	50.3–52.8	47.3–53.5	55.8
	60.3 ± 1.1	51.8 ± 0.6	51.6 ± 1.6	
Bill length	13.5–15.3	7.5–9.0	5.9–7.0	10.1
	14.5 ± 0.6	8.2 ± 0.4	6.5 ± 0.3	
Rectrix 1	22.1–24.9	19.8–22.4	24.3–27.0	25.3
	23.5 ± 0.9	21.0 ± 0.7	26.1 ± 0.8	
Rectrix 2	26.2–31.1	25.9–28.1	28.4–34.1	31.3
	28.8 ± 1.2	27.0 ± 0.7	31.2 ± 1.4	
Rectrix 3	39.2–44.4	36.0–40.4	35.7–41.0	40.5
	42.1 ± 1.7	38.0 ± 1.4	37.7 ± 1.4	
Rectrix 4	62.1–68.5	51.3–57.6	41.5–47.3	56.1
	65.2 ± 2.3	54.3 ± 1.9	43.4 ± 1.5	
Rectrix 5	149.0–189.0	94.1–109.0	46.0–51.0	85.0
	173.7 ± 10.4	99.9 ± 4.1	48.1 ± 1.4	

[a] Collected in Ecuador.

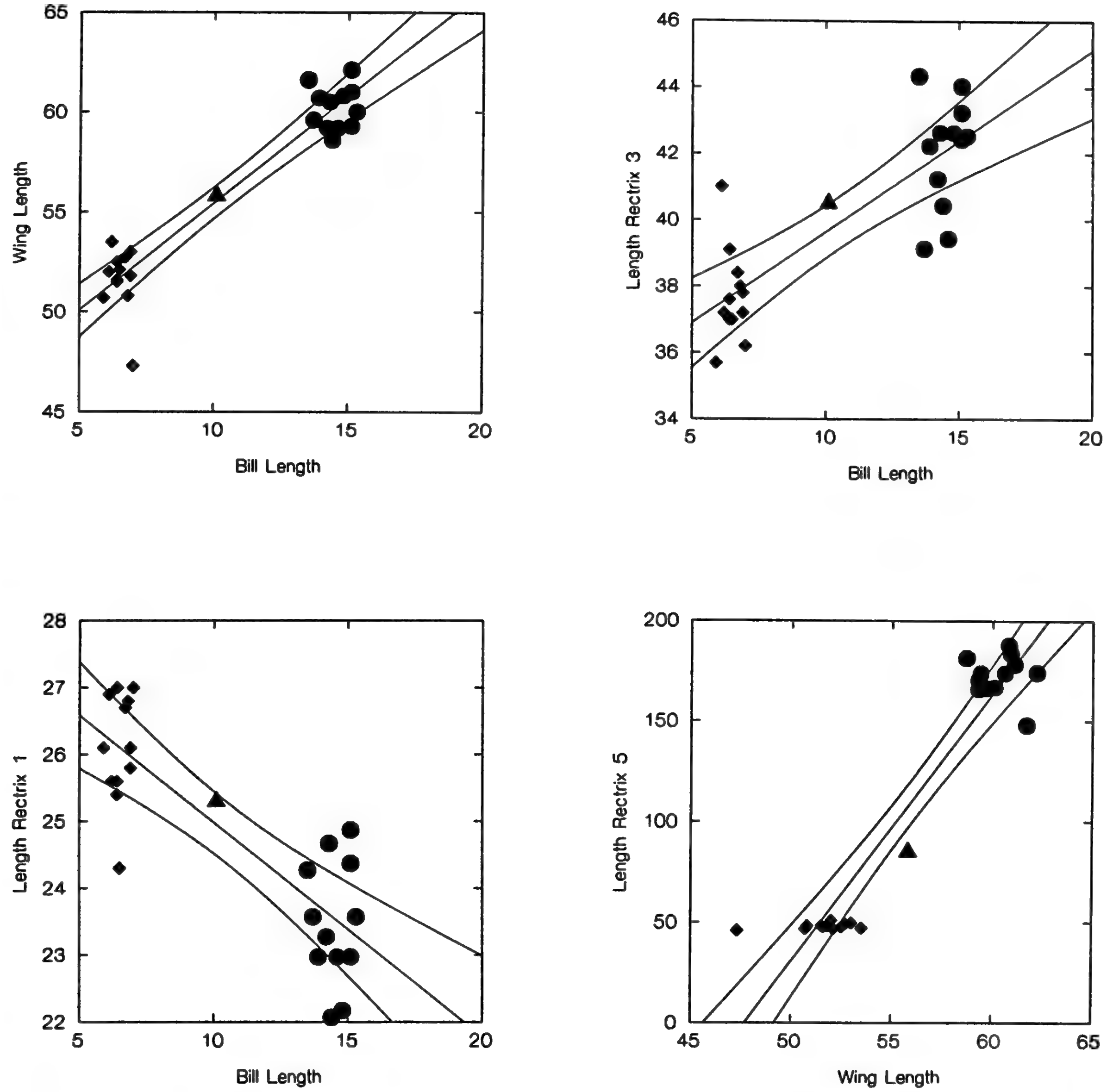

Fig. 3. Bivariate plots of mensural characters of males in definitive plumage: *Lesbia victoriae* (circles); *Ramphomicron microrhynchum* (diamonds); and their hybrid (triangle) (=*Lesbia ortoni,* AMNH 156651). Least squares regression lines and 95% confidence bands are illustrated for comparison.

cation of the *Lesbia* parent. Lengths of the hybrid's bill and wing chord exceed the cumulative range of those measurements for males of *L. nuna* and *R. microrhynchum* (Table 1). Morphological luxuriance has never been observed in trochiline hybrids; thus, *L. nuna* is not one of *L. ortoni*'s parental species. On the other hand, measurements of the hybrid fell between the character means of *R. microrhynchum* and *L. victoriae.* Of particular interest, bill and rectrix 1 measurements exhibit negative allometry in the pooled sample, whereas those of the bill and rectrix 3 show positive allometry (Fig. 3). In both cases, hybrid values approximate those predicted by the least squares regression line.

Geographic overlap.—The geographic and elevational ranges of the parental species, *Lesbia victoriae* and *Ramphomicron microrhynchum,* overlap broadly in the Andes (Fjeldså & Krabbe 1990). *Lesbia victoriae* inhabits forest edge and dry brushy slopes at 2600–4000 m elevation, whereas *R. microrhynchum* prefers cloud forest edge and paramo in more humid regions at 1700–3400 m (Graves 1985, Fjeldså & Krabbe 1990). Both species, particularly the former, are fairly common residents in the Quito region and were well represented in

19th century collections from Ecuador (Oberholser 1902, Lönnberg & Rendahl 1922, Chapman 1926).

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Literature Cited

Berlioz, J., & C. Jouanin. 1944. Liste de Trochilidés trouvés dans les collections commerciales de Bogota.—Oiseau 14:126–155.

Boucard, A. 1893. Genera of humming birds. Vol. 3, Part 2. Bournemouth, London.

Chapman, F. M. 1926. The distribution of bird-life in Ecuador.—Bulletin of the American Museum of Natural History 55:1–784.

Collar, N. J., L. P. Gonzaga, N. Krabbe, A. Madroño Nieto, L. G. Naranjo, T. A. Parker, III, & D. C. Wege. 1992. Threatened birds of the Americas: The ICBP/IUCN Red Data Book, 3rd edition, part 2. International Council for Bird Preservation, Cambridge, U.K., 1150 pp.

Cory, C. B. 1918. Catalogue of birds of the Americas. Part 2, No. 1.—Field Museum of Natural History Zoological Series 13:1–315.

Elliot, D. G. 1879. A classification and synopsis of the Trochilidae.—Smithsonian Contributions to Knowledge, No. 317.

Fjeldså, J., & N. Krabbe. 1990. Birds of the high Andes. Zoological Museum, University of Copenhagen, Denmark, 876 pp.

Gould, J. 1861. An introduction to the Trochilidae or family of humming-birds. Published by the author, London.

Graves, G. R. 1985. Elevational correlates of speciation and intraspecific geographic variation in Andean forest birds.—Auk 102:556–579.

———. 1990. Systematics of the "green-throated sunangels" (Aves: Trochilidae): valid taxa or hybrids?—Proceedings of the Biological Society of Washington 103:6–25.

———. 1993a. Relic of a lost world: a new species of sunangel (Trochilidae: *Heliangelus*) from "Bogota."—Auk 110:1–8.

———. 1993b. A new hybrid manakin (*Dixiphia pipra* × *Pipra filicauda*) (Aves: Pipridae) from the Andean foothills of eastern Ecuador.—Proceedings of the Biological Society of Washington 106:436–441.

———. 1996a. Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes.—Proceedings of the Biological Society of Washington 109:373–390.

———. 1996b. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 2. Hybrid origin of *Eriocnemis soderstromi* Butler.—Proceedings of the Biological Society of Washington 109:764–769.

———, & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* × *Heliangelus amethysticollis*) from northern Colombia.—Condor 92:754–760.

Greenway, J. C., Jr. 1978. Type specimens of birds in the American Museum of Natural History. Part 2.—Bulletin of the American Museum of Natural History 161:1–305.

Lawrence, G. N. 1869. Characters of some new South American birds, with notes on other rare or little known species.—Annals of the Lyceum of Natural History 9:265–275.

Lönnberg, E., & H. Rendahl. 1922. A contribution to the ornithology of Ecuador.—Arkiv for Zoologi 14:1–87.

Meyer de Schauensee, R. 1947. New or little-known Colombian birds.—Proceedings of the Academy of Natural Sciences of Philadelphia 99:107–126.

Morony, J. J., Jr., W. J. Bock, & J. Farrand, Jr. 1975. Reference list of the birds of the world. American Museum of Natural History, New York.

Mulsant, É., & É. Verreaux. 1876. Histoire Naturelle de Oiseaux-mouches ou Colibris, constituant la famille des Trochilidés. Part 3. Bureau de la Société Linnéenne, Lyon.

Oberholser, H. C. 1902. Catalogue of a collection of hummingbirds from Ecuador and Colombia.—Proceedings of the United States National Museum 24:309–342.

Peters, J. 1945. Check-list of birds of the world. Vol. 5. Museum of Comparative Zoology, Cambridge, Massachusetts, 306 pp.

Salvin, O. 1892. Catalogue of the birds in the British Museum, Vol. 16. London, 703 pp.

Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.

Simon, E. 1921. Histoire naturelle des Trochilidae (synopsis et catalogue). Encyclopedia Roret, L. Mulo, Paris.

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, 822 pp.

Appendix

General comparative description of definitive plumages of male *Lesbia victoriae, Ramphomicron microrhynchum,* and the hybrid, *L. victoriae* × *R. microrhynchum* (=*Lesbia ortoni* Lawrence, 1869; AMNH 156651). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

Dorsal feathering (capital and spinal tracts) of *victoriae* to the upper tail coverts is medium dull green; feather bases are gray and some lateral barbs are narrowly fringed with buff. These plumage areas of *microrhynchum* are deep purple; feather bases are gray separated from the purple terminal discs by a narrow greenish band.

The dorsum of the hybrid appears an amalgam of *victoriae* and *microrhynchum,* more closely resembling the latter species. The greenish subterminal band of crown and back feathers of the hybrid is wider and the purple terminal disc narrower than in *microrhynchum,* imparting a mottled purple and green appearance to the crown, hindneck and back. Scapulars are mottled green and purple; the rump and uppertail coverts of the hybrid are more uniformly purple, whereas a few feathers on the sides of the lower back are tipped with green. Purple feather tips occur ventro-laterally to the auriculars, sides of the neck, and sides of the rump.

In *victoriae,* a brilliant medium-green gorget extends from the chin to the upper breast the posterior border of the gorget is broadly lanceolate in shape. Feathers of the lores, auriculars, sides of neck, breast, and flanks are green, finely margined (10 × magnification) with buff in fresh plumage; feathers along the midline below the gorget and on the abdomen are extensively fringed with buff. Vent plumes are white; undertail coverts are buff with a muted and elongated grayish spot along the rachis; tibial plumes are buff.

The ventral color and pattern of *microrhynchum* are similar to *victoriae,* but the lores and auriculars are rich purple, the gorget more rounded and proportionally smaller. Gorget color is light green, subtly paler than in *victoriae.* Feathers of the breast and sides of *microrhynchum* are narrowly margined with grayish-buff, especially on the abdomen and along the midline below the gorget. Vent plumes in *microrhynchum* are white; undertail coverts are dark purplish brown, some tinted with green, and all broadly margined with buff or buffy–white; tibial plumes are brownish-black, narrowly tipped with buff.

The hybrid's gorget is light green, intermediate in color, size, and shape between those of the parental species. Barbs of auricular feathers are green tipped with purple. The lores are dull green with some purple reflections. The remainder of the underparts are intermediate in appearance between those of the parental species. Vent plumes are white, whereas the short tibial plumes are buff or light brown. Undertail coverts are buff with gray bases.

In *victoriae,* the rectrices (dorsally) are black with brownish-purple reflections in bright light, conspicuously (rectrices 1–4) or inconspicuously (rectrix 5) tipped with dark green. The proximal ⅓ of the lateral vane of rectrix 5 is gray (dorsally) and grayish-white (ventrally). The proximal ⅓ of the rachis (rectrix 5) is grayish–white on the ventral surface. Tips of the outermost rectrices (5) of *victoriae* are slightly subspatulate and "bowed" in cross-section. The rectrices of *microrhynchum* are black with bronzy–purple reflections, especially on rectrix 1; the rachises are blackish–brown. In cross-section, the outermost rectrices (5) are nearly flat.

The rectrices of the hybrid are intermediate between those of the parental species: (rectrix 1)—black with purplish tint proximally, shading to bronze, then coppery to coppery-purple at the tip; (rectrices 2–4)—black with bronzy reflections turning to coppery-purple at the tip; (rectrix 5)—black with faint bronzy reflections but lacking the coppery-purple tip present on the other rectrices. The lateral vane of rectrix 5 is margined dorsally with buffy–white to within 25 mm of the feather tip. Ventrally, the rachis is white or very pale buff proximally, becoming dark brownish–black near the middle of the long axis of the feather. In cross-section, rectrix 5 of the hybrid is intermediate in curvature between that shown by *victoriae* and *microrhynchum.*

Primaries and secondaries are dull dark brown in *victoriae,* and blackish-brown with purplish reflections in *microrhynchum.* The flight feathers of the hybrid are intermediate in color and iridescence. In *victoriae,* the greater wing coverts are green (same as back), the primary coverts are dark brown tipped with green, and the tiny coverts along the leading edge of the wing are green broadly edged with buff. Greater and primary coverts are blackish-brown in *microrhynchum*; the leading edge coverts are brownish-black, some narrowly margined with light brown. Wing coverts of the hybrid are intermediate in color and pattern.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 4. Hybrid origin of *Calothorax decoratus* Gould

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Abstract.—*Calothorax decoratus* Gould 1860 is shown to be a hybrid between *Acestrura heliodor* and *Acestrura mulsant.* Plumage characters of the hybrid are a blended combination of those of the parental species. External measurements of the hybrid approximate the values expected from least squares regression of parental measurements. This is the first conclusively documented case of hybridization among the diminutive woodstars (*Acestrura*).

The systematics and taxonomy of the Andean woodstars (Trochilidae: *Acestrura*) have yet to be resolved. In particular the validity of *Calothorax decoratus* Gould 1860 (hereafter *Acestrura decorata*), described from a unique specimen (No. 1888.7.25.203 in the Natural History Museum (formerly British Museum [Natural History]), has been questioned since Salvin (1892: 408) pronounced it "a species of doubtful value, intermediate between *A. mulsanti* and *A. heliodor.*" Since then, *A. decorata* either has been placed in the synonymy of *A. heliodor* (Cory 1918) or considered as a doubtful species or hybrid (Berlioz & Jouanin 1944, Peters 1945, Meyer de Schauensee 1949, Morony et al. 1975). In this paper I confirm the hybrid origin of *A. decorata* using the methods outlined in Graves (1990) and Graves & Zusi (1990).

Materials and Methods

Species of *Acestrura* are sexually dimorphic. The unsexed type of *A. decoratus* appears to be in definitive male plumage and lacks striations on the ramphothecum at 10 × magnification, indicating adulthood. Gould (1860) believed that the specimen was collected in Antioquia, Colombia. However, as pointed out by Berlioz & Jouanin (1944), specimens exported from "Bogotá" and other Colombian localities during the 19th century could have been collected nearly anywhere in northwestern South America. Assuming a hybrid origin of *A. decorata,* the pool of potential parental species would include all the hummingbirds known to occur in Colombia (Hilty & Brown 1986), and possibly Ecuador (Chapman 1926, Fjeldså & Krabbe 1990) and Venezuela (Meyer de Schauensee & Phelps 1978).

The diminutive type of *Acestrura decorata* as noted by Gould (1860), Salvin (1892), and Hartert (1922) is, in fact, so similar in appearance to *A. heliodor* and *A. mulsant* that I focused my analysis on adult males of the five unquestioned species of *Acestrura* (*heliodor, astreans, mulsant, berlepschi, bombus*; see Graves 1986), and on other species of "woodstars" known from northwestern South America (*Myrmia micrura, Chaetocercus jourdanii, Philodice mitchellii, Calliphlox amethystina*) (taxonomy of Sibley & Monroe 1990). I compared the type of *A. decorata* directly with series of these species in the Natural History Museum (BM[NH]), Tring. Photographs, videotape, and notes later were compared with specimens in the American

Fig. 1. Ventral and lateral views of male *Acestrura heliodor* (top), *A. mulsant* (bottom), and their putative hybrid, *A. decorata* (BM[NH] 1888.7.25.203; =*Calothorax decoratus* Gould).

Table 1.—Ranges and means (± standard deviation) of measurements (mm) of adult males of *Acestrura heliodor, A. mulsant,* and the hybrid, *A. heliodor* × *A. mulsant* [= *A. decorata* (Gould)].

	heliodor (*n* = 12)	*mulsant* (*n* = 9)	Hybrid BM [NH] 1888.7.25.203
Wing chord	26.8–29.0 27.5 ± 0.6	37.6–39.8 38.9 ± 0.8	32.1
Bill length	11.8–13.4 12.5 ± 0.5	15.8–17.3 16.3 ± 0.5	14.3
Rectrix 1	8.3–9.2 8.8 ± 0.4	14.8–16.9 15.6 ± 0.6	11.8
Rectrix 2	10.8–13.4 12.1 ± 0.7	18.0–20.6 18.0 ± 20.1	13.8
Rectrix 3	19.1–21.1 20.0 ± 0.6	22.8–26.1 24.5 ± 1.2	22.1
Rectrix 4	17.8–19.8 18.8 ± 0.6	22.8–25.4 24.3 ± 0.8	21.2
Rectrix 5	12.7–14.7 13.6 ± 0.6	19.3–21.6 20.4 ± 0.8	15.9

Museum of Natural History (AMNH), New York, and the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Color descriptions were made under natural light (Appendix). Measurements of 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) were taken with digital calipers and rounded to the nearest 0.1 mm (Table 1). Least squares regression lines and confidence intervals were projected on bivariate plots to illustrate size differences (Wilkinson 1989).

The hybrid diagnosis was approached in a hierarchical manner. I hypothesized the presumed parental species of *A. decorata* through the comparative analysis of plumage pattern and color, feather shape, and bill curvature. As a second step, the restrictive hypothesis was tested with the quantitative analysis of size and external proportions. Agreement of results is regarded as strong support for the hypothesis (Graves 1990, 1993, 1996; Graves & Zusi 1990).

Results and Discussion

Gould (1860:309) noted "this species [*Acestrura decorata*] might easily be mistaken for *Calothorax* [*Acestrura*] *heliodori* ··· it differs from it in several particulars,—in being larger, in having the frill in front of the throat not so prolonged on the sides (in which respect it more nearly resembles *C. mulsanti*), the two centre tail-feathers finer and more spiny, and the bill much longer." Could a rare developmental or genetic aberrancy affecting size of *A. mulsant* or *A. heliodor* be responsible for the unique specimen of *A. decorata*? Neither dwarfism nor gigantism has ever been documented within the Trochilidae, and bona fide cases of those phenomena are very rare within birds (Buckley 1982). Details of the plumage color of *A. decorata* differ from that of both *A. heliodor* and *A. mulsant* (Fig. 1, Appendix), indicating that it is not a scale version of either species. Thus, we may conclude that *A. decorata* represents a hybrid or a valid taxon. My analysis presented below shows that the hybrid hypothesis cannot be refuted.

Characters of *Acestrura decorata* relevant for hybrid diagnosis include: brilliant violet-purple gorget with elongated lateral feathers; white feathers on chin; grayish-white pectoral band below gorget; white feathers along midline of lower breast; lack of rufous pigment in rectrices; and widths of rectrices 4 and 5 <⅓ those of rectrices 1–3. This combination of characters can only be derived from *Acestrura heliodor* and *A. mulsant* among the nine species (36 possible pairs of species) in the restricted pool (see Appendix). The plumage of *A. decorata* is almost perfectly intermediate in appearance between *A. heliodor* and *A. mulsant,* whose geographic ranges and elevational distributions overlap in the Cordillera Central and Cordillera Oriental of the Colombian Andes.

Hybridization between other species could not have produced the plumage characters present in the type of *Acestrura decorata. Chaetocercus jourdanii, Acestrura bombus, Myrmia micrura, Philodice mitchellii,* and *Calliphlox amethystina* can be eliminated as possibilities because all pos-

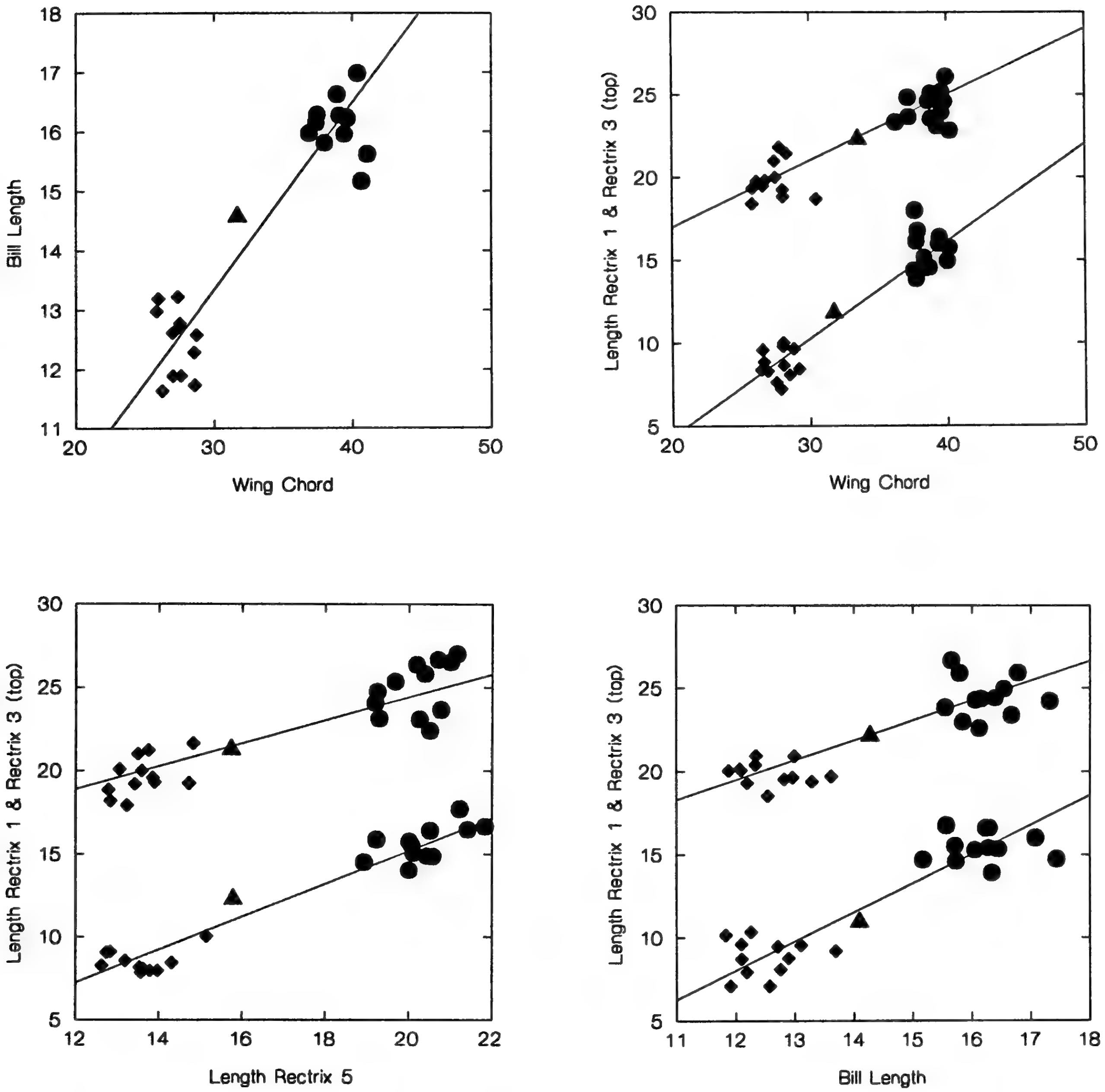

Fig. 2. Bivariate plots of selected measurements (see Table 1) of male *Acestrura heliodor* (diamonds), *A. mulsant* (filled circles), and their putative hybrid (triangle), *A. decorata* (BM[NH] 1888.7.25.203; =*Calothorax decoratus* Gould).

sess rufous, buff, or cinnamon-colored pigmentation on the rectrices and ventral plumage; *A. decorata* lacks any trace of such coloration. The geographic range of *Acestrura astreans,* which is restricted to the Sierra Nevada de Santa Marta, does not overlap the ranges of the other eight species in the restricted pool. *Acestrura astreans* also possesses a dark red gorget, which is not expressed in the type of *A. decorata.* The poorly-known woodstar *A. berlepschi* has a limited range in the lowlands of western Ecuador (Collar et al. 1992) and co-occurs only with woodstar species possessing buff or rufous plumage characters (e.g., *Myrmia micrura*). These facts constitute ample reason for removing *A. astreans* and *A. berlepschi* from the list of potential parental species.

External measurements.—Measurements of *Acestrura decorata* fall between the character means of the hypothesized parents (Table 1, Fig. 2). Despite the significant difference in size between the parental species (character means for *A. mulsant* are 22–77% larger than those for *heliodor*), both species and *A. decorata* share unusual tail proportions where rectrices 1, 2, and 5, are substantially shorter than rectrices 3 and 4. This offers additional support for the conclusion drawn from plumage pattern and color, that *A. decorata* is a hybrid between *A. mulsant* and *A. heliodor,* the first documented case of hybridization involving species of *Acestrura.* As such, *A. decorata* (=*Calothorax decoratus* Gould) should be removed from the synonymy of *A. heliodor* (contra Cory 1918) and relegated to the growing list of documented trochiline hybrids.

Acknowledgments

I thank Robert Prŷs-Jones and Michael Walters for permitting me to examine the type of *A. decorata* in The Natural History Museum, and the curators and staff of the American Museum of Natural History for access to their collections. I appreciate Richard Banks, Robert Prŷs-Jones, Tom Schulenberg, Michael Walters, and Richard Zusi for commenting on the manuscript. I thank Harry Taylor of The Natural History Museum photographic services for taking photographs and making prints. Travel was supported by the Department of Vertebrate Zoology and the Research Opportunities Fund, Smithsonian Institution.

Literature Cited

Berlioz, J., & C. Jouanin. 1944. Liste des Trochilidés trouvés dans les collections commerciales de Bogota.—L'Oiseau (n.s.) 14:126–155.

Buckley, P. A. 1982. Avian genetics. Pp. 21–110 *in* M. Petrak, ed., Diseases of cage and aviary birds. 2nd ed. Lea and Febiger, Philadelphia, 680 pp.

Chapman, F. M. 1926. The distribution of bird-life in Ecuador.—Bulletin of the American Museum of Natural History 55:1–784.

Collar, N. J., L. P. Gonzaga, N. Krabbe, A. Madroño Nieto, L. G. Naranjo, T. A. Parker III, & D. C. Wege. 1992. Threatened birds of the Americas: The ICBP/IUCN Red Data Book, 3rd edition, part 2. International Council for Bird Preservation, Cambridge, U.K., 1150 pp.

Cory, C. B. 1918. Catalogue of birds of the Americas. Part 2, No. 1.—Field Museum of Natural History Zoological Series 13:1–315.

Fjeldså, J., & N. Krabbe. 1990. Birds of the high Andes. Zoological Museum, University of Copenhagen, Denmark, 876 pp.

Gould, J. 1860. Descriptions of twenty-two new species of humming-birds.—Proceedings of the Zoological Society of London 28:304–312.

Graves, G. R. 1986. Systematics of the gorgeted woodstars (Aves: Trochilidae: *Acestrura*).—Proceedings of the Biological Society of Washington 99:218–224.

———. 1990. Systematics of the "green-throated sunangels" (Aves: Trochilidae): valid taxa or hybrids?—Proceedings of the Biological Society of Washington 103:6–25.

———. 1993. A new hybrid manakin (*Dixiphia pipra* × *Pipra filicauda*) (Aves: Pipridae) from the Andean foothills of eastern Ecuador.—Proceedings of the Biological Society of Washington 106:436–441.

———. 1996. Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes.—Proceedings of the Biological Society of Washington 109:373–390.

———, & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* × *Heliangelus amethysticollis*) from northern Colombia.—Condor 92:754–760.

Hartert, E. 1922. Types of birds in the Tring Museum. B. Types in the general collection. Trochili.—Novitates Zoologicae 29:403–412.

Hilty, S. L., & W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, 836 pp.

Meyer de Schauensee, R. M. 1949. Birds of the Republic of Colombia. Part 2.—Caldasia 5:381–644.

———, & W. H. Phelps, Jr. 1978. A guide to the birds of Venezuela. Princeton University Press, Princeton, New Jersey, 424 pp.

Morony, J. J., Jr., W. J. Bock, & J. Farrand, Jr. 1975. Reference list of the birds of the world. American Museum of Natural History, New York.

Peters, J. 1945. Check-list of birds of the world. Vol. 5. Museum of Comparative Zoology, Cambridge, Massachusetts, 306 pp.

Salvin, O. 1892. Catalogue of the birds in the British Museum, Vol. 16. London, 703 pp.

Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, 822 pp.

Appendix

Comparative descriptions of diagnostic plumage characters of adult male *Acestrura heliodor, A. mulsant,* and their hybrid, BM[NH] 1888.7.25.203 (=*Calothorax decoratus* Gould 1860). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

In *heliodor,* plumage of the capital and spinal tract is dark green, toned on the back, rump and uppertail coverts with bluish-green. Bluish reflections are slightly less evident on homologous plumage tracts in *mulsant* and the hybrid.

Gorget color in *heliodor* exhibits postmortem color change in specimens (Graves 1986), becoming pinker, less purple over time. The gorget color of the hybrid and 19th century specimens of *heliodor* and *mulsant* is pinkish-purple. Most specimens of *heliodor* possess a few buffy–white barbs on feathers at the anterior apex of the gorget. The pale chin spot of *mulsant* is significantly larger, whereas that of the hybrid is intermediate in size. The bases of gorget feathers in *heliodor* are grayish–buff separated from the pinkish-purple tip by a narrow transitional zone tinted green. Gorget feathers are patterned similarly in *mulsant* and in the hybrid, but the transitional bands are dark green and greenish–black, respectively. Lateral gorget feathers are much more elongated in *heliodor* (pinkish–purple tip, width = 1.6 mm, length = 4.7 mm) than in *mulsant* (width = 2.8 mm, length = 2.1 mm); gorget dimensions in the hybrid are intermediate (2.7 × 2.7).

The underparts of *heliodor* (posterior to the gorget) are similar in pattern but significantly darker than those of *mulsant* (Fig. 1). The hybrid is intermediate in appearance—in the darkness of the pectoral band, the width and intensity of the midline stripe, and in the distribution of white on the lower belly.

Rectrix color of *heliodor*: rectrix 1 is dark green; rectrix 2 is black medially and blackish–green laterally; rectrices 3–5 are black. Rectrix 1 of *mulsant* is dark green, the others (2–5) are black. Rectrices of the hybrid are intermediate in color: rectrix 1 is dark green with a blackish tip; rectrix 2 is black medially and blackish–green laterally; the outermost rectrices (3–5) are black.

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110(2):326. 1997.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 20 December 1996 in Vol. 53, 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.), % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case No.

2950 *Pseudofoenus* Kieffer, 1902 (Insecta, Hymenoptera): proposed designation of *Foenus unguiculatus* Westwood, 1841 as the type species.

2987 *Geopeltis* Regteren Altena, 1949, *Geoteuthis* Münster, 1843, *Jeletzkyteuthis* Doyle, 1990, *Loligosepia* Quenstedt, 1839, *Parabelopeltis* Naef, 1921, *Paraplesioteuthis* Naef, 1921 and *Belemnoteuthis montefiorei* Buckman, 1880 (Mollusca, Coleoidea): proposed conservation.

3016 *Gladiolites geinitzianus* Barrande, 1850 (currently *Retiolites geinitzianus*; Graptolithina) proposed designation of a neotype.

3007 *Trematospira* Hall, 1859 (Brachiopoda): proposed designation of *Spirifer multistriatus* Hall, 1857 as the type species.

2994 *Nothosaurus* Münster, 1834 (Reptilia, Sauropterygia): proposed precedence over *Conchiosaurus* Meyer, [1833].

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 20 December 1996 in Vol. 53, Part 4 of the *Bulletin of Zoological Nomenclature.* Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Opinion No.

1857. *Metabla tothrix* Sugonjaev, 1964 (Insecta, Hymenoptera): *Blastothrix isomorpha* Sugonjaev, 1964 designated as the type species.

1858. *Nectria* Gray, 1840 (Echinodermata, Asteroidea): *Nectria ocellata* Perrier, 1875 designated as the type species.

1859. Nine specific names of southern Afrotropical birds conserved.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(2):327–328. 1997.

BIOLOGICAL SOCIETY OF WASHINGTON

124th Annual Meeting, 9 May 1997

President Stephen Cairns called the meeting to order at 11:00 a.m. in the Waldo Schmitt Room, National Museum of Natural History. In summarizing the year's activities, Steve noted that in addition to the Council meeting held annually just prior to the general meeting, the Council met on 11 February 1997 and voted to donate a complete set of the *Proceedings* to the Labatorio de Invertebrados Bentonicos, Estacion Mazatlan, providing that institution would cover shipping and handling costs. The Council also authorized use of Society funds for compilation of an additional five sets of the *Proceedings,* which the Society hopes to sell for about $3,000 per set, plus postage. Wheldon & Wesley will advertise the availability of these sets, and receive 10% of profits from sales. In the future, the Society may not be able to compile additional complete sets because many issues are missing, and the large amount of photocopying necessary to produce a set is prohibitive.

Treasurer Chad Walter summarized Society finances for the period between 1 January and 31 December 1996. Total income was $72,372.30 ($40,130.10 from publication charges, $23,678.00 from dues and subscriptions, and $8,564.20 from sales of back issues and interest on Society accounts). Expenditures totalled $71,616.90 ($64,167.03 for publication costs, $7,118.70 for management costs, and $331.17 for bank charges). The net gain was $755.40 for this period (Table 1). The treasurer's report also indicated that the number of *Proceedings'* pages for which the Society received no remuneration was down in Volume 109 to 27.6%, vs. 45.6% in Volume 108 and 42.1% in Volume 107.

The President then summarized a report that Finance Committee Members Dick Banks and Austin Williams had presented to the Council. The report suggested that the Society (1) should look into better investment of endowment funds to increase the rate of return (currently less than 5%); (2) is subsidizing too many pages in the *Proceedings* which is depleting the General Fund residual; (3) should change the by-laws to indicate that interest from the endowment fund automatically be re-invested into the endowment fund, and that proceeds from sales of back-issues of the *Procedings* be used for general operating costs (these are currently the practices, but by-laws mandate the opposite, i.e., that proceeds from sales of back-issues by deposted into the endowment fund, and earnings from the endowment be used in the general operations of the Society); and (4) should adhere to the by-laws in the future by operating under an approved budget. Prior to the general meeting, the Council (1) voted to increase the amount authors are charged for a page in the *Proceedings* from $60.00 to $65.00, starting in 1988, (2) approved a motion allowing the Treasurer to continue current practices involving use of proceeds from sales of back-issues of the *Proceedings* until by-laws can be amended, and (3) approved a 1997 budget for the Society drafted by the Finance Committee.

President Cairns thanked Dick Banks, Chad Walter, and Austin Williams for their extraordinary efforts in maintaining and evaluating Society finances.

Council member Rafael Lemaitre then read the Editor's report, which was prepared by *Proceedings*' editor Brian Robbins. The report indicated that four issues of Volume 109 were published, comprising 70 papers and 770 pages. There were 80 submissions in 1996, down from the four

Table 1. Summary Financial Statement for 1996.

	General Fund	Endowment Fund	Total Assets
ASSETS: JANUARY 1, 1996	30,356.86	75,721.77	106,078.63
TOTAL RECEIPTS FOR 1996	68,744.73*	3,627.57**	72,372.30
TOTAL DISBURSEMENTS FOR 1996	71,616.90	00.00	71,616.90
ASSETS: DECEMBER 31, 1996	27,484.69	79,349.34	106,834.03
NET CHANGES IN FUNDS	−2,872.17	3,627.57	755.40

* A clause in the By-laws concerning the Endowment Fund states "The annual earnings from this Fund (as well as the proceeds from the sale of back issues) shall (may) be used in the general operations of the Society." The income from sales of back issues and bulletins inventory ($4,216) was not deposited into the Endowment Fund (Calvert Account) but into the General Fund (Riggs and Douglas Accounts).

** The interest generated by this Fund was not used.

previous years (86–93). However, as of 1 May 1997, there were 41 submissions, up from 34 in 1996 and 36 in 1995. There is no current backlog for accepted papers.

The meeting was adjourned at 11:14.

Respectfully submittted,
Carole C. Baldwin
Secretary

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

Submission of manuscripts.—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

Presentation.—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON" a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Appendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

Review.—One of the Society's aims is to give its members an opportunity for prompt publication of their shorter contributions. Manuscripts are reviewed by a board of Associate Editors and appropriate referees.

Proofs.—Authors will receive first proofs and original manuscript for correction and approval. Both must be returned within 48 hours to the Editor. Reprint orders are taken with returned proofs.

Publication charges.—Authors are required to pay full costs of figures, tables, **changes in proofs ($3.00 per change or revision),** and reprints. Authors are also asked to assume costs of page-charges. The Society, on request, will subsidize a limited number of contributions per volume. Payment of full costs will facilitate speedy publication.

Costs.—Printed pages @ $60.00, figures @ $10.00, tabular material @ $3.00 per printed inch per column. One ms. page = approximately 0.4 printed page.

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THE BIOLOGICAL SOCIETY OF WASHINGTON

PROCEEDINGS

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $25.00 (for USA and non-USA addresses) include subscription to the *Proceedings of the Biological Society of Washington.* Annual dues are payable on or before January 1 of each year. Renewals received after January 1 must include a penalty charge of $3.00 for reinstatement. Library subscriptions to the *Proceedings* are: $40.00 for USA and non-USA addresses. Non-USA members or subscribers may pay an additional $25.00 to receive the *Proceedings* by Air Mail.

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Identification and restriction of the type locality of the Manzano Mountains cottontail, *Sylvilagus cognatus* Nelson, 1907 (Mammalia: Lagomorpha: Leporidae)

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Abstract.—The locality from which the holotype of *Sylvilagus cognatus* Nelson, 1907 was collected is identified and restricted.

Nelson (1907:82) reported the type locality of *Sylvilagus cognatus* (currently regarded as *S. floridanus cognatus*) as "10,000 feet altitude, near summit of Manzano Mountains, New Mexico". Poole & Schantz (1942) subsequently reported the type locality as "Tajique, near summit of Manzano Mountains, altitude 10,000 feet, Valencia Co., N. Mex." The reference to Tajique as the specific locality where the holotype was collected has caused some question (Frey 1996). Tajique is a town at 2043 m on the eastern base of the Manzano Mountains located in the Tajique land grant, Torrance Co., New Mexico. In the southwestern U.S., cottontail taxa often are associated with distinctive vegetative communities. Accordingly, precise and accurate locations for type localities are important both to systematic and ecological studies of southwestern cottontails.

Nelson (1907) reported the holotype of *Sylvilagus cognatus* as collected by A. Rea in February 1905 and deposited in the Biological Survey Collection, USNM, as No. 136569; no additional specimens were mentioned. The USNM has three additional specimens of this taxon labeled as topotypes, also collected by A. Rea. Rea was not an employee of the Biological Survey of the museum and there are no field notes associated with these specimens. At that time, specimens received from non-employees were catalogued first into an intermediate catalogue (the "X catalogue") before formal cataloguing in the USNM catalogue. The four specimens of *cognatus* were X-catalogued on three separate occasions; therefore, they either were received at different times or processed at different times: first a single entry, later another, and finally two together, including the holotype (see Table 1). All four were catalogued as being from "Tajique, Manzano Mountains". The first entry, but not the later ones, has had added to it, in a different hand, "10,000 ft." These four specimens were then entered into the USNM catalogue at two different times, a single specimen first, and then later a series of three. Again all were entered in this catalogue as being from "Tajique, Manzano Mountains". The first entry has no elevation; the series of three, which includes the holotype, all have "10,000 ft." as part of the locality. Finally, all four specimen labels, which probably were produced at USNM rather than in the field, bear "10,000 ft." as part of the locality (variances with respect to locality among catalogues and specimen tags are summarized in Table 1). It thus would seem that Poole & Schantz (1942) included Tajique as part of the locality because it appears on all the labels and in both of the catalogues. Nelson (1907) may not have included Tajique in the original description because he had rea-

Table 1.—Data recorded on the specimen tags, in the intermediate "X catalogue," and in the museum catalogue of the Division of Mammals, U.S. National Museum for the holotype and three topotypes of *Sylvilagus cognatus*.

Source	Date	Locality	Remarks
X No. 4999	17 Jan 1905	New Mexico: Tajique	10,000 ft. (Manzano Mts.) topotype
USNM 135755	17 Jan 1905	New Mexico: Tajique	
skin tag	17 Jan 1905	New Mexico: Tajique	Manzano Mts. 10,000 ft.
X No. 5190	7 Feb 1905	New Mexico: Manzano Mts.	(Tajique) topotype
USNM 136567	7 Feb 1905	New Mexico: Manzano Mts.	Tajique (10,000 ft.)
skin tag	7 Feb 1905	New Mexico: Manzano Mts.	Tajique (10,000 ft.)
X No. 5330	Feb 1905	New Mexico: Tajique, Manzano Mts.	Topotype[a]
USNM 136568	Feb 1905	New Mexico: Manzano Mts.	Tajique (10,000 ft.)
skin tag	Feb 1905	New Mexico: Manzano Mts.	Tajique (10,000 ft.)
X No. 5331	Feb 1905	New Mexico: Tajique, Manzano Mts.	Type[a]
USNM 136569	Feb 1905	New Mexico: Manzano Mts.	Tajique (10,000 ft.)
skin tag	Feb 1905	New Mexico: Manzano Mts.	Tajique (10,000 ft.)

[a] Remarked for both entries "Skulls may be mismatched; received without tags."

son to believe that these specimens were not actually from Tajique. In his revision of the North American rabbits, Nelson (1909) reported five specimens from the Manzano Mountains and repeated the type locality in the synonymy as it was reported in the original 1907 description. However, he later remarked that "The topotypes of the present form from Tajique *ranch* [italics ours], at 10,000 feet altitude, near the highest part of the Manzano Mountains, vary [. . .], but a specimen from a short distance away and lower down on the east slope of the extreme south end of the range is larger . . . and agrees with those from Tajique" (Nelson 1909:192). We could not find "Tajique Ranch" on any map or gazetteer.

We were unable to find any correspondence concerning the actual place of capture of the rabbits in the Smithsonian Institution archives. However, Rea did send some miscellaneous bones to the Smithsonian Institution that he had uncovered in a cave on (or near) his ranch and they were cataloged as being from "Manzano Mts." or "Tajique, Manzano Mts." Further, in 1904 Rea sent a snake (*Pituophus*) to the Smithsonian Institution that subsequently was cataloged as being from "Tajique, ab. 10,000 alt". In a letter from A. K. Fisher to L. Stejneger in regards to this snake from Rea "captured near Tajique at about 10,000 ft. altitude," Fisher, discussing the unusual capture, quotes from Rea "speaking generally of rattlesnakes they are not found up here . . . suppose the climate is not warm enough for them. Rea's mailing address was given as "Tajique, Valencia Co., New Mexico." Torrance Co. was created from portions of Valencia and other counties on 16 March 1903 with additional portions of Valencia Co. (including most of the Manzano Mountains) added to Torrance Co. on 2 February 1905 (Coan 1965). Thus, it may be assumed that everything sent to the Smithsonian Institution by Rea was given the locality of Tajique because that was his mailing address rather than where the specimens were collected.

James H. Gaut, an employee of the Biological Survey, worked in the Manzano Mountains for three months during the fall and early winter of 1903 (Bailey 1928). Gaut's field notes (Smithsonian Institution Archives Record Unit 7176) describe camps made "near Tajique, altitude 7800 feet." Bailey (1928), in describing localities visited by Gaut describes Tajique, as "A *town* [italics ours] on the eastern slope of the Manzano Mountains, 30 miles southeast of Albuquerque; 7500 feet." This corresponds with the present town of Tajique and suggests that during the early 1900's Tajique commonly referred to the town. Interestingly, Gaut's field notes also describe a camp "at an elevation of 10,500 feet at Mr. A. Rea's ranch on the summit of the mountain due west of Tajique." The collector of the holotype and owner of this ranch probably are one and the same. Further, Gaut certainly knew the difference between Tajique and Rea Ranch. He cataloged a *Mustela* and several *Peromyscus* as being from "Summit of Ridge, Rea's Ranch, 10,000 ft." as opposed to others from "East slope near Tajique, 8400 ft.".

A map of the Cibola National Forest in the Manzano Mountains (USDAFS, 1938) labels a "house, cabin, or other building" symbol as "Rea." We believe this refers to the ranch owned by A. Rea from which the type specimen of *S. cognatus* was collected and herein restrict the type locality of *S. cognatus* to the vicinity of Rea Ranch. It is located 1.9 km N and 13.4 km W of Tajique (T6N, R5E, NE1/4 of NW 1/4 Sec. 9, N34°45′05.39″, W106°25′18.04″) on the northeast side of Bosque Peak, at 2880 m (= 9450 ft.) elevation. Bosque Peak is the highest peak of the north end of the Manzano Mountains; the relatively flat top of the peak covers approximately 2.5 km^2. Vegetation in the vicinity of the restricted type locality (vegetative communities follow Dick-Peddie, 1993) includes Upper Montane Coniferous Forest (i.e., mixed coniferous forest) characterized by Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*), small patches of Subalpine Coniferous Forest characterized by Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*), Subalpine-Montane Grassland, and Montane Scrub on dry, steep western slopes. The vegetative community in the vicinity of Rea Ranch is consistent with the observation that *Sylvilagus floridanus* is typically associated with montane forests in New Mexico. In contrast, Tajique, at a lower elevation, is a transition between Colorado Piñon (*Pinus edulis*)-One-seed Juniper (*Juniperus monosperma*) Woodland, One-seed Juniper Savanna, and Plains-Mesa Grassland.

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Literature Cited

Bailey, F. M. 1928. Birds of New Mexico. New Mexico Department of Game and Fish, 807 pp.

Coan, C. F. 1965. The county boundaries of New Mexico. New Mexico Legislative Council Services, Santa Fe, 27 pp.

Dick-Peddie, W. A. 1993. New Mexico vegetation; past, present, and future. University of New Mexico Press, Albuquerque, 244 pp.

Frey, J. K. 1996. Mammalian type localities in New Mexico.—Occasional Papers, Museum of Southwestern Biology 7:1–21.

Nelson, E. W. 1907. Descriptions of new North American rabbits.—Proceedings of the Biological Society of Washington 20:81–84.

———. 1909. The rabbits of North America.—North American Fauna, 29:1–314.

Poole, A. J., & V. S. Schantz. 1942. Catalog of the type specimens of mammals in the United States National Museum, including Biological Surveys Collection.—Bulletin of the United States National Museum 178:1–705.

U.S. Department of Agriculture Forest Service (USDAFS). 1938. Cibola National Forest (Manzano Division) New Mexico. Map.

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A new species of *Tantilla* (Serpentes: Colubridae) from northeastern Guatemala

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Abstract.—*Tantilla tecta* is described from near Laguna Yaxhá in northeastern Guatemala. This species belongs to the *taeniata* group and is the only member of this group known from the Petén region. It is characterized by: a narrow pale middorsal stripe restricted to the vertebral scale row; a narrow pale lateral stripe on adjacent portions of the third and fourth scale rows; a broad pale collar that is uninterrupted medially; and 54 subcaudals in the single known specimen. It is most similar to *T. jani* of the Pacific versant of northern Middle America and to *T. slavensi* of the Tuxtla region of southern Veracruz, Mexico, but may be differentiated from these species by the condition of the pale lateral stripes on the body, the extent of the pale nuchal collar, the coloration of the paraventral scale row, the number of ventrals and subcaudals, and relative tail length.

Resumen.—Se describe el colúbrido *Tantilla tecta* de las inmediaciones de la Laguna Yaxhá, Petén, Guatemala. Esta especie pertenece al grupo *taeniata* y es el único miembro del grupo conocido de la región petenera. Se caracteriza por poseer: una línea dorsal angosta restringida a la hilera vertebral de escamas; una línea lateral pálida en las areas adjacentes de las hileras de escamas tres y cuatro; un collar pálido y ancho no interrumpido dorsalmente; y 54 subcaudales en el único especimen conocido. Se parece más a *T. jani* de la vertiente pacífica de Guatemala y Chiapas y a *T. slavensi* de la región de Los Tuxtlas en el sur de Veracruz, México, pero se diferencia de estos por varias características, incluyendo la condición de la línea lateral pálida del cuerpo, la extención del collar pálido, la coloración de la hilera de escamas paraventrales, el número de escamas ventrales y subcaudales, y el largo relativo de la cola.

The extensive lowlands of the Petén region of Guatemala have been the focus of a number of herpetological investigations summarized by Campbell (1998), Duellman (1963), Lee (1980, 1996), and Stuart (1934, 1935, 1937, 1958). Relatively few species of reptiles probably remain to be discovered in this region, although our knowledge of the distributions and life histories for most species remains poor. Nevertheless, certain small, secretive snakes are notorious for their ability to escape detection. Among these are members of the genus *Tantilla,* of which several species are widespread in the Petén region. The *taeniata* group of *Tantilla* has a Middle American distribution and is composed of a dozen species, including the one herein described. The fact that half of the species in this group have been described since 1971, and that over half the species remain known from fewer than a dozen specimens, provides some indication of the difficulty of finding these snakes. It is likely that the combination of secretive habits, disjunct distributions, and perhaps rarity in nature contribute to the infrequency with which these snakes are encountered.

A single specimen of the *taeniata* group was recently discovered near Laguna Yaxhá in Petén, a locality from which no member of this group was known previously. We have compared this specimen with material housed in the University of Texas at Arlington and the University of Kansas collections, as well as carefully consulted the thorough descriptions provided by Pérez-Higareda et al. (1985), Savitsky & Smith (1971), Wilson (1982, 1983), and Wilson & Meyer (1971). This specimen cannot be allocated to any known species and we therefore propose that this species be known as

Tantilla tecta, new species

Figs. 1–2

Holotype.—The University of Texas at Arlington (UTA) R-41160 (previously UVG 1742), an adult female from the slope flanking the NE side of Laguna Yaxhá, Petén, Guatemala (17°03′43″N, 89°23′12″W). Collected by Cristian Granizo on 29 Jun 1992. This locality lies in Tropical Dry Forest at about 220 m.

Diagnosis.—A small species of *Tantilla* of the *taeniata* group (sensu Wilson, 1983) that may be distinguished from all other members of the genus by having: a narrow pale middorsal line restricted to the vertebral scale row; a narrow pale lateral line on adjacent portions of the third and fourth scale rows that extends onto the tail; a broad pale collar that is not interrupted medially; and 54 subcaudals in the single known specimen. In *T. briggsi, T. cuesta, T. cuniculator,* and *T. tayrae* the pale middorsal line is absent or restricted to a few scales on the anterior portion of the body, and in *T. taeniata* the middorsal stripe usually is expanded laterally to include all of the vertebral scale row and adjacent portions of the paravertebral rows. *Tantilla taeniata* can also be distinguished from *T. tecta* by the pale coloration on the top of the head which is distinctly paler than the dark borders of the nuchal collar. The dorsum of the head in *T. tecta,* in contrast, is about the same as the borders of the collar. *Tantilla flavilineata, T. oaxacae,* and *T. reticulata* differ from *T. tecta* in having a broader pale lateral stripe located on the fourth dorsal scale row and adjacent portions of the third and fifth rows.

Tantilla tecta differs from all species in the *taeniata* group except *T. jani* and *T. slavensi* in having a narrow pale middorsal line confined to the vertebral scale row. *Tantilla jani* differs from *T. tecta* in having less distinct pale lateral stripes that usually terminate on the posterior part of the body; a pale collar that includes the posterior portions of the parietals, posterior temporals, and ultimate supralabial; a pale postocular spot that includes the lingual margin of the fifth supralabial; the first pair of infralabials usually in contact; 37–47 subcaudals in females; and a relative tail length from 15 to 18% of the total length (versus 23% in female holotype of *T. tecta*). *Tantilla slavensi* may be distinguished from *T. tecta* in having part of the paraventral scale row pale (versus ground color from dorsum extending onto ventrals); a pale nuchal collar that is interrupted medially (versus not interrupted) and no more than one scale in length (versus two); a pale lateral line that becomes obscure on the base of the tail (versus evident even on distal portion of tail); the pale lateral line with a narrow dark brown border above, but not distinctly bordered below (versus a distinct dark border below pale lateral line which is darker than the border above); and 158–159 ventrals in two known females (versus 148 in single female). A higher number of ventrals is present in females of *T. flavilineata* (152–164) and *T. reticulata* (162–173) than in *T. tecta* (148), whereas slightly lower numbers are present in females of *T. oaxaca* (145), *T. tayrae* (140–146), and *T. cuesta* (147). A higher number of subcaudals is present in females of *T. taeniata* (58–65) and *T. reticulata* (58–70), and fewer subcaudals are present in females of *T. flavilineata* (43–49), *T. jani* (37–47), *T. striata* (31–34), *T. oaxacae* (48), *T. cuniculator* (48–53), *T. tayrae* (44–46), and *T. cuesta* (45) than in *T. tecta* (54). Undoubtedly, as many of

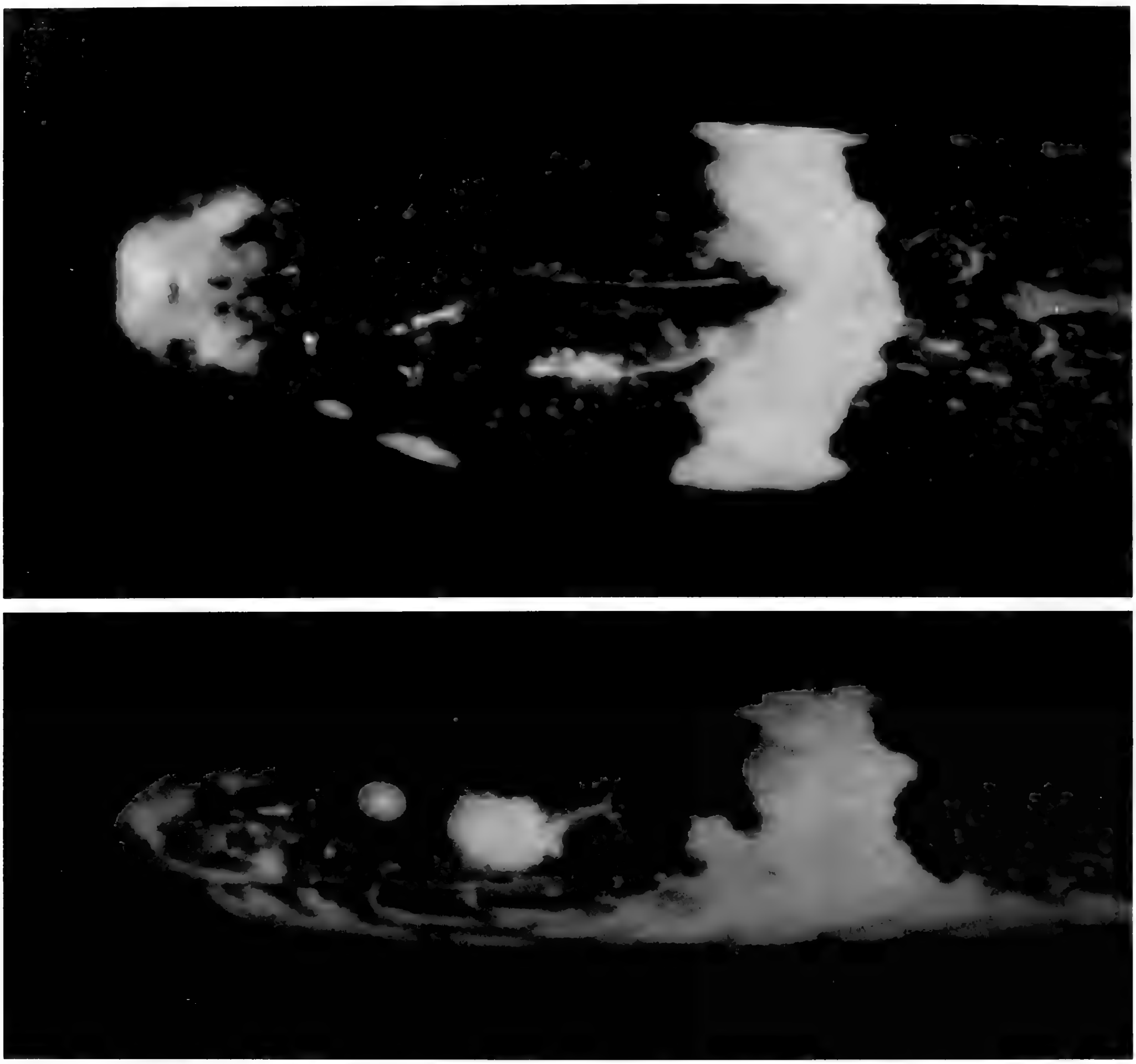

Fig. 1. Dorsal (upper) and lateral (lower) aspects of the head of *Tantilla tecta,* holotype (UTA R-41160). Head length 6.7 mm from front face of rostral to posterior end of mandible.

these species become known from more adequate samples, the ranges for some segmental counts will overlap.

Description.—An adult female, 222 mm in total length; tail length 51 mm (23% of total); head length 6.7 mm from front face of rostral to posterior end of mandible; head width 4.3 mm at broadest point (at level of angle of mouth); head scarcely distinct from neck; snout truncate in dorsal view; eye small, snout about 2.4 times as long as horizontal distance across eye; pupil subcircular; rostral about 1.6 times broader than high; internasals 1.7 times wider than long, laterally contacting anterior and posterior nasals; prefrontals large, slightly wider than long, laterally contacting posterior nasal, prefrontal, and narrowly contacting second supralabial; median prefrontal suture 0.4 times as long as frontal; frontal about 1.3 times longer than wide; parietals about 1.8 times longer than wide, median suture about 0.9 of frontal length; nasals completely divided, nostril located in posterior portion of anterior nasal; no loreal; 1/1 preoculars; 2/2 postoculars; temporals 1 + 1, separating fifth, sixth, and seventh supralabials from parietal; supralabials 7/7, the first contacting nasals, the second contacting postnasal, prefrontal, and preocular,

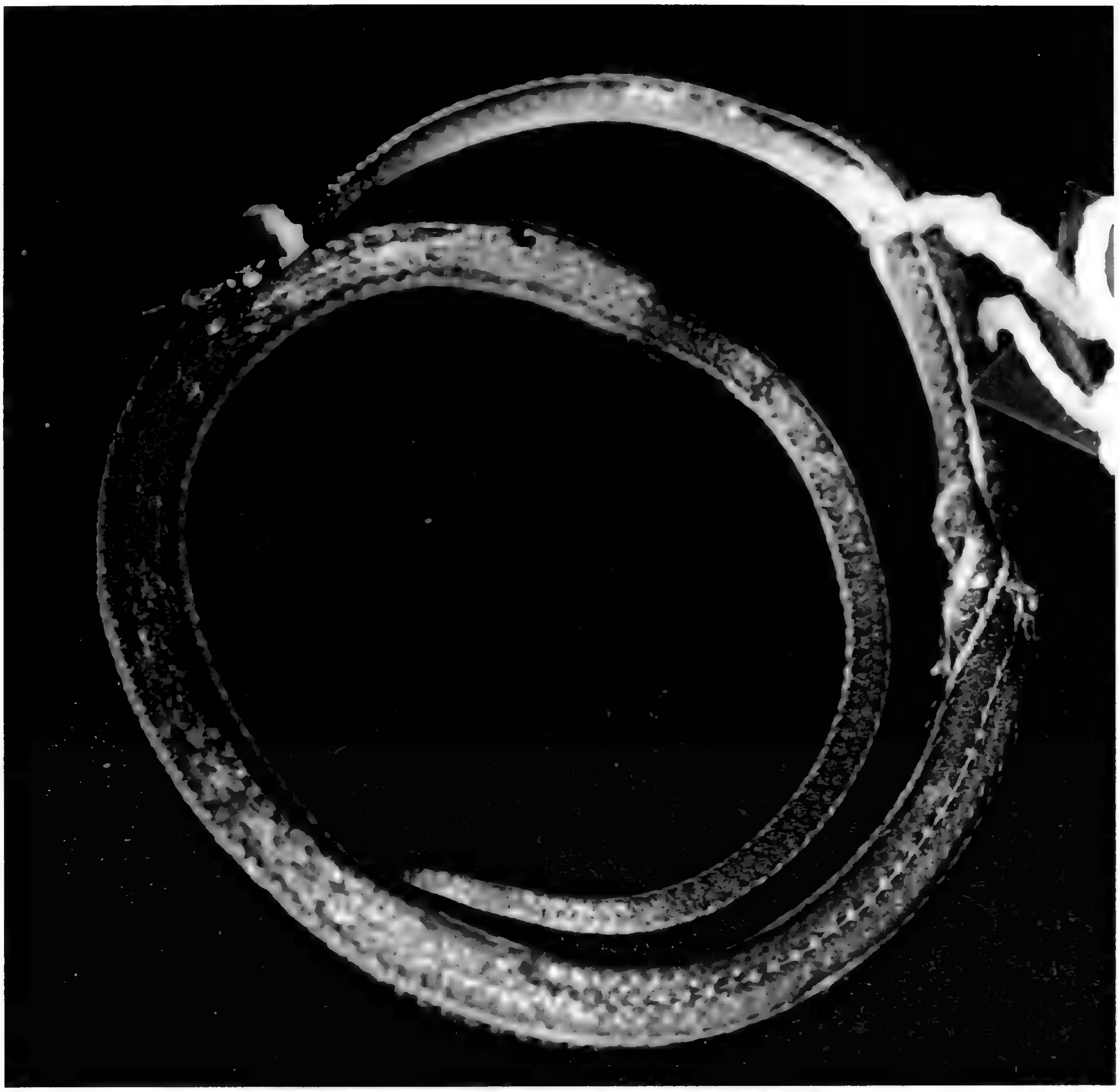

Fig. 2. *Tantilla tecta,* holotype (UTA R-41160), 222 mm TL (reproduced from UTA Slide No. 17660).

the third contacting preocular, the third and fourth contacting orbit, the fifth and sixth contacting anterior temporal, and the seventh the largest and contacting anterior and posterior temporals; mental about twice as broad as long, contacting anterior pair of chinshields; anterior chinshields well developed, about twice as long as wide; posterior chinshields well differentiated from gulars, about half of size of anterior chinshields; posterior chinshields separated from first ventral by two gulars and two preventrals; infralabials 6/6, first four pairs contacting anterior chinshields, fourth pair largest; dorsal scales smooth, in 15 longitudinal rows throughout length of body, no apical pits apparent; dorsal scales in 4 rows at level of tenth subcaudal; ventrals 148; anal divided; subcaudals 54, paired; anal glands extending posteriorly the length of four subcaudals.

In preservative (alcohol after formalin), ground color brown; a beige middorsal stripe arising about two scale lengths behind collar, extending most of the snout-vent length but becoming obscure on the posterior fourth of body; middorsal stripe occupying about median third of vertebral scale row, edged with dark brown laterally; beige lateral stripes on upper portion of scale row 3 and lower portion of scale row 4, edged with dark brown above and below, beginning about four scale lengths behind collar and extending to the tip of the tail; ground color below lateral stripe a bit darker than that on either side of the middorsal stripe; dorsal ground color extending to lateral portions of ventrals and subcaudals, paraventral scale row not pale; venter of body and tail cream-colored; top of head dark brown with pale spot on upper portion of rostral, internasals, and anterior two-thirds of prefrontals; a distinctive white nuchal collar immediately behind parietals and secondary temporals, collar 1–2 scales long, bordered posteriorly with black, merging with pale coloration of venter, not interrupted middorsally, a small intrusion of nuchal collar on lower posterior part of ultimate supralabial; a small, indistinct spot on adjacent portions of first and second supralabials; a prominent white postocular spot including most of fifth supralabial (but not lingual margin) and adjacent portions of lower postocular and anterior temporal; infralabials mostly pale except along lip margin and posterior portion of individual scales, fourth supralabial also with a dark margin medially.

The right maxillary bears 13 small teeth, which increase in size posteriorly; a small diastema separates the last two teeth which are enlarged and have lateral grooves. All maxillary teeth are compressed anteroposteriorly and bladelike.

Etymology.—The trivial name is derived from the Latin *tectus,* meaning concealed or secret, in allusion to the ability of this species to escape detection despite many years of field work in the region.

Remarks.—The *taeniata* group of *Tantilla,* as presently envisioned (Wilson 1983, Pérez-Higareda et al. 1985), consists of 12 species, including the species described here: *briggsi, cuesta, cuniculator, flavilineata, jani, oaxacae, reticulata, slavensi, striata, taeniata, tayrae,* and *tecta.* Based on the presumably derived condition of the pale longitudinal stripes on the body, *T. tecta* appears to be most closely related to *T. jani* and *T. slavensi.* Both *T. jani* and *T. slavensi* are geographically remote from *T. tecta* and occur in more mesic, less seasonal habitats (Tropical and Premontane Wet Forests). *Tantilla jani* is found at elevations of 305–960 m (Wilson 1985) along the Pacific versant of Middle America from eastern Oaxaca, Mexico, into Guatemala. *Tantilla slavensi* occurs in the Los Tuxtlas region of southern Veracruz, Mexico, over 600 km to the WNW of the type-locality for *T. tecta,* and is known from 50–800 m (Pérez-Higareda et al. 1985). Although the holotype of *Tantilla tecta* comes from an area usually considered to be covered with Tropical Dry Forest, Laguna Yaxhá is often thought to be near the boundary between Tropical Dry and Tropical Moist Forest, with the latter extending to the south shore of the lake. Certainly, the demarcation between these two types of forest is not clear and many of the hillsides and depressions to the north of the lake are covered with patches of forest that might be associated with Tropical Moist Forest. Nevertheless, the entire region around Laguna Yaxhá experiences a highly seasonal climate with most of the precipitation falling from May to December and a dry season extending from January through April.

The only species of *Tantilla* with which *T. tecta* is possibly sympatric in the Petén faunal area of Campbell & Vannini (1989) are *T. moesta, T. cuniculator,* and *T. schistosa. Tantilla moesta* has a long pale nuchal collar that extends posteriorly from the parietals for a length of at least three dorsal scales and usually includes the posteriormost three supralabials, the dorsum is uniformly dark brown or black without any longitudinal striping, and the venter is uniformly dark. *Tantilla cuniculator* has only the slightest indication of (or completely lacks) a pale middorsal stripe, the pale lateral stripe is less distinct than in *T. tecta,* the pale nuchal collar is usually broader, and the pale postocular spot usually includes the lingual margin of the fifth supralabial. *Tantilla schistosa* has a uniformly colored dorsum without longitudinal stripes and 24–40 subcaudals. *Tantillita canula* and *T. lintoni* also occur in Petén, but they are easily distinguished from *T. tecta* in lacking pale nuchal collars and pale lateral stripes, and having the middorsal stripe (if present) ill-defined and confined to the posterior part of the body and the tail.

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Literature Cited

Campbell, J. A. 1998. The Amphibians and Reptiles of northern Guatemala, Yucatan, and Belize.—The University of Oklahoma Press, Norman, Oklahoma, in press.

———, & J. P. Vannini. 1989. Distribution of amphibians and reptiles in Guatemala and Belize.—Proceedings of the Western Foundation of Vertebrate Zoology 4:1–21.

Duellman, W. E. 1963. Amphibians and reptiles of the rainforests of southern El Petén, Guatemala.—University of Kansas Publications, Museum of Natural History 15:205–249.

Lee, J. C. 1980. An ecogeographic analysis of the herpetofauna of the Yucatan Peninsula.—Miscellaneous Publications, Museum of Natural History, Univiversity of Kansas 67:1–75.

——— 1996. The Amphibians and Reptiles of the Yucatan Peninsula. Cornell Univiversity Press, Ithaca, New York. 500 pp.

Pérez-Higareda, G., H. M. Smith, & R. B. Smith. 1985. A new species of *Tantilla* from Veracruz, Mexico.—Journal of Herpetology 19:290–292.

Savitsky, A. H., & H. M. Smith. 1971. A new snake from Mexico of the *taeniata* group of *Tantilla*.—Journal of Herpetology 5:167–171.

Stuart, L. C. 1934. A contribution to a knowledge of the herpetological fauna of El Peten, Guatemala.—Occasional Papers of the Museum of Zoology, University of Michigan 292:1–18.

———. 1935. A contribution to a knowledge of the herpetology of a portion of the savanna region of central Petén, Guatemala.—Miscellaneous Publications, Museum of Zoology, University of Michigan 29:1–56.

———. 1937. Some further notes on the amphibians and reptiles of the Peten forest of northern Guatemala.—Copeia 1937:67–70.

———. 1958. A study of the herpetofauna of the Uaxactun–Tikal area of northern El Peten, Guatemala.—Contributions from the Laboratory of Vertebrate Biology, University of Michigan 75: 1–30.

Wilson, L. D. 1982. A review of the colubrid snakes of the genus *Tantilla* of Central America.—Milwaukee Public Museum Contributions in Biology and Geology 52:1–77.

———. 1983. A new species of *Tantilla* of the *taeniata* group from Chiapas, Mexico.—Journal of Herpetology 17:54–59.

———. 1985. *Tantilla jani* (Günther).—Catalogue of American Amphibians and Reptiles, Society for the Study of Amphibians and Reptiles, 369.1.

———., & J. R. Meyer. 1971. A revision of the *taeniata* group of the colubrid snake genus *Tantilla*.—Herpetologica 27:11–40.

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Geographic variation in the frog genus *Vanzolinius* (Anura: Leptodactylidae)

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Abstract.—*Vanzolinius discodactylus,* a forest-dwelling frog species of western Amazonia in South America, varies in characters of color pattern, morphology, and advertisement call. Analysis of this variation indicates that very local (site) differentiation results in mosaic patterns of differentiation, largely obfuscating larger geographic patterns. Comparison of available genetic estimates of differentiation for *V. discodactylus* are consistent with the morphologically and advertisement call-based conclusions. A previously studied forest-dwelling lizard and another forest-dwelling frog also demonstrate local differentiation patterns suggesting that the variation in *V. discodactylus* may represent a general pattern for forest-dwelling amphibians and reptiles in Amazonia.

During examination of specimens for a study of *Leptodactylus* species (Heyer 1994), several *Vanzolinius* specimens were encountered. Dr. Claude Gascon found *Vanzolinius* to be relatively common along the Rio Juruá in Brazil and used the species to test the riverine barrier hypothesis (Gascon et al. 1996). A cursory examination of these additional materials suggested that there was considerable variation, which might profitably be studied. The purpose of this paper is to analyze geographic variation in *Vanzolinius.*

Materials and Methods

As many adults, larvae, and recordings of advertisement calls as possible were assembled from major museum collections (Appendix 1).

The sex of individuals was determined either by examination of vocal slits, or dissection to examine gonads. The following categories are used: adult male—vocal slits present; juvenile male—testes present, but vocal slits not broken through; adult female—oviduct folded at least in part; juvenile female—ovaries present, but oviduct straight; juvenile—condition of gonads indeterminate (in some cases, gonads had been removed by previous workers).

Analyses differ depending on the type of data gathered for the characters examined. The following descriptions of characters are arranged by analytical groups.

Color patterns and external morphological features of adult form individuals.—These qualitative traits are categories recorded as either binary or multistate characters. For the latter, states were added to the series as they were encountered during the data-taking phase. The states within each series have no intended or implied relationships or transformation series. Intermediate conditions between states were recorded with the first letter of the state that most nearly approached the condition observed in the specimen examined.

Dorsal snout pattern: Three basic states were encountered: a relatively uniform dark pattern (Fig. 1A); a variegated pattern (Fig. 1B); and a uniform light pattern (Fig. 1C).

Light postorbital eye stripe: A series of symbols define the distinctiveness of the postorbital eye stripes: − [absent]; (+) [indistinct]; + [distinct]; +! [sharply defined].

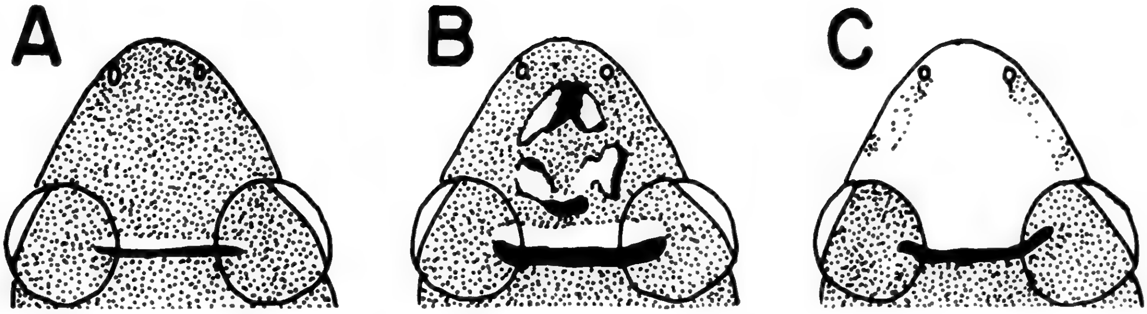

Fig. 1. Dorsal snout pattern standards.

In cases where the two sides of the head differed, both conditions were recorded.

Light subocular bar: The distinctiveness of the bar was noted by the same symbols as for the previous character, except the +! category was not encountered.

Dorsal pattern: Dorsal pattern variation forms a continuum among the more distinctive states recorded. The states recognized are: State A—either an uniform dorsum (brown or tan) or indeterminately blotched (Fig. 2A); State B—the dorsum with very distinct dark markings in the interorbital and interscapular areas (Fig. 2B); State C—distinct interorbital blotch, well defined chevron markings anteriorly and blotches posteriorly on the body (Fig. 2C); State C-1—as previous state except chevrons continuous; State D—a distinct darker straight edged band extending from behind eyes on full extent of dorsum (Fig. 2D); State D-1—as previous state, except sides irregular.

Dark mid-dorsal pin stripe: An interrupted dark mid-dorsal pin stripe was recorded as either present or absent.

Throat and chest pattern.—Variation in this character is continuous among the states encountered: State A—variegated pattern (Fig. 3A); State A-1—as previous state, but light; State B—uniform light pattern (Fig. 3B); State B-1—as previous state, but lateral portions darker; State C—dark speckled pattern (Fig. 3C); State C-1—as previous state, but dark spotting more extensive; State D—dark pattern (Fig. 3D); State E—dark pattern with light spots (Fig. 3E).

Belly pattern: Variation in this character is continuous among the states encountered:

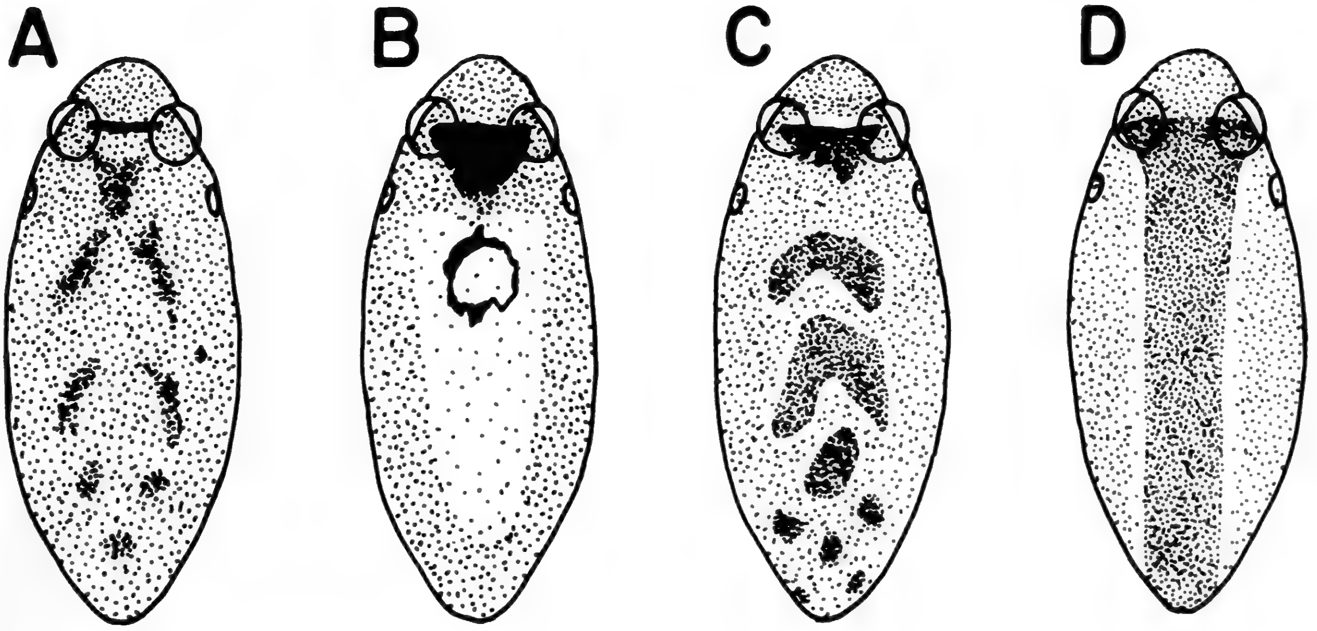

Fig. 2. Dorsal pattern standards.

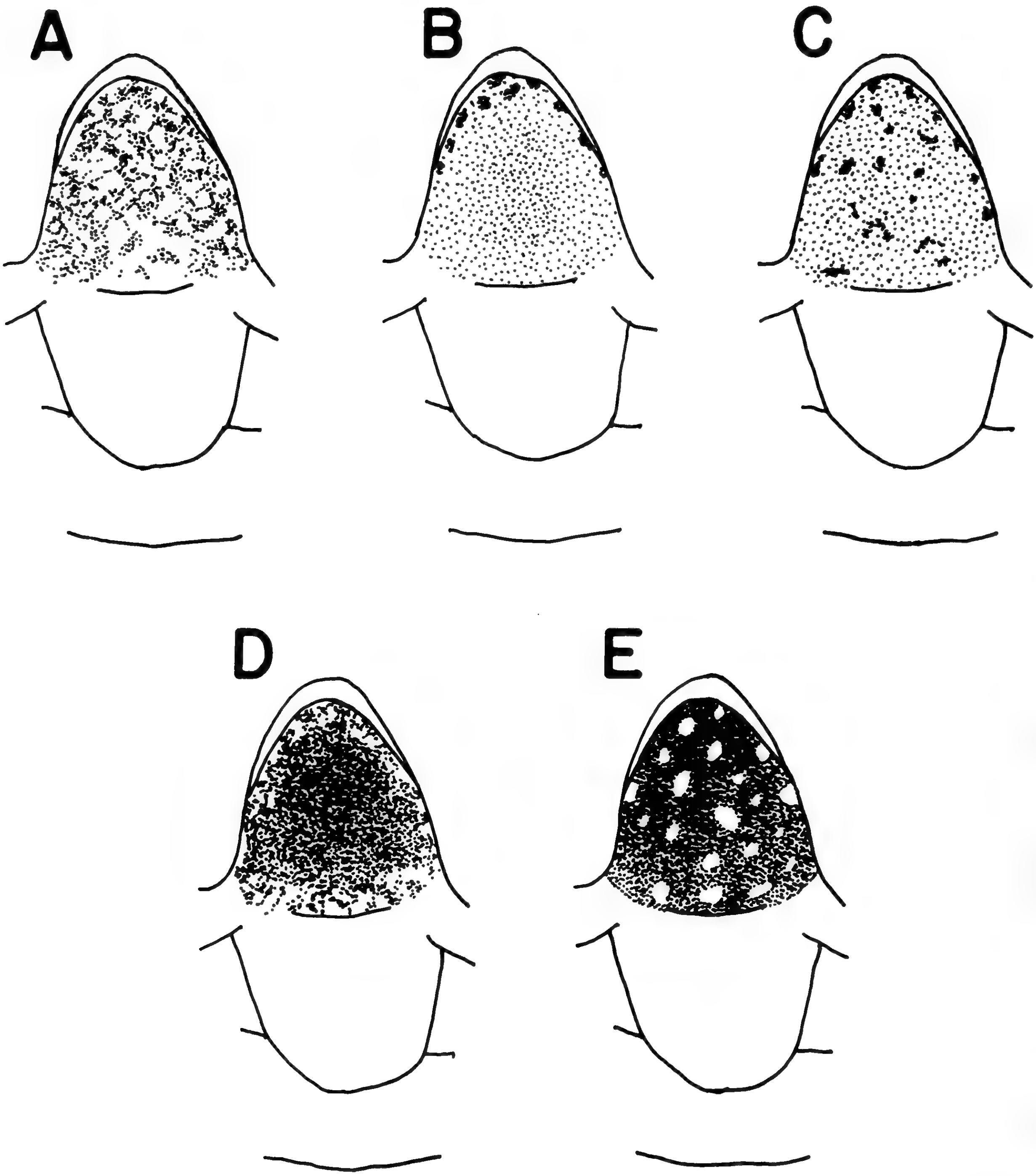

Fig. 3. Throat and chest pattern standards.

State A—speckled pattern (Fig. 4A); State A-1—almost uniform cream pattern; State B—indistinctly mottled, more intense anteriorly (Fig. 4B); State B-1, as previous state, but lighter; State C—distinctly mottled, rather uniform over belly (Fig. 4C); State C-1—as previous state, but lighter; State C-2—as State C but dark anteriorly and no melanophores posteriorly; State D—distinctly variegated dark and light pattern (Fig. 4D).

Posterior thigh pattern: Variation in this character is continuous among the states encountered: State A—indistinctly mottled (Fig. 5A); State B—indistinctly mottled with indistinct dark longitudinal band (Fig. 5B); State C—distinctly mottled (Fig. 5C); State D—speckled with indistinct dark longitudinal band (Fig. 5D); State E—speckled with distinct dark longitudinal band (Fig. 5E); State F—speckled with dark longitudinal band bordered above by light longi-

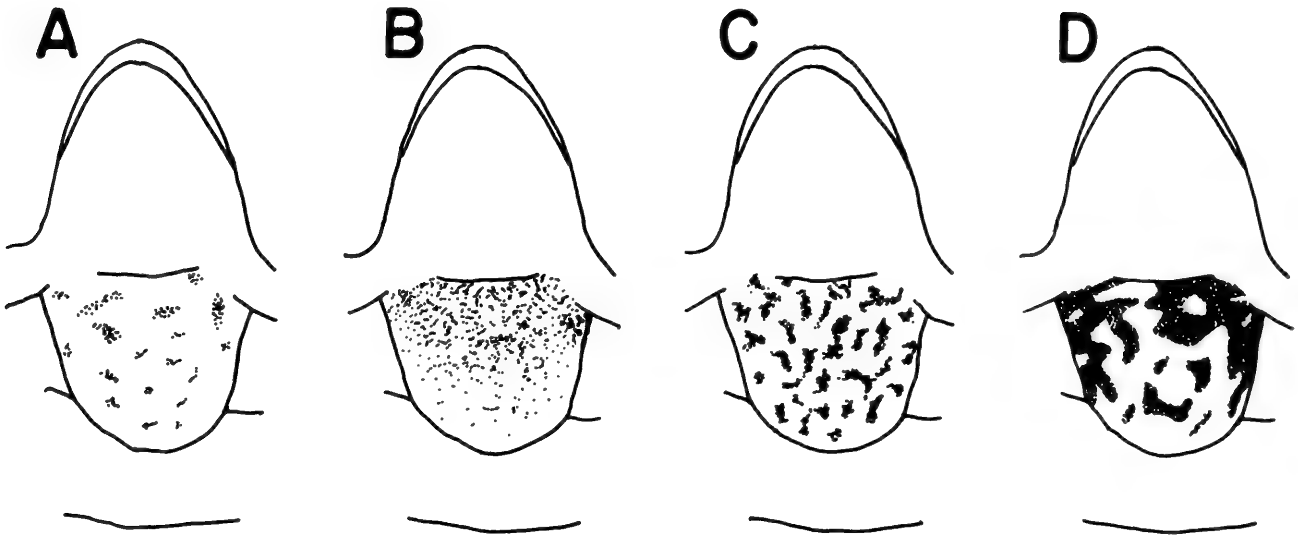

Fig. 4. Belly pattern standards.

tudinal stripe (Fig. 5F); State F!—as for State F except light stripe very distinct.

Outer tarsal pattern: Data were taken on the distinctiveness of the outer tarsal pattern relative to the dorsal tarsal pattern. However, variation turned out to be minimal and scoring could not be done consistently. These data are not analyzed further.

Dorsolateral fold condition: There is relatively little variation in this character and the variation that exists is difficult to evaluate in terms of the impact preservation has on recognition of fold condition. Most individuals have no dorsolateral folds. In a few individuals, a short ridge or elongated warts lie in the dorsolateral fold region posterior to the eye. The variation in this character is not analyzed further.

Male secondary sexual characters: All males lack secondary sexual characters of thumb or chest pads or spines or male arm hypertrophy as found in *Leptodactylus.*

Male vocal sac: Variation in this character is minimal and difficult to evaluate in terms of preservation artifact. In most males, the vocal sac is single and internal; in a few males, the single vocal sac has external indications of weak lateral folds. Variation of this character is not analyzed further.

Textures: Data were taken on textures of the dorsum, the upper shank, the outer tarsus, and sole of foot. In all cases the degree of development of shagreen and tubercles was difficult to categorize consistently and differentiate from preservation artifact. The

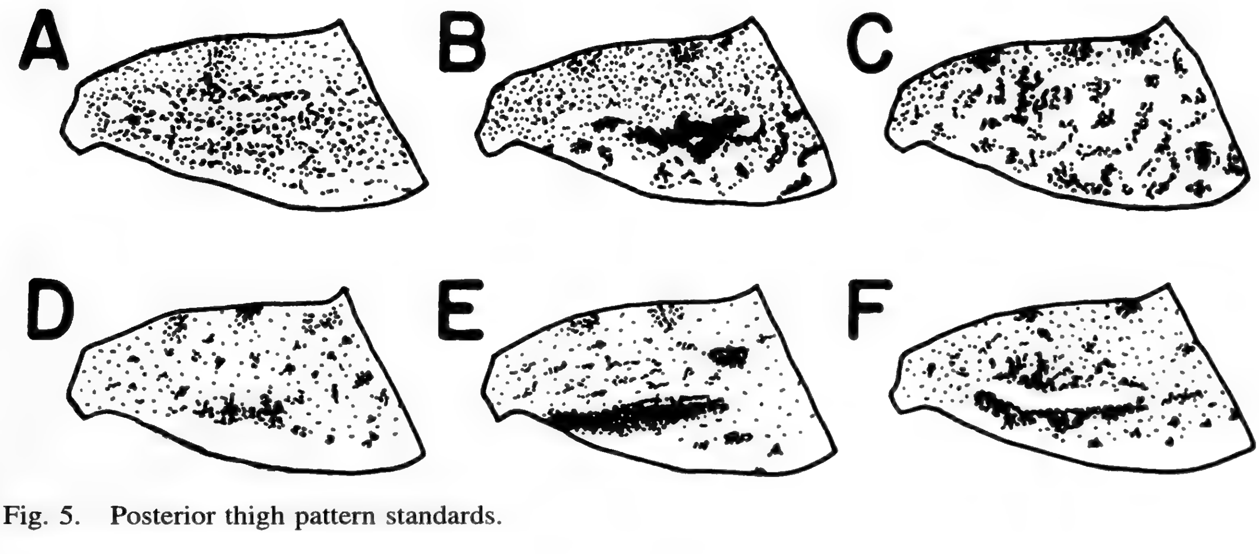

Fig. 5. Posterior thigh pattern standards.

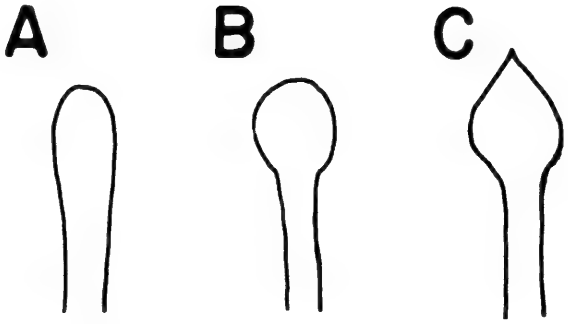

Fig. 6. Digit tip dorsal outline standards.

dorsum is tuberculate, with either small black-tipped or white-tipped tubercles, usually more densely packed posteriorly. The dorsum may also be somewhat granular, have a shagreen, or be smooth. The upper shank and outer tarsus consistently have tubercles, black and/or white tipped, and the surfaces may also be shagreened. The foot is either smooth or the outer margin has a few black/white tipped tubercles and/or a shagreen. Variation for these characters is not analyzed further.

Finger tip dorsal outline: For both finger and toe tip shapes, the outline shapes standardized by Savage (1987) for *Eleutherodactylus* were used. For both finger and toe tip dorsal outlines, only three of Savage's (1987) shapes were encountered corresponding to his unexpanded even (Fig. 6A), expanded even (Fig. 6B), and expanded pointed or lanceolate (Fig. 6C) states. The third finger tip is the most expanded and is the digit from which data were taken. Very little variation was encountered, suggesting that observer variation in interpreting shape was probably as large as actual variation. The conditions recorded ranged from not expanded, just A, A, A-B, or A-C. Variation is not analyzed further for this character.

Toe tip dorsal outline: The same standards were used for toe tips as for finger tips (Fig. 6). Data were recorded for both the third and fourth toe tips. The conditions for the third and fourth toe dorsal outlines are very similar. For 165 individuals, the conditions are identical, for 9 individuals the fourth toe dorsal outline is perceptibly more expanded than for the third, and for 75 individuals, the third toe dorsal outline is perceptibly more expanded than the fourth. As the third toe tip is a bit more expanded in the total sample, data are analyzed only for the third toe tip.

Dorsal toe grooves: The dorsal surfaces of the toes typically have from 2–5 grooves involving the epidermis and dermis. The grooves are almost parallel to each other along the long axis of the toe, but radiate slightly outward from the proximal toe tip to the distal tip. Usually the grooves extend almost the entire length of the expanded portion of the toe tip, but the grooves do not reach the tip of the toe. Counting the exact number of grooves is not always precise as the grooves are sometimes incomplete and preservation artifact can obscure the definition of the grooves. Data were taken for both the third and fourth toes. As for the dorsal outline, the conditions within individuals are similar, but typically the third toe has one more groove than the fourth. For 96 individuals, the third and fourth toes have the same number of grooves, for 18 individuals, the fourth toe has more grooves than the third, and for 132 individuals the third toe has more grooves than the fourth. Because the raw data indicate that the variation in the fourth toe mirrors that seen in the third, only the data for the third toe are analyzed further.

Analysis of preceding characters: The preceding characters are recorded as discrete entities even though variation is mainly continuous. Because the data are discrete, chi-square analyses are used to determine whether occurrence frequencies of states differ significantly. The 0.05 convention is used to determine significance. Data were adjusted, when necessary, to reach a minimum cell size of an average expected frequency of 5 (Hayek 1994:239). Data were first examined to determine whether states for adult males and females differed significantly. If they did not, then data recorded for juveniles were added to both the male and female data to provide more robust data sets for statistical analysis among geographic regions (see definitions of regions below).

Measurement data and analyses.—Measurements were taken on the following variables, as defined by Gascon et al. (1996): snout-vent length (SVL), nostril separation, eye width anterior, eye width posterior, head width, head length, eye to nostril distance, thigh length (=femur length of Gascon et al. 1996), shank length (=tibia length of Gascon et al. 1996), foot length, tympanum diameter (=tympanum height of Gascon et al. 1996), eye length, maximum width of third finger, and maximum width of fourth toe. Measurements were taken with a Helios dial calipers and recorded to the nearest 0.1 mm.

Only adult specimens are used for the measurement data analyses. As males and females are sexually dimorphic in size, they are analyzed separately (L. C. Hayek, C. Gascon, and W. R. Heyer (unpublished data) discuss multivariate analyses on morphometric data on *Vanzolinius.*) The data are analyzed using the software program SYSTAT 5 (Wilkinson et al. 1992).

Larval data.—To my knowledge, the only larvae available are those reported on by Duellman (1978) from a single locality in Ecuador (Mera, Pastaza). Specimens KU 121362–121363 are larvae ranging from Gosner stages 30–38. Specimens KU 121360–121361 are just metamorphosed individuals. There is no internal evidence from study of these specimens to either establish that they are *Vanzolinius* or they are not. Dr. John Lynch collected the specimens and informs me (pers. comm.) after he consulted his field notes, " . . . it appears that I guessed on the identification . . . on the basis of habitat selection. Hence, don't trust the identification." As nothing can be determined about geographic variation based on these specimens (even assuming they are *Vanzolinius discodactylus*), larvae are not treated further in this paper.

Advertisement call data and analyses.—Recordings of single individuals from five localities are available for analysis.

Brazil: Acre; Nova Vida, Rio Juruá, USNM Tape 256 Cut 12. Recorded at 1900 h on 17 March 1992 by Claude Gascon at a temperature of 25°C, no voucher specimen.

Brazil: Amazonas; Altamira, Rio Juruá, USNM Tape 255 Cut 2. Recorded at 1915 h on 17 November 1991 by Claude Gascon at a temperature of 25°C, voucher INPA 5021.

Brazil: Amazonas; Barro Vermelho, Rio Juruá, USNM Tape 254 Cut 5. Recorded at 1900 h on 27 October 1991 by Claude Gascon at a temperature of 24.4°C, voucher INPA 3352.

Brazil: Amazonas; Jainú, Rio Juruá, USNM Tape 254 Cut 13. Recorded at 1740 h on 2 November 1991 by Claude Gascon at a temperature of 26.1°C, no voucher specimen.

Ecuador: Napo; Limoncocha, USNM Tape 18 Cut 1. Recorded at 2000–2034 h on 9 July 1971 by Ronald Heyer at an air temperature of 23.4°C, water temperature 23.6°C, voucher LACM 92001.

Calls were analyzed using Canary 1.2 software (Charif et al. 1995) on a Power Macintosh 8500 computer. Calls were digitized for analysis at a sample rate of 22050 Hz and a sample size of 16 bits. Call rate was determined directly from recordings for periods ranging from 45 to 180 s per recording. Other call parameters were taken from a combination of waveform, audiospectrogram (=spectrogram as used in Canary manual), and spectrum analyses based on ten calls for each individual. Most of the recordings had considerable noise. Many parameters were taken from filtered calls. The filter around option was used for determining some parameters for USNM Tape 256 Cut 12 (filtered around 520–5000 Hz), USNM Tape 255 Cut 2 (filtered around 500–5000 Hz), USNM Tape 254 Cut 5 (filtered around 330–4000 Hz), and USNM Tape 18 Cut 1 (filtered around 500–4500 Hz).

Definition of geographic areas for analysis.—The primary purpose of this study is to determine the nature of geographic variation found within *Vanzolinius discodactylus.* Sample sizes are insufficient to analyze the data from each locality independently. Localities were plotted on a map and localities were grouped on the basis of geographic proximity (Fig. 7). The rationale used for grouping localities involved trying to maximize three criteria simultaneously: to have as many groups as possible in order to characterize geographic variation; to have as many individuals as possible in each group to permit robust statistical analyses; and to maintain geographic integrity. With respect to geographic integrity, a rule of thumb of keeping localities within the same major river drainage basins was generally applied (Areas A, B, C, D, F, G, H), but not exclusively so (Area E). Initially 10 geographic area groupings were made. When the data were examined for these groupings to see if they were sufficient, three of the groups lacked sufficient data for analysis. Two Colombian localities were sufficiently isolated from each other as well as other samples to be placed in their own groups; unfortunately, the specimens from both localities are faded such that data are incomplete for them. Thus, data for the Colombian localities of Caldas; Villa María and Caquetá; Florencia, are not included in the geographic analyses (Fig. 7, upper two squares). A single Peruvian locality (Ucayali, Yarinacocha) also formed a distinct geographic group by itself and contains one faded specimen, unsuitable for further geographic analysis (Fig. 7, lower square). Eight geographic groupings remain and are identified by letter in further discussion: (A) northern Amazonian Ecuador; (B) southern Amazonian Ecuador; (C) Amazonian Peru; (D) the Brazil-Colombia border region; (E) easternmost known localities for *Vanzolinius* in Amazonian Brazil; (F) the mid-region of the Rio Juruá of Brazil; (G) the upper region of the Rio Juruá in the Brazilian State of Amazonas; and (H) the upper region of the Rio Juruá in the Brazilian State of Acre.

As there are but five individuals available from Region D, (1 female, 1 male, 3 juveniles), Region D data are omitted from the analyses by areas, unless otherwise noted.

Results

Dorsal snout pattern.—This was the only character for which some individuals clearly demonstrated two states (this exception involved only conditions B and C both occurring in the same individual), suggesting partial independent genetic control of this character. The states (Appendix 2) were collapsed for analysis to three: (1) pure A, (2) any B, and (3) any C. Because several individuals had both states (2) and (3), the total number of state conditions analyzed exceeds the number of individuals examined for this character only.

The chi-square analysis by sex was not significant ($\chi^2 = 1.35$; $df = 2$; $P = 0.50 > 0.30$). Thus, male, female, and juvenile data were combined to analyze by geographic area. The chi-square analysis by geographic area is significant ($\chi^2 = 69.92$; $df = 12$; $P < 0.001$). In partitioning the results, regions A+B are distinct from regions E+F+G+H. Region C is not distinct from either of the other two area groupings.

Light postorbital eye stripe.—For individuals having different states on either side of the head, the more distinctive state was scored for statistical analysis (e.g., an individual recorded as having state (+) on one side of the head and + on the other was treated as having the + state for statistical analysis). The chi-square analysis by sex was significant ($\chi^2 = 6.43$; $df = 2$; $P = 0.05 > 0.02$); therefore the variation among geographic areas has to be analyzed separately by sex. For females, the chi-square analysis by geographic area is significant ($\chi^2 = 42.43$; $df = 12$; $P < 0.001$). In partitioning the significance, regions B+E are distinct from regions A+C+F+G+H. In order to meet the minimum expected cell size criterion for statistical robustness for males, the data had to be collapsed by rec-

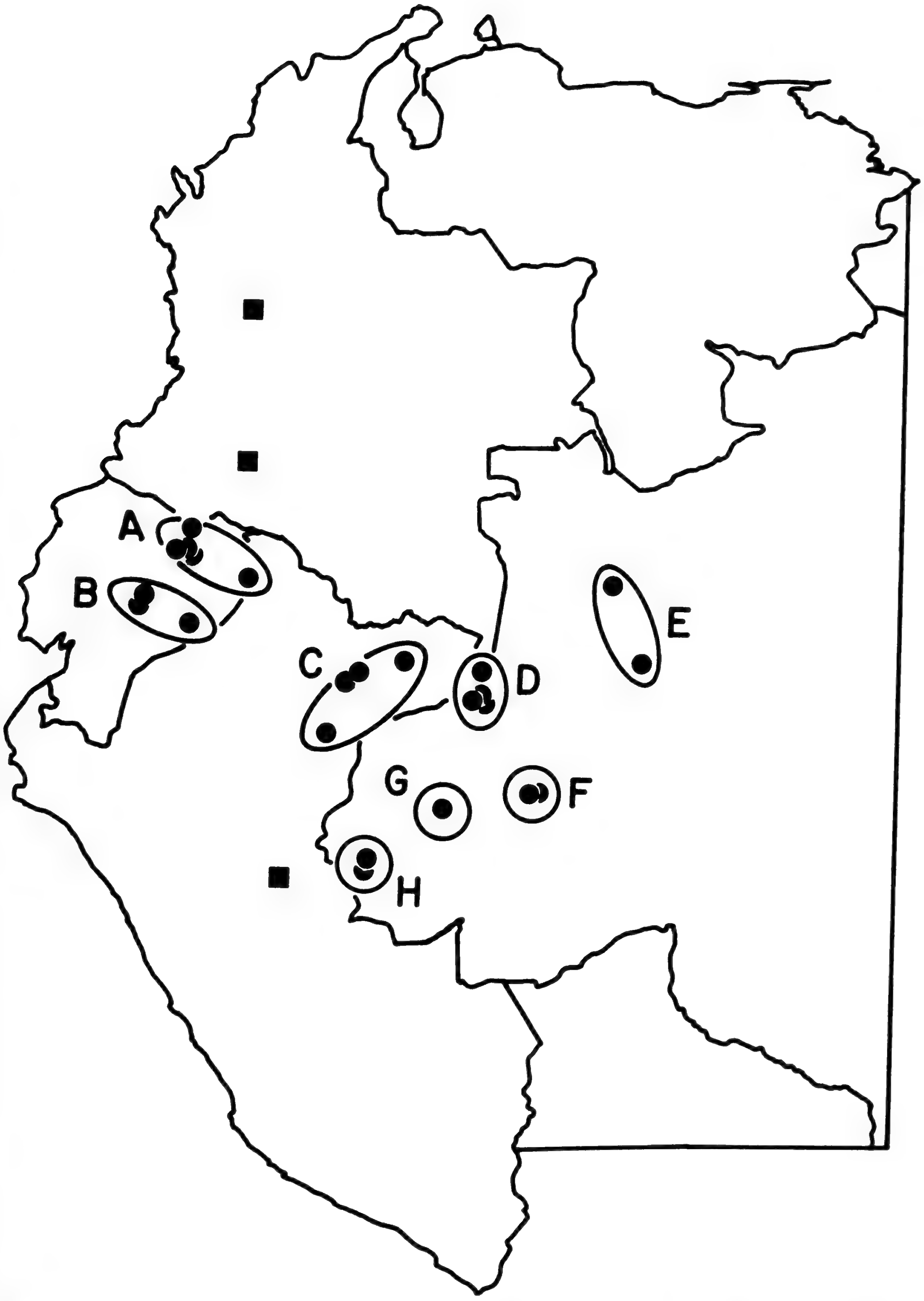

Fig. 7. Map of northwestern South America showing known distribution of *Vanzolinius discodactylus*. Guyana and Brazil are truncated by the 60°W meridian; Bolivia and Brazil by the 15°S parallel. Squares are single localities excluded from analysis of geographic variation. Circles and ellipses labelled A–H indicate groupings of localities (dots) used for analysis of geographic variation. A dot may represent more than one locality.

ognizing but two character states: absent (− state) or present (combined (+), +, +! states). The chi-square results are significant ($\chi^2 = 27.80$; $df = 6$; $P < 0.001$). In partitioning the results, the significance is due entirely to the distinctiveness of the Area B specimens.

Light subocular bar.—For individuals having different states on either side of the head, the more distinctive state was scored for statistical analyses. The chi-square analysis by sex was significant ($\chi^2 = 6.85$; $df = 2$; $P = 0.05 > 0.02$). In order to meet the assumption of minimum expected cell size for females, the data for Area H were deleted. The resultant chi-square analysis is not significant ($\chi^2 = 15.49$; $df = 10$; $P = 0.20 > 0.10$). To meet the minimum expected cell size for the male data, the states were collapsed to two: absent (− state) and present ((+) and + states). The resultant chi-square analysis is not significant ($\chi^2 = 9.59$; $df = 6$; $P = 0.20 > 0.10$).

Dorsal pattern.—For statistical analyses, the first state recorded for intermediate conditions is used (e.g., a specimen recorded as having condition A−B is scored as having condition A for the statistical tests). The chi-square analysis by sex is not significant ($\chi^2 = 2.93$; $df = 3$; $P = 0.50 > 0.30$); female, male, and juvenile data were combined to analyze by geographic area. To meet the assumption for minimum expected cell size, States D and D-1 are combined; however, Area D is included. The chi-square result among areas is significant ($\chi^2 = 203.09$; $df = 28$; $P < 0.001$). In partitioning the results the following area groupings are distinct from each other: A; B; C+D+E; F+G+H.

Dark mid-dorsal pin stripe.—The chi-square analysis by sex is significant ($\chi^2 = 5.86$; $df = 1$; $P = 0.02 > 0.01$). To meet the minimum expected cell size criterion for females by area, Area H was deleted. The chi-square result is significant ($\chi^2 = 11.47$; $df = 5$; $P = 0.05 > 0.02$). Partitioning the results indicates the following area groupings are distinct from each other: A+B; C+E+F+G. For males, the chi-square analysis of character states by area is not significant ($\chi^2 = 9.43$; $df = 6$; $P = 0.20 > 0.10$).

Throat and chest pattern.—As for dorsal pattern, the first state recorded for intermediate conditions is scored for the statistical analyses. State E was scored for only one individual and is not considered in the analyses. As only two known-sex individuals have State B-1, and only one known-sex individual has State C-1, State B-1 is combined with State B and State C-1 is combined with State C in the analyses. The chi-square analysis by sex is significant ($\chi^2 = 23.20$; $df = 4$; $P < 0.001$). To satisfy the minimum expected cell frequency assumption for females, drastic manipulations are required. Areas B and H are excluded. States A-1 and A are combined. The resultant chi-square analysis is significant ($\chi^2 = 23.39$; $df = 8$; $P = 0.01 > 0.001$). In partitioning the results, only areas E+F are distinct. Drastic manipulations are also required to analyze the male variation. States C and C-1 are deleted. Areas C, E, G, and H are deleted. States A-1 and A are combined. The resultant chi-square test is not significant ($\chi^2 = 1.90$; $df = 4$; $P = 0.90 > 0.50$).

Belly pattern.—As for dorsal pattern, the first state recorded for intermediate conditions is scored for statistical analyses. To meet the minimum expected cell frequency assumption for the analysis by sex, the following states are combined: A and A-1; B and B-1; C, C-1, and C-2; State D is deleted. The resultant chi-square analysis is significant ($\chi^2 = 8.60$; $df = 2$; $P = 0.02 > 0.01$). To analyze females, the same state combinations described above are used and Areas B and H are deleted to meet the minimum expected cell size assumption. The chi-square result is statistically significant ($\chi^2 = 56.20$; $df = 8$; $P < 0.001$). Partitioning the results indicates that the following area groupings are distinct from each other: A; C+E; F+G. To meet the minimum expected cell size assumption for males, only the combined states (as above) from Areas B, E, and F could be analyzed. The chi-square results are significant (χ^2 = 24.43; *df* = 4; *P* = 0.001); however, there are too few areas involved for meaningful partitioning.

Posterior thigh pattern.—As for dorsal pattern, the first state recorded for intermediate conditions is scored for statistical analyses. As only three individuals have State F!, it is combined with State F. The chi-square analysis by sex is not significant (χ^2 = 9.95; *df* = 5; *P* = 0.10 > 0.05); females, males, and juveniles are combined to analyze character states by geographic areas. The chi-square analysis by area is significant (χ^2 = 101.30; *df* = 30; *P* < 0.001). Partitioning the results indicates the following geographic area groupings are distinct from each other: A+B; C; E; F+G; H.

Third toe tip dorsal outline.—Only one individual was scored with any indication of State C, and it was an intermediate State B−C; for statistical analyses, that individual was scored as having State B. As only two individuals had the unexpanded state, that state is combined with the "Just A" State for analyses. The chi-square analysis by sex is not significant (χ^2 = 6.90; *df* = 4; *P* = 0.20 > 0.10); females, males, and juveniles are combined for analysis of state frequencies among geographic areas. The chi-square analysis by area is significant (χ^2 = 158.78; *df* = 24; *P* < 0.001). In partitioning the results, the following area groupings are distinct from each other: A; B+C; E; F+G+H.

Third toe tip dorsal grooves.—Because so few individuals had only one groove (Appendix 2), the individuals are combined with those having two grooves. The resulting chi-square analysis by sex is not significant (χ^2 = 0.58; *df* = 3; *P* = 0.80 > 0.70); females, males, and juveniles are combined for analysis of state frequencies among geographic areas. The resultant chi-square analysis is significant (χ^2 = 34.90; *df* = 18; *P* = 0.01 > 0.001). Partitioning the results indicates that the following geographic groupings are distinct from each other: C; E; A+B+F+G+H.

Measurements.—Because only two adult males represent Area G, they are deleted from the analyses.

MANOVA analyses were run on the two data sets (male and female). All univariate F tests were statistically significant ($P \leq 0.001$). The multivariate tests are also significant for both data sets (e.g., Wilks' Lambda for male data = 0.022, $F_{(70),\ 237}$ = 4.136, *P* < 0.001; for female data Wilks' Lambda = 0.025, $F_{(84),\ 312}$ = 3.501, *P* < 0.001). Thus, there is significant variation of the measurement data among the geographic areas.

In order to understand the nature of the geographic variation, discriminant function analyses were performed on untransformed data and are discussed separately for the male and female data.

The male data post-classification results (Table 1) indicate that sizes and shapes are distinctive for each area, with lesser distinctiveness in morphologies between Areas A and B. A plot of the first two canonical scores (Fig. 8) indicates that the Area A and B samples overlap each other to a greater extent than any of the other samples. The male measurement data support the following area groupings as distinct from each other: A+B; C; E; F; H.

The female data post-classification results (Table 2) also indicate that the morphologies are distinctive within each region, with less differentiation between Areas C and E and among Areas F, G, and H. The plot of the first two canonical scores (Fig. 9) demonstrates extensive overlap of specimen data for Areas C and E and Areas F, G, and H. The female measurement data indicate the following area groupings to be distinct from each other: A; B; C+E; F+G+H.

Comparison of the male and female data underscore that the males and females from Area C differ markedly in their association with the other samples. The Area C males are quite similar to those of Area H but dif-

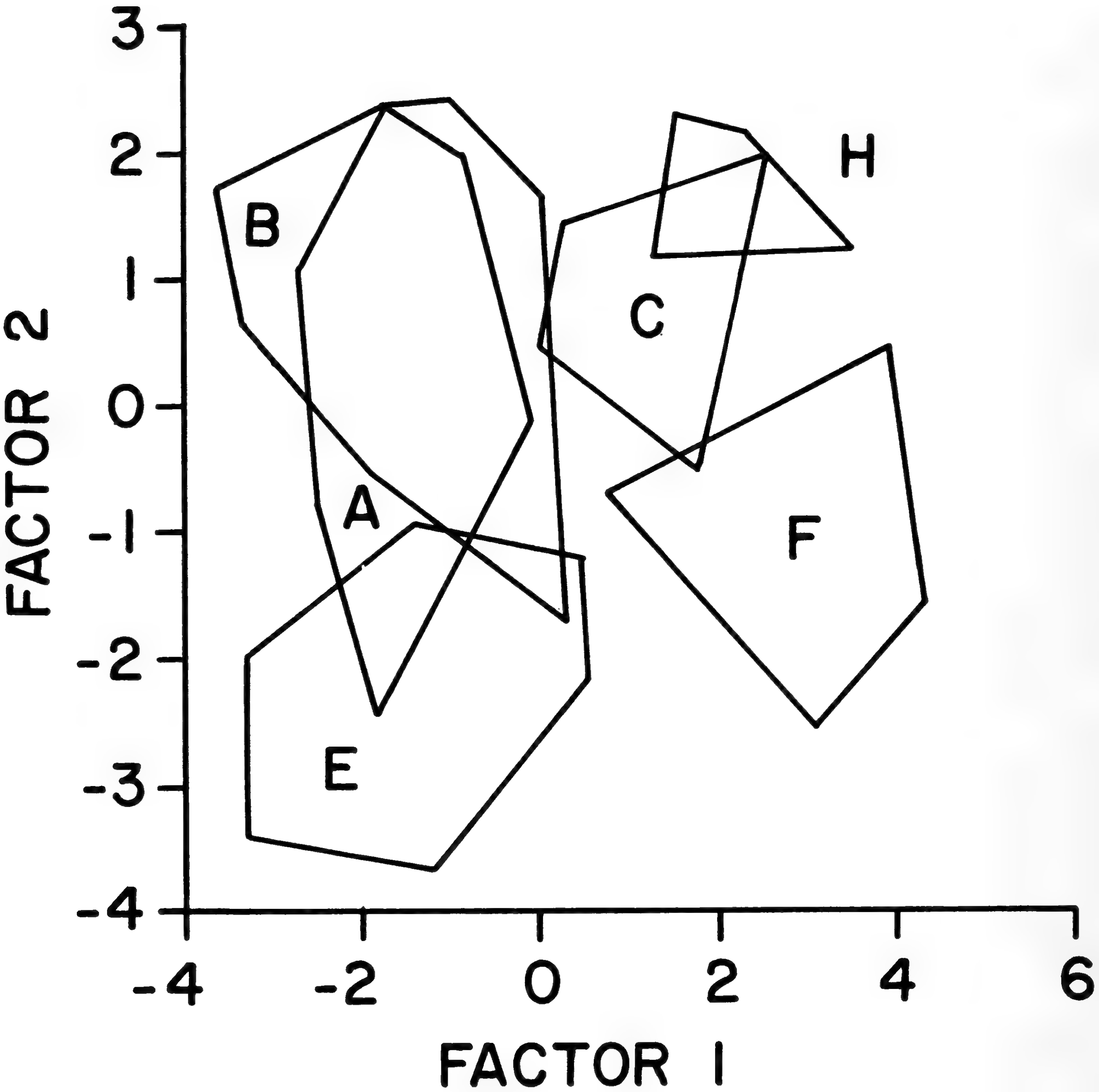

Fig. 8. Graph of first and second canonical factors for Area A–C, E–F, H males.

fer strikingly from those of Area E. Conversely, the Area C females are quite similar to those of Area E but distinct from those of Area H. These patterns suggest that size and shape have responded to separate selection pressures for males and females in *Vanzolinius.*

Advertisement calls.—The call from Limoncocha, Ecuador has been analyzed and described previously (Straughan & Heyer 1976).

Calls consist of individual notes which are partially pulsed. The basic call parameters are similar among all five recordings (Table 3). The exact durations of the calls are difficult to determine, as it appears that there is microphone ringing.

The most variation among calls involves: packaging of pulses; relative sharpness of attack; one or two distinct broadcast frequency bands; and maximum broadcast frequency energy. (The recording qualities are insufficient to adequately evaluate harmonic structure.) There is a continuum of variation from a note that has relatively weak partial pulses to a note that has a few strong pulses, almost or entirely complete, each of which may or may not be partially pulsed

Table 1.—Discriminant function analyses for male *Vanzolinius* measurement data by geographic areas.

	Number of observations classified into areas					
	A	B	C	E	F	H
Area A	5	2	0	1	0	0
Area B	1	18	0	1	0	0
Area C	0	0	9	0	0	1
Area E	0	0	0	12	0	0
Area F	0	0	0	0	12	0
Area H	0	0	0	0	0	6

Table 2.—Discriminant function analyses for female *Vanzolinius* measurement data by geographic areas.

	Number of observations classified into areas						
	A	B	C	E	F	G	H
Area A	7	0	0	0	0	0	0
Area B	0	4	0	0	0	0	0
Area C	0	0	5	1	0	0	0
Area E	1	0	5	22	0	0	0
Area F	0	0	1	0	14	1	4
Area G	0	0	0	0	0	5	2
Area H	0	0	0	0	0	1	2

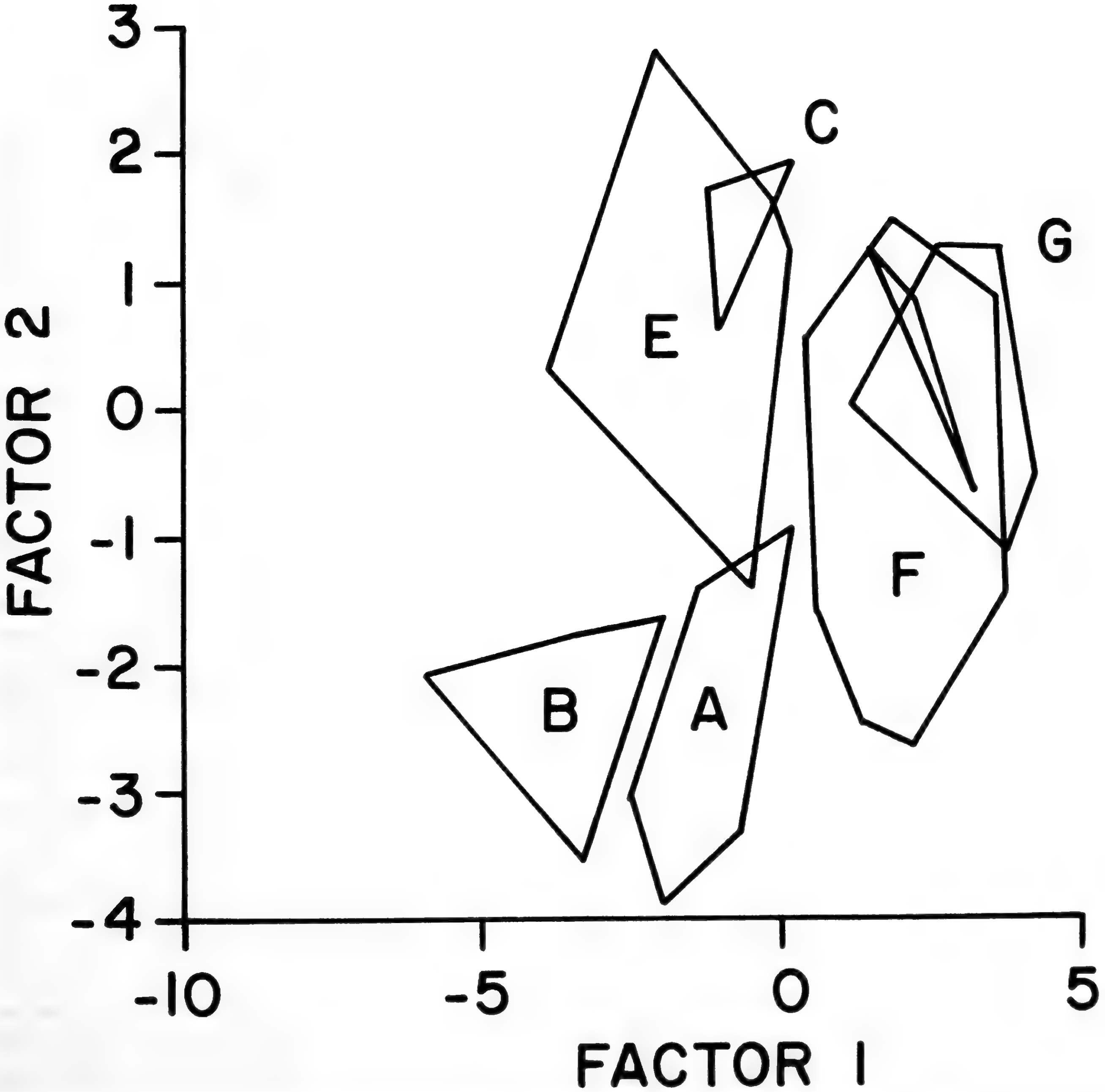

Fig. 9. Graph of first and second canonical factors for Area A–C, E–H females. The polygon for Area H is not labeled and occurs entirely within polygon F.

Table 3.—Advertisement call data for *Vanzolinius* specimens from five localities.

	Geographic area				
	A	F	F	F	H
USNM Tape & Cut	18,1	254,5	254,13	255,2	256,12
Call rate per s	0.8	1.1	1.3	1.4	0.9
Mean call duration (s)	0.14	0.14	0.12	0.13	0.14
Modal # of strong pulses	1	5	4	1	1
Mean # of total partial pulses	16.8	21.7	18.3	13.9	18.5
Very sharp attack	+(?)	—	—	+	+
Portion of call with most energy	First half to middle	First half to middle	Middle to first half	First half	First half
Two distinct broadcast bands	—	+	+	+	weak
Modal value of most intense frequency for lower broadcast band	—	1630	1560	1730	1980
Modal value of most intense frequency for higher broadcast band	2850	2570	2410	2590	2590
Modal values of total frequency range	2260–3190	1330–2930	1160–2830 1250–	1320–3020	1490–3010 –3090
Harmonics	—	—	weak	weak?	weak?

(Fig. 10). All calls are frequency modulated, increasing over a short time span. The relative sharpness of attack varies from moderate to sharp (Fig. 11). During the frequency rise at the beginning of the call, there is variation in how much energy is broadcast during the beginning of the call (1 or 2 broadcast bands, Fig. 12). The dominant frequencies of frog calls are known to vary with temperature, typically in an increasing manner (Duellman & Trueb 1986: 104). Although there is relatively little variation of environmental temperatures at times of recordings, the few data points suggest an inverse relationship with temperature with maximum broadcast frequency energy (Fig. 13). This, in turn, suggests that the variation in dominant frequencies is due to something other than temperature.

Given such small sample sizes, it is not clear how much of the observed variation among calls is due to individual variation versus population or regional differentiation. The recordings from the paired sites of Barro Vermelho and Jainú (see Gascon et al. 1996) share distinctive call features of pulse packaging and sharpness of attack; these features are not found in the other call from the same geographic area (F), Altamira. Thus, this call variation appears to be very local. Two other features vary among the geographic areas, the presence of one or two broadcast frequency bands and dominant broadcast frequencies (Table 3).

Differentiation Patterns

Color patterns, morphology, measurements, calls.—Two trends are apparent from the preceding results (summarized in Table 4).

1) There is a strong component of differentiation at the local geographic area as defined by Areas A–H in this study. There is a suggestion that local differentiation is more pronounced throughout the region covered by Areas A–E than for the region covered by Areas F–H.

2) There is also a component of geographically related differentiation. Areas A and B share a set of states; Areas C, (D), and E share a set of states (evidence for including D based on only one available character, however); and Areas F, G, and H also share a set of states.

The above characterizations are conservative. The actual levels of differentiation in *Vanzolinius* doubtless are greater than those demonstrated in this study. In many cases, insufficient sample sizes forced col-

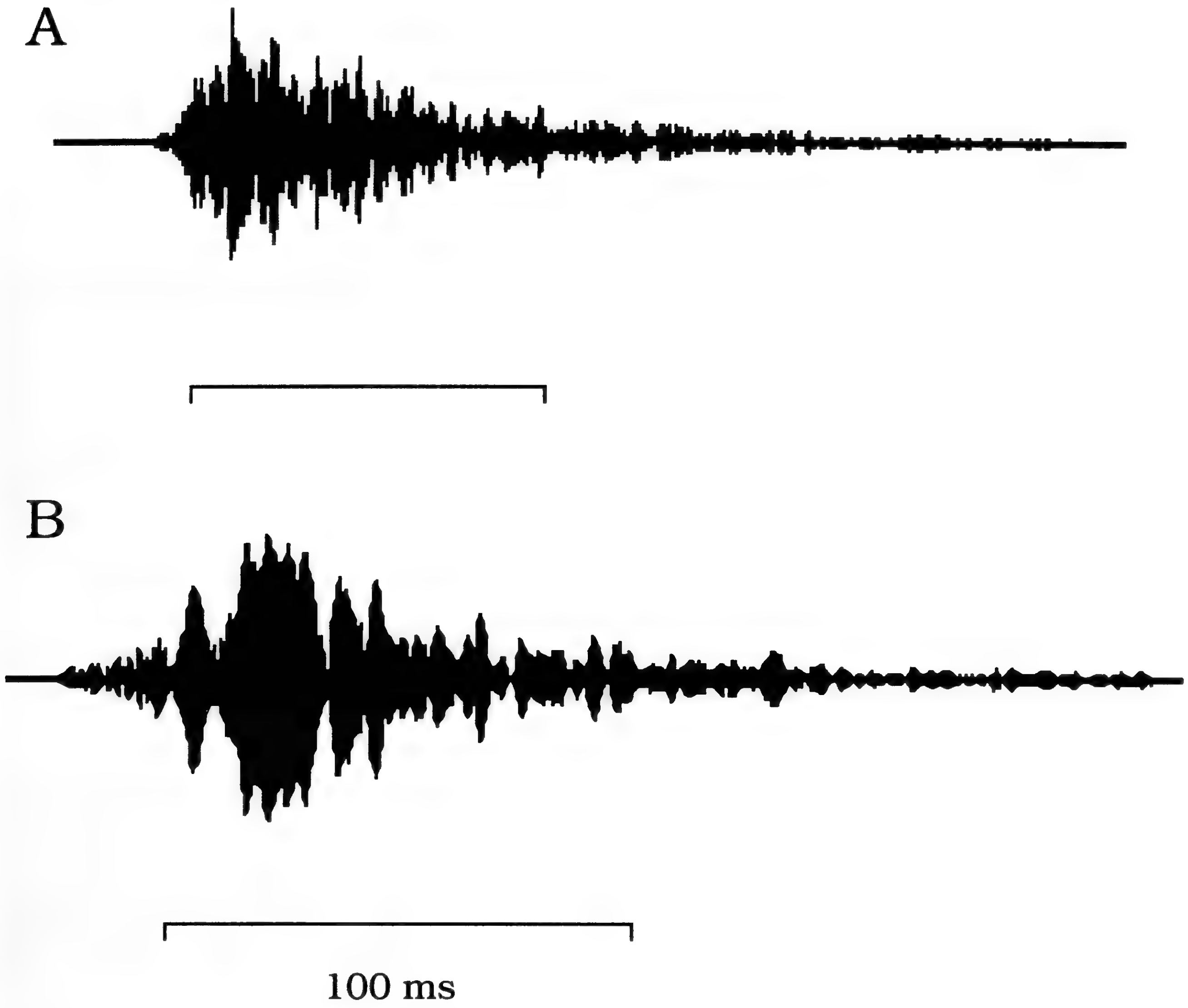

Fig. 10. *Vanzolinius* advertisement call, wave forms. A. Weakly pulsed call, USNM Tape 256, Cut 12. B. Strongly pulsed call, USNM Tape 254, Cut 5. (Both calls filtered.)

lapsing of either the extent of variation observed, deletion of geographic areas, or both during the statistical analyses. It is likely that larger sample sizes would reinforce the patterns described above and perhaps better delineate the patterns of differentiation among areas C-D-E and F-G-H.

Enzymes.—Gascon et al. (1996) published protein starch gel electrophoretic results for 20 presumptive loci for samples corresponding to Areas E, F, G, and H as defined in this study. Using their published data, the samples sizes for each geographic area are E = 41, F = 24, G = 13, and H = 2. Results using Nei's (1972) genetic distance values in a multidimensional scaling analysis (Wilkinson et al. 1992) indicate a general similarity to the morphologically and advertisement call based results. Each area shows some genetic-estimate differentiation (Fig. 14). There is not complete concordance of genetic-estimate differentiation with geography in that adjacent areas E and F are the most distinctive area pair in the data set (Fig. 14).

As indicated with advertisement call data, the actual area/population structure unit where differentiation occurs is at a finer scale than the size of the geographic areas A–H used to group samples for morphological and call analyses. In order to examine the effect of genetic-estimate differentiation among sites where sample

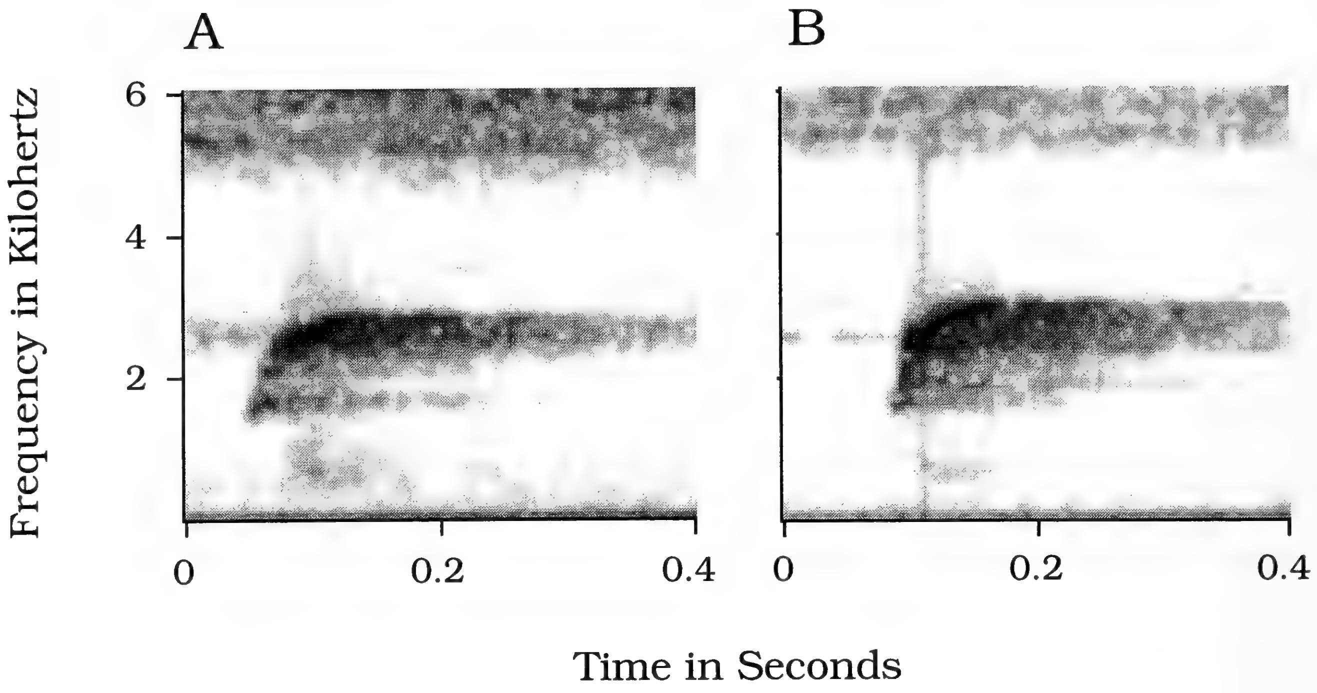

Fig. 11. *Vanzolinius* advertisement call, audiospectrograms. A. Sharp attack, USNM Tape 254, Cut 5. B. Very sharp attack, USNM Tape 256, Cut 12. (Neither call filtered.)

sizes were appropriate, all sites for which at least 5 individuals were available were analyzed using Nei's distances (1972) in a multidimensional scaling analysis (Wilkinson et al. 1992). The results indicate that there is differentiation among localities (Fig. 15, note however, that the separation on the y-axis is 1/10 that of the x-axis). As might be expected, one of the nearby pairs of localities from the same side of the river (Gascon et al. 1996, locality numbers 6 and 7, Fig. 1, Vira-Volta

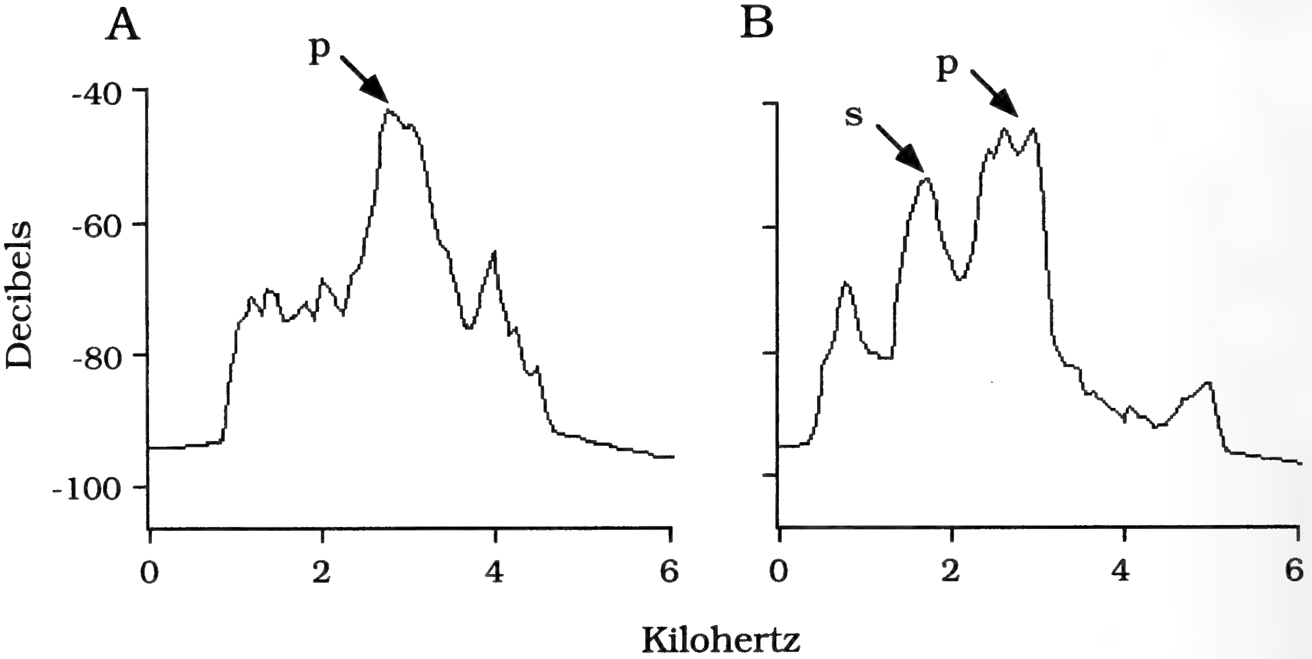

Fig. 12. *Vanzolinius* advertisement call, spectrum analyses. A. Call with virtually all of the broadcast energy in a single peak (p, maximum energy at 2750 Hz), USNM Tape 18, Cut 1. B. Call with significant energy in a second broadcast peak (primary peak, p, with maximum energy at 2590 and 2920 Hz, secondary peak, s, with maximum energy at 1700 Hz), USNM Tape 255, Cut 2. (Both calls filtered.)

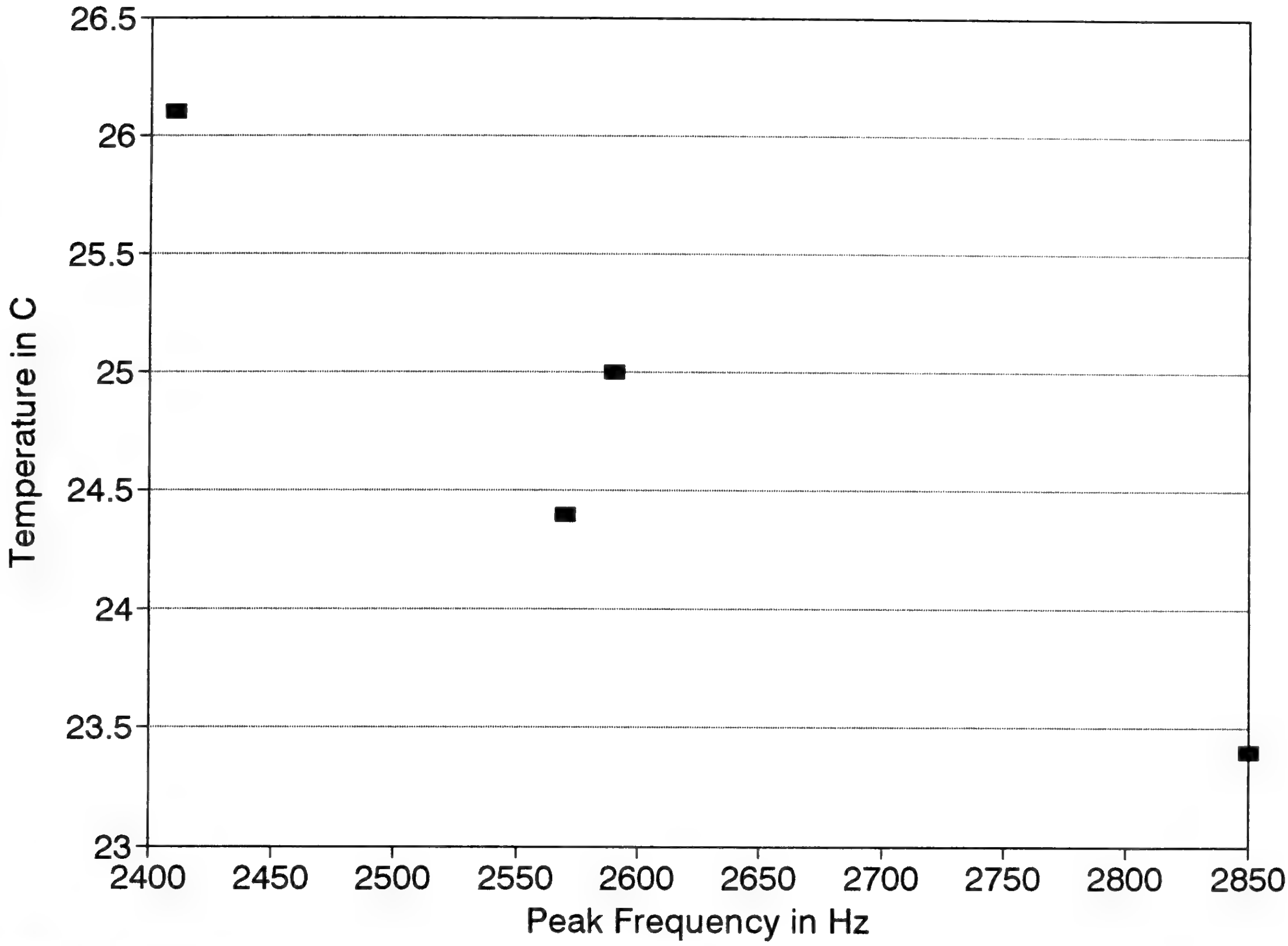

Fig. 13. Plot of temperature versus maximum broadcast energy in *Vanzolinius* calls.

varzea and terra firme sites) shows essentially no differentiation. However, the amount of differentiation between the other nearby pair of localities from the same side of the river (Gascon et al.'s locality numbers 10, Altamira and 11, Jainu (=Barro Vermelho), both varzea) are about as different from each other as any other pair of localities analyzed (Fig. 15). This distinctiveness is due to the Altamira sample. The pronounced genetic-estimate differentiation at this scale is unexpected. Such small-scale differentiation (in a geographic sense) results in an overall mosaic pattern of differentiation. Such a mosaic pattern of differentiation obfuscates any

Table 4.—Unique or shared character states among geographic area samples. Upper matrix with number of shared distinctive states. Diagonal with number of unique character states/total number of states analyzed. Lower matrix with total number of characters compared between areas.

	A	B	C	D	E	F	G	H
A	5/13	5	2			2	2	2
B	10	3/10	2		1	1	1	1
C	12	10	3/12	1	5	3	3	2
D	1	1	1	0/1	1			
E	12	10	12	1	4/12	3	2	1
F	13	10	12	1	12	1/13	9	7
G	11	9	11	1	11	11	0/11	6
H	10	9	9	1	9	10	8	2/10

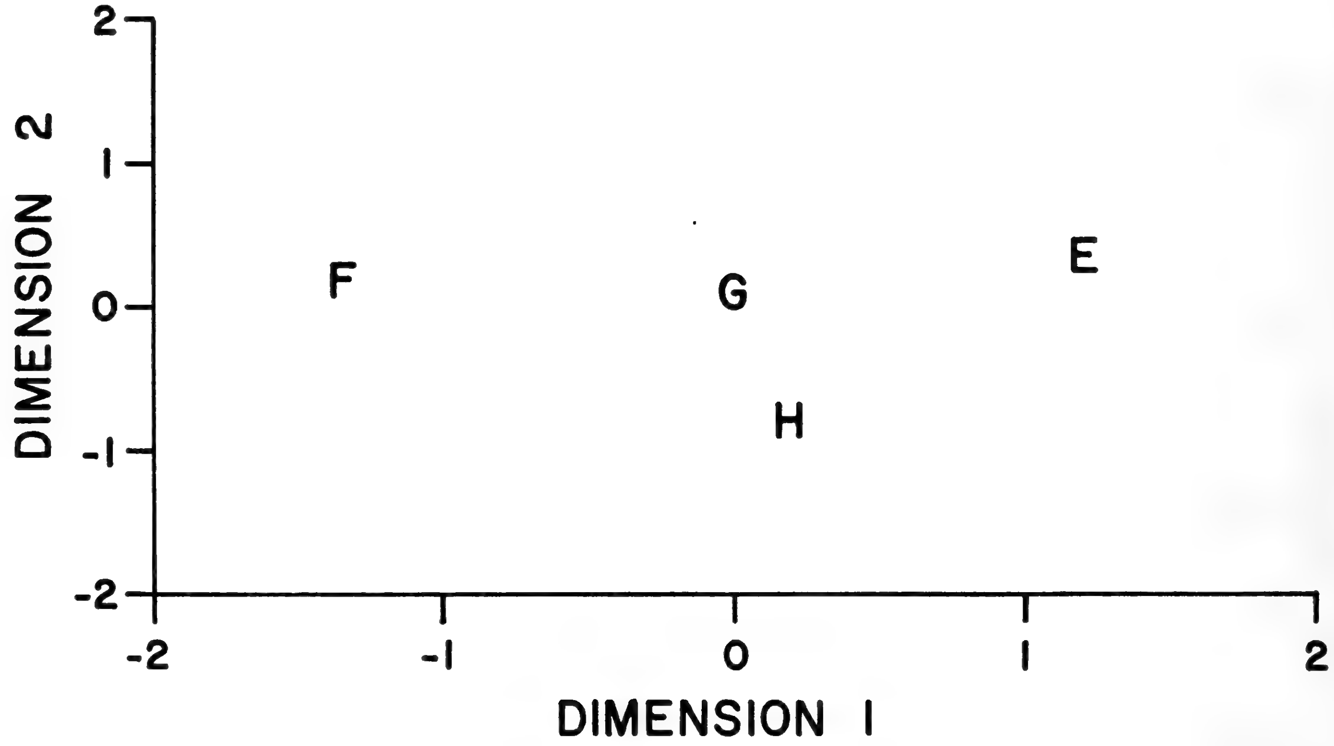

Fig. 14. Multidimensional scaling results for electrophoretic data given in Gascon et al. (1996), grouped by geographic areas as used in present study.

larger pattern of geographic differentiation.

The very local genetically based differentiation pattern provides corroboration and explanation of the results based on the morphological and advertisement call analyses presented previously.

Discussion

Distribution.—As indicated previously, specimens USNM 146971–146973 from Colombia: Caldas; Villa María are faded. I have no doubt that they are *Vanzolinius,* however. As seen from the distribution based on other known localities (Fig. 7), the interandean locality of Villa María is curious. The specimens were part of the collection donated to the Smithsonian by Hermano Niceforo María. The specimens were originally in the Museo La Salle collection as numbers 45, 45a, and 45b. Adjacent to these specimen records in the USNM catalogue ledger, Museo La Salle numbers 44, 44a, 44b, 44c, 44d, and 231 are also listed from the same locality. Dr. John Lynch identified the 44 series (USNM 146974–146978 respectively) as *Eleutherodactylus fitzingeri* and 231 (USNM 146979) as *Eleutherodactylus* sp. Lynch and Myers (1983) reported *E. fitzingeri* from Nicaragua through Panama, the Chocó of Colombia, and the interandean valleys of Colombia, but not from the Amazonian versant of the Andes in Colombia (see their Map 6, p. 535). Although Lynch & Myers (1983:560–561) do not include USNM 146974–146978 in their list of specimens examined, the locality of Villa María falls within the distribution described by them. Thus, some specimens from the La Salle collection from Villa María are geographically appropriate. In order to determine whether a transcription error had occurred in relation to the locality data for the *Vanzolinius* specimens (USNM 146971–146973), I asked Dr. Lynch who was in charge of the Museo La Salle herpetological collection in Bogotá. My intention was to determine the original catalogue entries for these specimens. Dr. Lynch (pers. comm.) informed me that the Director of the Mu-

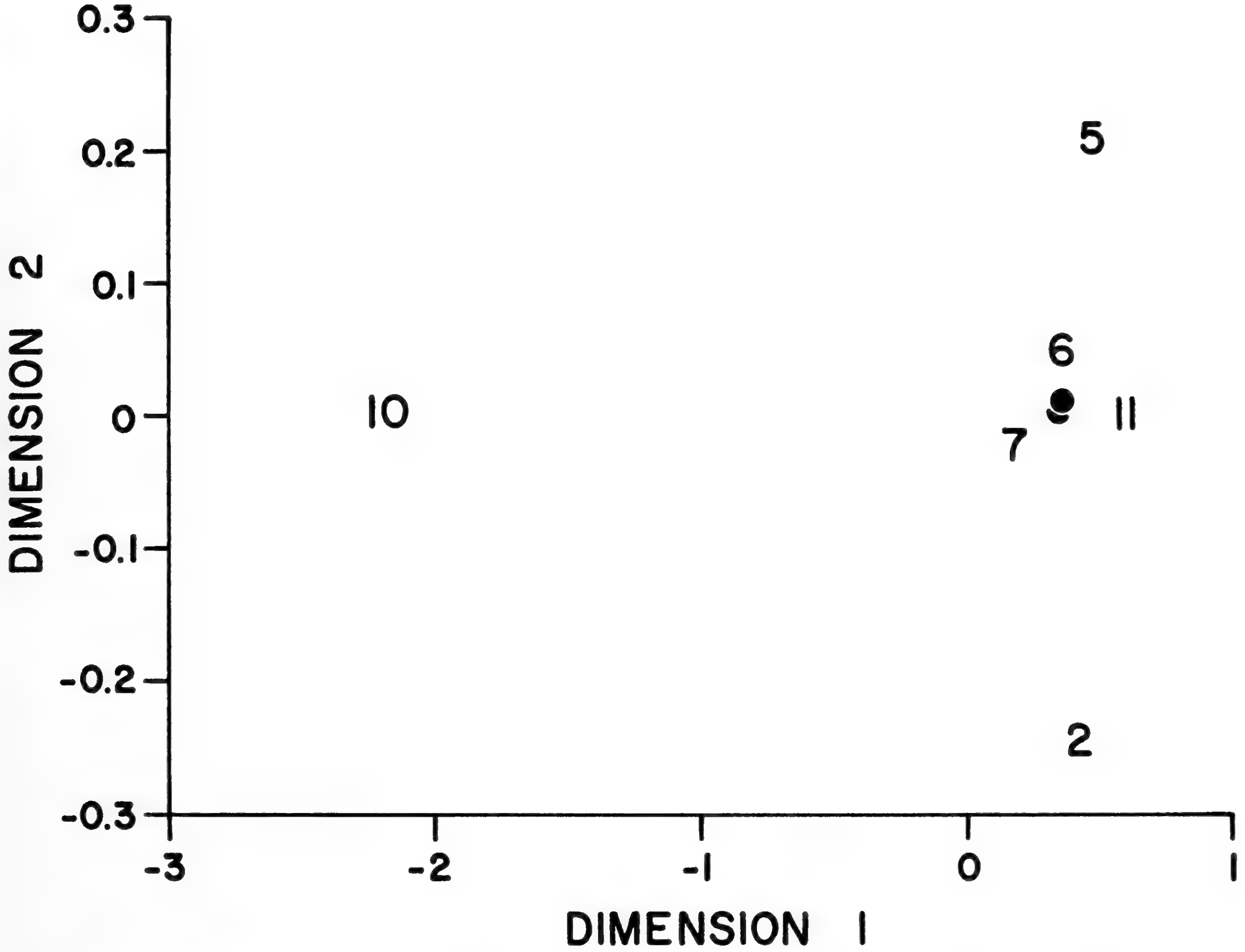

Fig. 15. Multidimensional scaling results for electrophoretic data given in Gascon et al. (1996), for individual localities represented by 5 or more specimen samples.

seo La Salle, in an effort to reduce duplicate information, had a student write new bottle labels for specimens in the herpetological collection and the Director discarded the original catalogues. Given the suspect nature of a species of amphibian with a western Amazonian distribution having a single disjunct population in an interandean Colombian valley, the locality of Villa María, Caldas, Colombia must be treated with extreme suspicion and not included in any distributional analyses until new collections verify the presence of *Vanzolinius* in Colombian interandean valleys.

Thirty six percent of the localities listed in Appendix 1 represent new locality records since 1990. The present patchy distribution (Fig. 7) certainly is due in part to collecting artifact. The current data indicate that the species has a distribution limited to western Amazonia. Exact knowledge of distributional limits of the species can only be approximated at this point, however. Sufficient collecting efforts have been undertaken in two critical areas for which absence data have some validity. *Vanzolinius discodactylus* has not been found in the Manaus, Brazil region, nor in the State of Madre de Dios, Peru. Thus the eastern and southern distributional limits likely fall between the currently known localities and Manaus and the Manú National Park.

Differentiation patterns.—Almost all studies of variation of the Amazonian herpetofauna have been directed at the species level. This is certainly appropriate, as much work remains before the species limits of the Amazonian herpetofauna are well defined, particularly for amphibians.

A classic exception is the detailed study by Vanzolini and Williams (1970) on *Anolis chrysolepis,* where they studied geographic variation at the population level over the entire range of forms that had been associated with *A. chrysolepis.* A portion of their methods is pertinent to the present discussion (1970:25):

> The investigation of each character was begun by the joint consideration of 13 "major samples" and carried forward by the analysis of "transects"—series of localities more or less linearly arranged between major samples. In this manner a two dimensional differentiation pattern of each character was obtained.
>
> The organization of the major samples and transects was decided initially only on the basis of the materials available and of the geometry of a map of the area of study. The results of a first analysis were then used to adapt the methods to permit better clarification of the patterns perceived. For example, the evidence (in fact known beforehand but not taken into consideration in the first study) of the existence of a well differentiated form, previously believed to be a well set-off species, in the area from Surinam to eastern Pará, led to a preliminary arrangement of the Guianan and Guiano-Brasilian transects, and to their subsequent modification in order to show to better advantage the phenomena of transition between these populations and adjacent ones.
>
> This sort of feedback and even bias in the analysis is not only unavoidable but highly desirable in studies of geographical differentiation in South America. If we had a perfect network of localities, each one represented by good samples—with statistically sufficient numbers of males and females, and with all age classes represented—a system of isophenes would emerge from the analysis, which might even be computerized.
>
> In fact, the available collections are, as is usual with museum collections, not made for a specific purpose, an irregular and patchy representation of the group range, and the study must begin by the setting of preliminary hypotheses, to be tested. In our case the hypothesis is, in all instances, that differences between the major samples correspond to geographic patterns and not to mosaics, and this hypothesis must be tested by adaptations of the analysis to the materials available, to the numbers of specimens and their position on the map, in other words, by the consideration of transects.

Although the number of localities and samples for Amazonian amphibians and reptiles has certainly increased since 1970, the overall assessment as described by Vanzolini and Williams still holds true. The organization of current studies on differentiation patterns of Amazonian amphibians must still be decided on the basis of materials available and the geometry of a map of the study area. As a consequence, direct comparison of results among studies is not possible at present. However, the comparisons that can be drawn suggest some statements that can be tested for generality with additional studies.

Vanzolini & Williams (1970) found differences between samples from the geographic areas represented by the areas defined in this paper as A+B and C+D+F+G+H (see their map 8, p. 180). They also found that samples from the nearby localities of Limoncocha and Santa Cecilia, Ecuador differed in some characters (e.g., fourth toe lamellae in males, p. 38).

The only other study I am aware of that treats intraspecific geographic variation for an Amazonian amphibian that occurs in the same region with *Vanzolinius discodactylus* is that of Duellman and Morales (1990) for *Edalorhina perezi.* Duellman & Morales (1990) analyzed variation of dorsal texture and belly pattern of *E. perezi* by river drainage systems. Comparison of their map (fig. 1:21) with the geographic areas used in this study indicate coincidence of the following: Region A (this study) = Napo drainage samples (their study); Region B = Pastaza drainage samples; Regions C+D = Amazonas drainage samples. Their data (table 2:23) indicate the following: The Amazonas drainage and Napo drainage samples are similar for dorsal texture conditions, but both differ from the Pastaza drainage sample; the Napo and Pastaza drainage samples are similar for ventral pattern condition and differ from the Amazonas drainage samples. Thus the two characters they analyzed in detail show independent patterns of variation and both demonstrate patterns of differentiation at the regional level.

Anolis chrysolepis, Edalorhina perezi, and *Vanzolinius discodactylus* are all forest denizens within Amazonia. All three taxa demonstrate some level of geographic differentiation at rather restricted regional levels. Much of the variation is difficult to put in a broad geographic context in all three species studies, however, suggesting a strong differentiation at the very local level which results in a mosaic pattern of differentiation that tends to obfuscate any larger scale geographic patterns. This is underscored by the genetic estimate data available for *Vanzolinius.* Rather than eschew the null hypothesis of differentiation being a mosaic, rather than having a geographic basis as implied by Vanzolini & Williams (1970:25), perhaps we need to embrace the mosaic concept.

One avenue that needs exploration is to determine the lower spatial limits of differentiation. At present, all we can say is that differentiation occurs at the geographic level that collectors have traditionally used to define distinct, but nearby, collecting localities. Does differentiation occur at even a finer scale than that for forest associated Amazonian amphibians?

Prognosis for further studies.—The corroboration of results from studies of differentiation of *Vanzolinius discodactylus* based on morphological features and on genetic estimate data is most encouraging. We should be able to undertake strictly morphological analyses of other taxa of forest associated Amazonian amphibians with confidence that the resultant patterns of differentiation reflect evolutionary processes and are not strictly phenotypic responses to localized environmental conditions.

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Literature Cited

Charif, R. A., S. Mitchell, & C. W. Clark. 1995. Canary 1.2 User's Manual. Cornell Laboratory of Ornithology. Ithaca, New York, 229 pp.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador.—University of Kansas Museum of Natural History Miscellaneous Publication 65:1–352.

———, & V. R. Morales. 1990. Variation, distribution, and life history of *Edalorhina perezi* (Amphibia, Anura, Leptodactylidae).—Studies on Neotropical Fauna and Environment 25:19–30.

Gascon, C., S. C. Lougheed, & J. P. Bogart. 1996. Genetic and morphological variation in *Vanzolinius discodactylus:* A test of the river hypothesis of speciation.—Biotropica 28:376–387.

Hayek, L. C. 1994. Analysis of amphibian biodiversity data. Pp. 207–269 *in* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds., Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press: Washington, D.C., 364 pp.

Heyer, W. R. 1994. Variation within the *Leptodactylus podicipinus-wagneri* complex of frogs (Amphibia: Leptodactylidae).—Smithsonian Contributions to Zoology 546:1–124.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985: 802–832.

Nei, M. 1972. Genetic distance between populations.—American Naturalist 106:283–292.

Savage, J. M. 1987. Systematics and distribution of the Mexican and Central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia: Leptodactylidae).—Fieldiana, Zoology, New Series 33(1375):1–57.

Straughan, I. R., & W. R. Heyer. 1976. A functional analysis of the mating calls of the Neotropical frog genera of the *Leptodactylus* complex (Amphibia, Leptodactylidae).—Papéis Avulsos de Zoologia 29(23):221–245.

Vanzolini, P. E., & E. E. Williams. 1970. South American anoles: The geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae).—Arquivos de Zoologia 19:1–298.

Wilkinson, L., M. Hill, J. P. Welna, & G. K. Birkenbeuel. 1992. SYSTAT for Windows: Statistics, Version 5 Edition. SYSTAT, Inc.: Evanston, Illinois, 750 pp.

Appendix 1. Specimens examined.

Geographic area assignments in parentheses.

BRAZIL. *Acre:* Nova Vida, (H), INPA 4490; Porongaba, (H), INPA 4271, 4287, 4291, 4294, 4296, 4350–4351; Porto Walter, (H), MZUSP 51574–51575; Sobral, (H), INPA 4348. *Amazonas:* Altamira, (F), INPA 3571–3573, 3584–3585, 3649, 3651, 5010, 5021, 5051, 5060, 5062–5063, 5103, 5132, 5166, 5173, 5177–5178, 5214, 5217–5218; Barro Vermelho, (F), INPA 3076, 3092, 3109, 3154, 3161, 3163, 3177–3178, 3198, 3229, 3352, 3385, 3387, 3397, 3399, 3405, 3411, 3454, 3507; Benjamin Constant, (D) CAS-SU 11835; Condor, (G), INPA 2573, 2587, 2608, 2640, 2642, 2644, 2883, 2904–2905, 2912, 2919–2921; Igarapé Tucuxi, Auati-Paraná, (E), MZUSP 28124; Nova Empreza, (G), INPA 2371, 2373, 2388, 2433, 2503; Nova Olinda, (F), INPA 3041; Parana (near Penedo), (G), INPA 2291, 2399; Penedo, (G), INPA 2410–2412, 2514; Rio Itacoaí, (D), MZUSP 9810; Vira-Volta, (E), INPA 5694, 5696–5703, 5720, 5727–5728, 5730, 5732, 5735–5737, 5757, 5761, 5763, 5766–5767, 5790, 5797–5803, USNM 348954–348983.

COLOMBIA. *Amazonas:* Leticia, left margin of Río Loreto Yacu (D), ICNMNH 11274; headwaters of Río Caiwima, ca 70 km NNE Puerto Nariño, (D), MCZ 97025, 97033. *Caldas:* Villa María (not assigned to area), USNM 146971–146973. *Caquetá:* Florencia (not assigned to area), USNM 147036–147037.

ECUADOR. *Napo:* Coca, 290–320 m, (A), KU 158609, 175463–175464; near Laguna Taracoa, 30 km downriver from Coca, ca 250 m, (A), MCZ 94884–94885, MZUSP 56380; Payamino, (A), USNM 196882; Río Yasuní (150 km upstream from Río Napo) (A), KU 175132–175133; Santa Cecilia, 340 m, (A), KU 104666, 109163, 111403, 111424, 111429, 119347, 119350, 126241–126242, 143518, 149295–149308, 152396, 175460. *Pastaza:* Mera, 1140 m, (B), KU 119303–119318, 178274–178282; Montalvo, 250 m, (B), RMNH 23990; Puyo and environs, (B), KU 119319–119322, 202647–202648, MCZ 90385, USNM 196878–196881, 343426–343427; Shell Mera (B), KU 99069, 99081–99082, 99085, 99090.

PERU. *Loreto:* Aldeia dos Indios Bora, 2 km N mouth of Zumun, (C), MZUSP 54189–54191; Estirón, Río Ampiyaco (C), AMNH 115691, MZUSP 23083, 24006, 24782–24786, 24793, 24797, 24803–24804, 24810, 24814, 24816, 24825; Moropon, (C), TCWC 41484; Requena, Jenaro Herrera, 140 m, (C), LR 4382 (to be deposited in Museo de Historia Natural, Universidad Nacional Mayor de San Marcos); Yanamona, (C), TCWC 41739. *Ucayali:* Yarinacocha, Río Ucayali, (not assigned to area), FMNH 56285.

Appendix 2. Color patterns and morphological data state distribution by sex among geographic areas.

Character	Sex	State	Geographic Area							
			A	B	C	D	E	F	G	H
Dorsal Snout Pattern	♀	A	6	6	3	1	7	2	3	1
		A-B		1	1		2			
		B-A								
		B	2	1	2		3	2		1
		B-C					2		1	1
		C-B	1				2	3	5	
		C	1	1	2		12	15	4	
		A-C					7		1	
		C-A			1		5	1		1
	♂	A	4	13	3		1	4		
		A-B	2	2	2		1			1
		B-A		1						1
		B	1	3	1		1	1		
		B-C	1			1			1	1
		C-B	1				3	1	1	1
		C	2	1	2		7	6	4	1
		A-C		2	2		1	1		
		C-A	1					1	1	1
	J	A	8	12	2	1	2	2		
		A-B								
		B-A	1							
		B	1							
		B-C					1		2	
		C-B	1				1			
		C	1	2		1	2	3	1	
		A-C	1	1		1				1
		C-A					1			

Light Postorbital Eye Stripe	♀	-	3	6	1		22	1	1	
		(+)	5	1	2	1	13	8	5	1
		+	2	1	6		5	14	8	3
		+!								
	♂	-	1	11			2			
		(+)	6	6	1	1	8	5	3	1
		+	5	4	6	1	3	9	5	5
		+!			3		1			
	J	-	5	14		2	2			
		(+)	7	1	2		3	3	1	1
		+	1				2	2	1	
		+!								
Light Subocular Bar	♀	-	2	4	2	1	23	9	5	1
		(+)	5	3	2		14	8	6	1
		+	3	1	5		3	6	3	2
	♂	-	1	10	1		5	3	2	
		(+)	6	7	1	2	7	6	5	1
		+	5	5	5		2	5	1	5
	J	-	5	7		1	4	3		
		(+)	5	7	2	1	2	2	2	1
		+	3		3		1			
Dorsal Pattern	♀	A	5	1	7	1	38	16	12	2
		B	1	1	1		2	4	2	2
		C	2	1				2		
		C-1	2							
		D		4						
		D-1		1						

	♂	A	8	11	9	1	14	7	6	5
		B	1					4	2	1
		C	1	1	1			2		
		C-1	2							
		D								
		D-1		9						
	J	A	6	3	2	3	6	7	1	1
		B	1				1		1	
		C	1	2						
		C-1	5							
		D		4						
		D-1		6						
Dark Mid-Dorsal Pin Stripe	♀	-	6	6	3	1	10	7	3	2
		+	4	2	5		30	15	11	2
	♂	-	8	12	7	1	5	5	2	5
		+	4	9	3		9	9	5	1
	J	-	8	6	1	1	1	2	1	1
		+	5	9	1	2	6	4	2	
Throat & Chest Pattern	♀	A	7	4			5	9	10	3
		A-1			3		16	7	3	
		B	2	3	6		8	4	1	1
		B-1				1				
		C					11	3		
		C-1								
		D	1	1						
		E								
	♂	A	5	7	4	1	2	2	5	2
		A-1	1				2	4		

		B	2	6	5		4	3	3	2
		B-1						1		
		C			1		5	1		1
		C-1								1
		D	3	8			1	3		
		E	1							
	J	A	9	10	1			4	1	1
		A-1	2	4	1	1	5			
		B	2			1	1	1	1	
		B-1								
		C		1			1			
		C-1								
		D								
		E								
Belly Pattern	♀	A	1		2		4	20	7	1
		A-1			1		6	1	4	
		B	2				13			1
		B-1		4	6	1	12			
		C	1				2	2	3	2
		C-1		1			3			
		C-2	4	3						
		D	2							
	♂	A		1		1	2	8	4	2
		A-1		3			1	4	1	
		B	2	1	2		4			
		B-1	1	6	3		4	1		
		C			2		3		3	4
		C-1	3	2	3					
		C-2	4	8						
		D	2							
	J	A					2	4	2	

		A-1		6		1	3			
		B	1		1					1
		B-1		4	1	1	1	1		
		C	1				1	1		
		C-1	2							
		C-2	6	5						
		D	3							
Posterior Thigh Pattern	♀	A	2	3	1		1		2	1
		B	2		1	1	12	7	1	1
		C	3	3			1	3	2	2
		D	2	1			5	6	7	
		E	1		4		19	5	2	
		F		1	2		1	2		
		F!			1		1			
	♂	A	1	5			1		2	3
		B	5	7	5		6	3	3	2
		C	4	4				3		1
		D	1	4		1	3	5	2	
		E	1		2		4	3	1	
		F			3					
		F!		1						
	J	A	5	3	1	2		1		1
		B		1			1			
		C	2	1		1				
		D	3	8			1	3		
		E	2	2	1		3	1	2	
		F	1				2			
		F!								
Third Toe Tip Dorsal Outline	♀	N.E.+		2						

		A	6	3	4		7			
		A-B	2	3	4		19	6	6	
		B-A					11	11	7	2
		B	2		1	1	3	6	1	2
	♂	N.E.+		4	1					
		A	8	11	3		1			
		A-B	2	4	4	1	9	6	3	4
		B-A		2			2	6	4	
		B	2		2		2	2	1	2
	J	N.E.+	1	6	1					
		A	9	7						
		A-B	1	2	1	1	2		1	
		B-A	2				3	4	1	1
		B				1	2	1		
Third Toe Tip Dorsal Grooves	♀	1								
		2	1	2			7	3	2	
		3	4	2	2	1	27	13	6	2
		4	4	3	6		6	5	5	1
		5	1	1	1			2	1	1
	♂	1						1		
		2	2	5	1		5			1
		3	5	8	2	1	8	9	7	3
		4	3	6	5		1	4	1	2
		5	2	2	2					
	J	1			1	1				
		2	2	5		1	2	1		
		3	7	9			4	3	1	1
		4	4	1	1		1	1	1	
		5								

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Two new species of salamanders (Caudata: Plethodontidae) of the genera *Bolitoglossa* and *Nototriton* from Parque Nacional La Muralla, Honduras

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Abstract.—Two new species of salamanders of the genera *Bolitoglossa* and *Nototriton* are described from the isolated cloud forests of Parque Nacional La Muralla, Honduras. The *Bolitoglossa* is a member of the *B. dunni* group and differs from all other group members by having well-defined yellow spots on the lateral surfaces of the body. The *Nototriton* appears to be most closely related to *N. barbouri* and can be distinguished from that species by its shorter tail and smaller size.

Parque Nacional La Muralla, in the northwestern portion of Departamento de Olancho, Honduras, is herpetologically one of the best known national parks in Honduras (Espinal et al. 1997). Espinal et al. (1997) included some recently collected salamanders from the park under the name *Nototriton* "*barbouri.*" Subsequent study of these salamanders demonstrated that they were likely an undescribed species related to *N. barbouri.* Thus, in July 1996, we returned to Parque Nacional La Muralla hoping to collect additional specimens of these salamanders. About mid-day on 29 July, we set up a camp at 1430 m elev. at the nearest known source of drinking water to the *Nototriton* locality. As the *Nototriton* locality was still a four hour walk from camp, we decided to collect that afternoon and night in the environs of our campsite and go to the *Nototriton* locality the following day. Unexpectedly, we discovered a brillantly colored undescribed species of *Bolitoglossa* around the campsite. The following day we made a successful visit to the previously known *Nototriton* locality. Study of this new material confirmed the distinctness of the Muralla *Nototriton.* We herein provide a formal description of each of these two salamanders.

Methods and Material

All measurements were made to the nearest 0.1 mm with dial calipers under a dissecting microscope. Abbreviations used are SVL (snout to posterior end of vent), HL (head length; snout to gular fold), HW (head width), TL (tail length), HLL (hind limb length), FLL (forelimb length), CLL (combined forelimb and hind limb lengths), HFW (hind foot width), and NL (nostril length). For ease of comparison, the format for the 'Description' and 'Measurements of the holotype' sections for the *Bolitoglossa* follow that of McCranie & Cruz (1996), whereas those sections for the *Nototriton* follow the format of McCranie & Wilson (1997). The numbers in parentheses in the color in life descriptions refer to the color codes in Smithe (1975). McCranie & Cruz (1996) listed the adult material of the *Bolitoglossa dunni* group recently examined and McCranie & Wilson (1997) listed all material of *Nototriton* recently examined. The following specimens of *Nototriton barbouri* were re-examined for this study: AMNH 54949; USNM 339700–12. Additionally, a recently collected specimen of *N. barbouri* (USNM 497552: Depto. Atlántida, Honduras) was compared to the new

Fig. 1. Adult female holotype of *Bolitoglossa decora* (USNM 500000), SVL 62.1 mm.

species of *Nototriton* (thus a total of 27 specimens of *N. barbouri* have been examined).

Systematics

Bolitoglossa decora, new species
Fig. 1

Holotype.—National Museum of Natural History, USNM 500000, an adult female from along the trail to Cerro de Enmedio near the Monte Escondido campground (15°05′N, 86°44′W), Parque Nacional La Muralla, 1440 m elev., Departamento de Olancho, Honduras, collected 29 Jul 1996 by D. Almendarez, J. R. McCranie, and L. D. Wilson. Original number LDW 11032.

Paratypes.—USNM 497534, an adult female, USNM 497533, 497535, both apparently immature males, all from the same hillside as the holotype, 1440–1550 m elev.

Referred specimens.—USNM 497536–38, all subadult females, all from the same hillside as the holotype, 1430–1500 m elev.

Diagnosis.—*Bolitoglossa decora* is a member of the *B. dunni* group as defined by Elias (1984). *Bolitoglossa decora* can be distinguished from all other members of the group—*B. carri* McCranie & Wilson, *B. celaque* McCranie & Wilson, *B. conanti* McCranie & Wilson, *B. cuchumatana* (Stuart), *B. dunni* (Schmidt), *B. engelhardti* (Schmidt), *B. helmrichi* (Schmidt), *B. longissima* McCranie & Cruz, *B. porrasorum* McCranie & Wilson, and *B. rostrata* (Brocchi)—by having well-defined Buff-Yellow (in life) or pale yellow (after a short time in preservative) spots on the lateral surface of the body. Individuals of some of the above mentioned species may have pale flecks on the lateral surfaces or pale dorsolateral stripes, but not well-defined pale spots laterally. Additionally, *B. decora* has less webbing (two to slightly over two phalanges on both sides of digit III on both forelimbs and hind limbs free of webbing) than all of the above named species except for *B. longissima, B. rostrata,* and some specimens of *B. celaque* (see table 1 in McCranie & Cruz 1996, for a comparison to the remaining Honduran members of the *B. dunni* group). *Bolitoglossa decora* also has shorter limbs than *B. longissima* (male HLL/SVL 24.9–26.4%, $\bar{X}$ = 25.7 versus 31.9% in one male *longissima*; female

HLL/SVL 24.1–25.3%, $\bar{X}$ = 24.7 versus 31.0–31.9%, $\bar{X}$ = 31.6 in *longissima*).

Description.—Relatively large (SVL 36.5–40.2, $\bar{X}$ = 38.4 in two apparently immature males; 61.0–62.1, $\bar{X}$ = 61.6 in two adult females) member of *B. dunni* group; snout nearly truncate to broadly rounded in dorsal aspect, broadly rounded in profile; females more robust than relatively slender males; labial protuberances well developed in males, weakly developed in females; mental gland very weakly developed in largest male, mental gland not evident in smaller male; head relatively narrow (HW/SVL 15.7–16.4%, $\bar{X}$ = 16.1 in two males; 16.1–16.3%, $\bar{X}$ = 16.2 in two females); eyes slightly protuberant, not or only barely visible beyond margin of jaw when viewed from below in both sexes; postorbital groove shallow, extending posteriorly from eye before turning sharply ventrally to connect with gular fold, another groove proceeding sharply ventrally just posterior to mandible and extending irregularly across throat anterior to gular fold; sublingual fold absent; maxillary teeth moderately abundant (47–54, $\bar{X}$ = 50.5 in two males; 68–70, $\bar{X}$ = 69.0 in two females), extending beyond level of center of eye; vomerine teeth abundant (23–31, $\bar{X}$ = 27.0 in two males; 29–31, $\bar{X}$ = 30.0 in two females), in long, single or slightly irregular, arched series extending slightly beyond level of medial border of choanae; premaxillary teeth (2 in both males; 5–6, $\bar{X}$ = 5.5 in two females) enlarged, piercing lip or located just posterior to lip in males, not enlarged, located posterior to lip in females; tail laterally compressed, constricted basally; tail relatively short (TL/SVL 74.9% in one male; 75.7–77.0%, $\bar{X}$ = 76.4 in two females); limbs slender, long, adpressed forelimb and hind limb slightly overlapping to limb interval of 1/2 costal fold in two males, limb interval 1/2–1 costal fold in two females (HLL/SVL 24.9–26.4%, $\bar{X}$ = 25.7 in two males; 24.1–25.3%, $\bar{X}$ = 24.7 in two females); webbing reduced, with two to slightly over two phalanges on both sides of digit III on both forelimbs and hind limbs free of webbing; digit tips bluntly rounded, bearing well-developed subdigital pads; relative length of digits on forelimbs I<IV≈II<III, those on hind limbs I<V<II<IV<III.

Color in life was recorded as follows for the adult female holotype (USNM 500000): middorsal region of back and top of head Amber (36), this color grading laterally to Burnt Umber (22); lateral surface of body with variously-sized prominent Buff-Yellow (53) spots; dorsal surface of tail Burnt Umber (22) with Warm Buff (118) spots; dorsal surfaces of limbs Warm Buff (118) with Buff-Yellow (53) spots and Burnt Umber (22) crossbars; side of head Raw Umber (23) with Buff-Yellow (53) spots; all ventral surfaces Drab (27) with Buff-Yellow (53) spots; iris mottled gold and rust color. A subadult female (USNM 497536) was colored as follows: dorsal surfaces of body and tail Fuscous (21) with slightly paler middorsal line of irregular markings; top of head Russet (34); lateral surfaces of body Fuscous (21) with row of Buff-Yellow (53) spots; dorsal surfaces of limbs Amber (36) with darker smudging; all ventral surfaces Drab (27) with very few scattered Buff-Yellow (53) spots on chin and chest; iris mottled gold and rust color.

Color in preservative: dorsum of body dark brown, sometimes with paler brown middorsal region; top of head usually paler brown than body ground color; lateral surfaces of body dark brown with pale yellow spots of varying sizes, ranging from small and few in number to numerous and large in size; most specimens also have small to moderately large pale yellow spots on dorsal and lateral surfaces of tail; dorsal surfaces of limbs usually with pale brown spots covering at least the knee region; ventral surfaces of body and tail vary from cream-colored with numerous tiny brown flecks to dark brown with numerous tiny pale iridophores, some specimens also have numerous large pale spots on ventral and subcaudal surfaces; large females have more numerous and larger pale spots on lateral surfaces of body and tail, on dorsal surfaces of tail and limbs, and on all ventral and subcaudal surfaces.

Measurements of holotype.—HW 10.1; HL 15.5; head depth at posterior angle of jaw 4.7; eyelid length 3.7; eyelid width 2.7; anterior rim of orbit to snout 4.1; horizontal orbital diameter 1.7; interorbital distance 3.3; distance between vomerine teeth and parasphenoid tooth patch 0.2; snout to forelimb 8.5; distance separating choanae 2.5; distance separating external nares 2.3; snout projection beyond mandible 1.0; SVL 62.1; body length 46.6; snout to anterior angle of vent 56.0; axilla to groin 28.9; TL 47.0; tail width at base 4.0; tail depth at base 3.9; right FFL 14.6; right HLL 15.7; right forefoot width 5.4; right HFW 6.4.

Natural history notes.—*Bolitoglossa decora* is known from 1430 to 1550 m in the Lower Montane Wet Forest formation of Holdridge (1967). One specimen was lying exposed among leaves in the trail during the day. At least one member of our party had stepped on, and possibly uncovered the individual prior to its discovery. The remaining specimens were collected at night from vegetation 1 to 2 m above the ground. Most of these were taken from fronds of a small palm. Another specimen was collected on the stalk of a small bamboo. Two newly hatched juveniles, that were not retained, were exposed at night on a bamboo leaf and on an arboreal bromeliad lying on the ground.

Etymology.—The specific name *decora* (pronounced with emphasis on first syllable) is an adjective formed from the Latin word *decorus,—a,—um* (ornamented, elegant, or beautiful). The name alludes to the spectacularly ornamented and beautiful color pattern of the large females of this taxon.

Nototriton lignicola, new species

Fig. 2

Holotype.—National Museum of Natural History, USNM 497539, an adult male from Cerro de Enmedio (15°06′N, 86°44′W) along the trail above the Monte Escondido campground, Parque Nacional La Muralla, 1780 m elev., Departamento de Olancho, Honduras, collected 30 Jul 1996 by D. Almendarez, J. R. McCranie, and L. D. Wilson. Original number LDW 11036.

Paratypes.—USNM 497540–43, 497546–47, all adult males, USNM 497544–45, 497548, all adult females, all from within ca. 0.5 airline km of the locality for the holotype, 1760–1780 m elev.

Referred specimens.—USNM 497549–51, all subadults from within ca. 0.5 airline km of the locality for the holotype, 1760–1770 m elev.

Diagnosis.—*Nototriton lignicola* is most similar morphologically to *N. barbouri* (Schmidt) of the *N. nasalis* group (see Papenfuss & Wake 1987). *Nototriton lignicola* differs from *N. barbouri* by having a shorter tail (adult male TL/SVL 0.898–1.059, $\bar{X} = 0.987$ versus 1.191–1.398, $\bar{X} = 1.295$ in *barbouri*; adult female TL/SVL 0.840–1.006, $\bar{X} = 0.935$ versus 1.031–1.146, $\bar{X} = 1.088$ in *barbouri*; also, all three subadult *N. lignicola* have TL/SVL ratios of ≤ 1.0) and smaller adult size (male SVL 28.3–33.9, $\bar{X} = 31.1$ versus 35.6–38.3, $\bar{X} = 37.0$ in *barbouri*; female SVL 31.0–32.8, $\bar{X} = 31.7$ versus 30.2–39.9, $\bar{X} = 35.3$ in *barbouri*). *Nototriton lignicola* is most easily distinguished from the remaining species placed in the *N. nasalis* group by McCranie & Wilson (1997) and Papenfuss & Wake (1987)—*N. alvarezdeltoroi* Papenfuss & Wake, *N. nasalis* (Dunn), *N. sanctibarbarus* McCranie & Wilson, and *N. veraepacis* (Lynch & Wake)—by having much smaller nostrils (NL/SVL 0.006–0.009 versus 0.017–0.029).

Description.—The seven adult males and three adult females in the type series, respectively, have the following measurements and proportions (means in parentheses): SVL 28.3–33.9 (31.1), 31.0–32.8 (31.7); HL/SVL 0.180–0.194 (0.186), 0.177–0.183 (0.181); HW/SVL 0.104–0.118 (0.113), 0.103–0.112 (0.108);

Fig. 2. Adult male paratype of *Nototriton lignicola* (USNM 497540), SVL 28.3 mm.

TL/SVL 0.898–1.059 (0.987, *n* = 6), 0.840–1.006 (0.935); HLL/SVL 0.163–0.181 (0.171), 0.158–0.163 (0.160); FLL/SVL 0.151–0.160 (0.156), 0.137–0.151 (0.144); CLL/SVL 0.314–0.340 (0.327), 0.296–0.314 (0.304); HFW/SVL 0.029–0.040 (0.035), 0.032–0.037 (0.034); NL/SVL 0.006–0.009 (0.007), 0.006 in all three females.

Snout broadly rounded to nearly truncate in dorsal aspect, broadly rounded to nearly vertical in profile; nostrils small; labial protuberances well developed in males, weakly developed in females; males with rather indistinct oval-shaped mental gland; eyes somewhat protuberant, narrowly visible to not visible beyond margin of jaw when viewed from below; postorbital groove shallow, extending posteriorly from eye before turning sharply ventrally to connect with gular fold, another groove proceeding sharply ventrally just posterior to mandible; head weakly demarcated from trunk; parotoid glands indistinct or absent; sublingual fold present; maxillary teeth 46–50 (48.3, *n* = 6) in males, 52–54 (53.3) in females, extending to level beyond center of orbit; vomerine teeth 16–20 (18.3, *n* = 6) in males, 16–24 (20.0) in females, in long, single, arched series extending to level well beyond outer edge of choanae; premaxillary teeth 4–5 (4.4) in males, 6 in all three females, slightly enlarged, located just posterior to lip and slightly offset from maxillary series in males, not enlarged, located posterior to lip and in line with maxillary series in females; costal grooves 13; tail laterally compressed, slightly constricted basally; limbs slender, short, limb interval four to five costal folds in males, five costal folds in females; digits differentiated, with about one phalanx of digit III between digits II–III on forelimbs free of webbing, and about two phalanges of digit III between digits III–IV on hind limbs free of webbing; digit tips bluntly rounded, bearing well-developed subdigital pads; relative length of digits on forelimbs I<IV<II<III, those on hind limbs I<V<II<IV<III; postilliac glands fairly distinct to indistinct; males with cloacal papillae, females with shallow cloacal folds.

Coloration in life was recorded as follows for the adult male holotype (USNM

497539): all dorsal surfaces Burnt Umber (22) with Buff (24) and white flecking visible to unaided eye; all ventral surfaces Hair Brown (119A) with scattered white flecks visible to unaided eye; iris rust red with copper spots. Another adult male (USNM 497540) was colored as follows: all dorsal surfaces Burnt Umber (22) except middorsum of body slightly paler; all dorsal surfaces with scattered white flecks visible to unaided eye; all ventral surfaces Hair Brown (119A); iris copper.

Color in preservative: all dorsal surfaces medium brown to dark brown with numerous pale colored iridophores, iridophores frequently joined to one another; ventral and subcaudal surfaces paler than dorsal surfaces as result of more numerous joined pale iridophores.

Measurements of holotype.—HW 3.9; head depth at posterior angle of jaw 2.2; eyelid length 1.9; eyelid width 1.1; anterior rim of orbit to snout 1.3; interorbital distance 1.1; snout to forelimb 9.3; NL 0.2; distance between external nares 0.8; projection of snout beyond mandible 0.1; HL 6.0; SVL 33.1; snout to anterior angle of vent 30.5; axillary to groin 18.0; TL 32.5; tail depth at base 2.0; tail width at base 2.0; FLL 5.0; forefoot width 0.7; HLL 5.4; HFW 1.0; length of digit III on hind foot 0.8; length of digit V on hind foot 0.3.

Natural history notes.—*Nototriton lignicola* is known from 1760 to 1780 m in the Lower Montane Wet Forest formation of Holdridge (1967). All specimens were taken from inside rotten logs. Six specimens were taken from inside one log on 14 September 1995. Three other individuals were also found inside this same log when it was revisited on 30 July 1996. Also on 30 July 1996, four specimens of *N. lignicola* and two of *Oedipina cyclocauda* were collected from inside a single rotten log.

Etymology.—The specific name *lignicola* is used as a noun in apposition formed from the Latin words *lignum* (wood) and *cola* (an inhabitant). The name refers to the microhabitat of this species as all known specimens were collected from inside rotten logs.

Discussion

Relationships among the species of the *B. dunni* (or *B. rostrata*) group are poorly understood (McCranie & Cruz 1996). *Bolitoglossa decora* occurs in an isolated mountain range about 55 km SSE of and 80 km NNW of the nearest known populations for other members of the *B. dunni* group (*B. porrasorum* and *B. longissima,* respectively). The reduced webbing in *B. decora* most closely resembles that of *B. longissima* among the Honduran species of the *dunni* group. However, *B. longissima* has essentially unpatterned dorsal and lateral surfaces and longer limbs. In recent years, we have collected tail tips (stored in 95% ETOH in the MVZ collection) from three of the Honduran species placed in the *B. dunni* group (*conanti, decora,* and *porrasorum*). An effort will be made to collect tail tips from the remaining Honduran species of the group as well. It is hoped that DNA analysis of this material will be forthcoming and will elucidate the ingroup relationships of these species that are not currently determinable with the diversity of morphological characteristics demonstrated by these species.

Nototriton lignicola appears to be most closely related to *N. barbouri.* These two species have similarly-sized nostrils that are considerably smaller than those of the remaining species placed in the *N. nasalis* group by McCranie & Wilson (1997) and Papenfuss & Wake (1987). *Nototriton barbouri* also can be found inside rotten logs like *N. lignicola. Nototriton lignicola* occurs in an isolated mountain range about 55 km SSE of and 70 km E of the two nearest known *N. barbouri* localities (Atlántida: Cerro Búfalo; Yoro: Montaña Macuzal; respectively). Tail tips of both *N. barbouri* and *N. lignicola* are also on deposit in the MVZ collection.

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Literature Cited

Elias, P. 1984. Salamanders of the northwestern highlands of Guatemala.—Natural History Museum of Los Angeles County Contributions in Science 348:1–20.

Espinal, M. R., J. R. McCranie, & L. D. Wilson. 1997. The herpetofauna of Parque Nacional La Muralla, Honduras. *in* J. D. Johnson, R. G. Webb, & O. Flores-Villela, eds., Middle American herpetology: Systematics, natural history, and conservation. Texas Western Press, El Paso (in press).

Holdridge, L. R. 1967. Life zone ecology. Revised edition. Tropical Science Center, San José, Costa Rica, 206 p.

McCranie, J. R., & G. A. Cruz. 1996. A new species of salamander of the *Bolitoglossa dunni* group (Caudata: Plethodontidae) from the Sierra de Agalta, Honduras.—Caribbean Journal of Science 32:195–200.

———, & L. D. Wilson. 1997 [1996]. A new species of salamander of the genus *Nototriton* (Caudata: Plethodontidae) from Montaña de Santa Bárbara, Honduras.—The Southwestern Naturalist 41:111–115.

Papenfuss, T. J., & D. B. Wake. 1987. Two new species of plethodontid salamanders (genus *Nototriton*) from Mexico.—Acta Zoologica Mexicana, nueva serie 21:1–16.

Smithe, F. B. 1975. Naturalist's color guide. Part I. Color guide. The American Museum of Natural History, New York, 182 color swatches.

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Protoblepharon rosenblatti, a new genus and species of flashlight fish (Beryciformes: Anomalopidae) from the tropical South Pacific, with comments on anomalopid phylogeny

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Abstract.—*Protoblepharon rosenblatti* is described from a single large specimen collected at 274 m off Rarotonga, Cook Islands. It differs from other anomalopids most notably in having a low number of gill rakers on the first arch (21 vs. 24 or more), high number of body scale rows (ca. 145 vs. 130 or fewer), no postorbital papillae, and a very small gap between the lacrimal and nasal for passage of the fibrocartilaginous stalk, which is twisted and not broadly exposed posteriorly. *Protoblepharon* is a primitive member of the lineage of flashlight fishes characterized by a shutter mechanism for light-organ occlusion.

The Anomalopidae comprise a small group of nearly circumtropically distributed, marine beryciform fishes characterized most conspicuously by a subocular luminous organ in which symbiotic luminous bacteria are cultured (e.g., Harvey 1922, Haygood & Cohn 1986). Since a review of the family by McCosker & Rosenblatt (1987), in which five species were recognized in three genera, Johnson & Rosenblatt (1988) erected a new genus, *Phthanophaneron,* for the eastern Pacific *Kryptophanaron harveyi* Rosenblatt & Montgomery, and Rosenblatt & Johnson (1991) described a new genus and species from Tahiti, *Parmops coruscans.* With the exception of *Photoblepharon,* with two species, all genera are monotypic.

Using derived morphological features, including aspects of the occlusion mechanism of the light organ, Johnson & Rosenblatt (1988) hypothesized the following relationships (in phyletic sequence) among four anomalopid genera: *Anomalops, Phthanophaneron, Kryptophanaron, Photoblepharon.* Rosenblatt & Johnson (1991) placed *Parmops* as the sister group of the *Phthanophaneron* + *Kryptophanaron* + *Photoblepharon* clade.

We have examined a very large (229 mm SL) flashlight fish from the preserved collections at the Australian Museum that cannot be assigned to any known species. The specimen was collected on hook and line in deep water off Rarotonga, Cook Islands. A comparison of the single known specimen of the new species with other anomalopids suggests that it is a primitive member of the group of flashlight fishes characterized by a shutter mechanism for light-organ occlusion, i.e., all anomalopid genera except *Anomalops* (Johnson & Rosenblatt 1988). Our phylogenetic placement of the new species is best served by erecting a new genus for it.

Flashlight fishes observed by divers and those preserved in fish collections typically are small (<100 mm SL), and thus the large size of the holotype of the new species is unusual. However, several large specimens (>200 mm SL) are known for *Anomalops* (McCosker & Rosenblatt 1987), and *Phthanophaneron harveyi* is known from a 20-mm SL juvenile, the 67.7-mm SL holotype, and a 204-mm SL specimen (Rosenblatt & Montgomery 1976, McCosker & Rosenblatt 1987, Allen & Robertson 1994). Large flashlight fishes typically are taken in deeper water than small ones (e.g., McCosker & Rosenblatt 1987), and may be more common than their poor representation in fish collections suggests. Further collecting efforts are needed to find small specimens of the new species, the holotype of which is from an area of the Cook Islands where small specimens of both *Anomalops* and *Photoblepharon* occur. Our purposes here are to describe the new species and discuss its relationships in the context of an existing phylogenetic hypothesis of anomalopid genera.

Methods

Measurements were made with needlepoint dial calipers or an ocular micrometer to the nearest 0.1 mm. Terminology of structures associated with the light organ follows Johnson & Rosenblatt (1988). Gillraker counts include all rudiments. Scale bars in illustrations represent 1 mm. We follow Johnson & Rosenblatt (1988) in using the name "Trachichthyoidei" for the clade comprising the Anomalopidae, Monocentridae, and Trachichthyidae, the monophyly of which was proposed by Zehren (1979) and Moore (1993). The Monocentridae and Trachichthyidae were considered the first and second outgroups, respectively, for the phylogenetic analysis of anomalopid genera based on the hypothesized monophyly of the Trachichthyoidei and a proposed sister-group relationship between the Monocentridae and Anomalopidae (Konishi & Okiyama 1997). Following Zehren (1979), Moore (1993) suggested a sister-group relationship between the Monocentridae and Trachichthyidae, but the single character cited as evidence involves the infraorbital series, which is modified in all anomalopids to accommodate the light organ. Further study is needed to test Konishi & Okiyama's (1997) Anomalopidae + Monocentridae hypothesis, which also is based on a single character: presence of a separate spinous dorsal fin in monocentrids and all anomalopids except *Photoblepharon.* Recognizing that neither hypothesis of trachichthyoid interrelationships is well supported, we initially included the sister group of trachichthyoids, the Anoplogastridae + Diretmidae (Zehren 1979, Moore 1993, Baldwin & Johnson 1995), as an additional outgroup in our analysis, but this inclusion had no effect on the topology of the tree and will not be discussed further. All characters included in the phylogenetic analysis were weighted equally, and multistate characters were treated as unordered.

Protoblepharon, new genus

Diagnosis.—An anomalopid with 21 gill rakers on the first arch, about 145 body scale rows, a small (14.5% HL) rotatable light organ, no postorbital papillae, and a very small gap between the lacrimal and nasal for passage of the stalk, which is twisted and not broadly exposed posteriorly. The following combination of characters also is useful in distinguishing *Protoblepharon:* a separate spinous dorsal fin, a pelvic-fin spine, two anal-fin spines, 59–60 enlarged lateral-line scales, an elastic shutter, and a broad strap-like ethmomaxillary ligament with no groove or swelling.

Type species.—Protoblepharon rosenblatti, new species.

Etymology.—From the Greek *protos,* first, and *blepharon,* eyelid, in reference to the cladistic position of the genus as first in the lineage of flashlight fishes that occlude the light organ with an erectable shutter.

Protoblepharon rosenblatti, new species

Fig. 1

Holotype.—AMS I.24275-001. A 229-mm SL female specimen caught by hook and line northwest of Matavera, Rarotonga, Cook Islands (21°12′S, 159°45′W), at 274 m on 30 Nov. 1983, and donated by

N. Sims of the Cook Islands Fisheries Department.

Description.—Counts and measurements, in mm, of the holotype: Dorsal-fin rays VI-I, 14; anal-fin rays II, 11; pectoral-fin rays ii15i; pelvic-fin rays I,5; caudal-fin rays 10, 10+9, 9 (all procurrent rays spinous except the posteriormost in the upper and lower caudal-fin lobes); branchiostegals 8; gill rakers on first arch 21 (5+12 rakers, plus two flat plates at dorsal end of epibranchial and two at anterior end of ceratobranchial); pored lateral-line scales 59 (60 on right side); scale rows above lateral line ca. 18; abdominal scutes 9; vertebrae 14+16. Head length 83.4; predorsal length 96.9; prepelvic length 112; body depth at origin of dorsal fin 81.9; caudal-peduncle depth 23.3; caudal-peduncle length 50.5; snout length 23.7; eye diameter 19.4; orbit diameter 20.5; light-organ length 12.1; pectoral-fin length 51.9; pelvic-fin length 41.2; first dorsal-spine length 12.2; third dorsal-spine length 17.0; sixth dorsal-spine length 6.8; seventh dorsal-spine length 20.0; first anal-spine length 5.8; second anal-spine length 12.3.

Body compressed (width 1.9 in depth) and deep (depth at origin of dorsal fin 1.8 in length without head). With mouth open, profile sloping gradually from occiput to snout, somewhat convex in region of mesethmoid, then dropping slightly to symphysis of upper jaw; upper-jaw symphysis at level of horizontal through middle of eye. Nostrils anterior and completely dorsal to eye with mouth open, the anterior with thickened posterior rim. With jaws forced closed, mouth oblique, lower jaw originating anteriorly near horizontal through middle of eye, and maxilla extending posteriorly to vertical through middle of eye. Posterior supramaxilla ovoid, anterodorsal surface with small pointed process extending anteriorly along posterodorsal edge of small anterior supramaxilla. Posterior supramaxilla covering most of posterior portion of maxilla, the posteroventral corner of maxilla exposed and covered with tiny black papillae. Distinct notch at symphysis of premaxillae, presumably accommodating small dentigerous knobs at symphysis of dentaries when mouth closed. Premaxillae, including most of lateral and medial surfaces, covered with bands of villiform teeth; no teeth at symphyseal notch. Each dentary with narrow band of villiform teeth posteriorly, patch of slightly larger teeth near symphysis extending onto lateral and medial surfaces. Vomer edentulous, palatines with well-developed bands of villiform teeth.

Bones of head and pectoral girdle covered with numerous, rugose to minutely serrate ridges. Cleithrum with large exposed surface posteriorly, margin smooth. Supracleithrum almost completely beneath opercle, only posterodorsal corner exposed, margin smooth. Anterior infraorbitals enlarged, covering anteroventral corner of orbit, and slightly flared laterally forming a medially sloping plate. Laterosensory canals of head appearing as channels of dark skin surrounded by bone, skin covered with small black papillae and perforated frequently by pores.

Eye small, diameter 4.1 in head. No fleshy papillae on posterior rim of orbit. Luminous organ below eye small, length 6.9 in head. Light organ free posteriorly, supported by fibrocartilaginous cup anteriorly, which is ligamentously bound to a fibrocartilaginous stalk. Organ capable of being rotated downward into pocket below eye and medial to infraorbitals. When occluded, dorsal margin of light organ well below infraorbital rim. Black elastic shutter membrane attached along outer margin of suborbital pocket.

Numerous small, spinoid scales (cf. Roberts 1993, = Ct' of Johnson 1984) covering body, about 145 lateral body rows but difficult to count because of irregular distribution of scales. Lateral line covered by enlarged scales, and abdomen with series of about 9 enlarged, keeled scutes. Head mostly scaleless, a few thick, heavily sculptured scales at anterodorsal corner of opercle, scales coalescing on cheek to form strong

Fig. 1. Holotype of *Protoblepharon rosenblatti,* AMS I.24275-001, 229 mm SL. Photograph by C. Bento, AMS.

bony covering. Gular region naked, with low, pigmented, transverse ridges.

Most rakers on first gill arch long and lath-like, length of first raker below angle nearly two-thirds diameter of eye. Four anteriormost and two dorsalmost rakers on first arch and rakers on remaining arches less than half that long. Pseudobranch well developed, about 27 filaments.

Spinous dorsal fin lower than soft dorsal fin, the longest spine (seventh) 1.7 in length of longest unbroken soft ray (the fifth). Length of first spine 1.2 in second, second 1.1 in third and fourth, fifth 1.3 in first, sixth 1.7 in first, and seventh 0.6 in first. First anal spine shorter than any dorsal spine, second anal spine about equal in length to first dorsal spine. Longest anal soft ray (second) about equal to longest dorsal soft ray. Caudal fin deeply forked.

Pectoral-fin base nearly horizontal, fin directed posterodorsally. Pectoral-fin length about 1.6 in head, third through sixth rays the longest. Pelvic fin shorter than pectoral, 2.0 in head, and falling well short of anus. Color in alcohol dark brown to black; fins, posterior trunk, and cheek darkest. Lateral-line scales pale.

Occlusion mechanism (Fig. 2).—The cup supporting the light organ is connected to a fibrocartilaginous stalk that is continuous with its contralateral member across the snout, with no attenuation at the commissure. Anteriorly, the stalk lies flat against the snout, with the broad surface facing outward; posteriorly, where the stalk passes through a small gap between the lacrimal and nasal, it twists such that its broad surface lies nearly in the horizontal plane (Fig. 2B). The posteroventral portion of the stalk and anteroventral corner of the cup each terminate in a short ventral process, and these are loosely joined dorsally by a short ligament. There is no ventral stalk hook. The shutter is slightly thickened near its anterodorsal corner, but there is no discrete shutter knob. The cup supports the anterior end of the light organ and extends posteriorly along about two-thirds of its ventral surface (Fig. 2B). A large section of it is exposed anterolaterally between the light organ and stalk; anteromedially, the cup forms a medially projecting shelf. The stalk muscle is not differentiated into dorsal and ventral bundles and inserts on the ligament connecting the stalk and cup. The Ligament of Diogenes originates on the rostral cartilage, curves around the ethmomaxillary ligament as a broad strap, and then narrows posteriorly before inserting broadly on the ventral process and anteromedial shelf of the cup. The ethmomaxillary ligament descends anteroventrally from its origin on the mesethmoid to insert on the maxilla with a short branch to the palatine. This ligament is broad and flat, lacks a groove where it is crossed by the Ligament of Diogenes, has no pronounced forward flexure, and bears no swellings.

Etymology.—It is our pleasure to name this species in honor of Dr. Richard H. Rosenblatt, a mentor to one of us (GDJ), friend and valuable colleague to all of us. His contributions to the systematics and functional morphology of flashlight fishes have shed much light on the evolution and biology of the Anomalopidae.

Remarks.—States for *P. rosenblatti* of characters not associated with the light organ used by Johnson & Rosenblatt (1988) and Rosenblatt & Johnson (1991) to reconstruct the evolutionary history of anomalopid genera are given in Table 1, those associated with the light organ in Table 2. In Table 3, we list states of characters among anomalopids and outgroups not considered in previous publications that are useful in diagnosing *P. rosenblatti:* number and relative size of lateral-line scales, number of gill rakers, relative size of light organ, least distance between nasal and lacrimal, and orientation of fibrocartilaginous stalk. The relatively small size of the light organ of *P. rosenblatti* could be a function of the large size of the holotype, as comparisons with *Phthanophaneron harveyi* indicate an inverse relationship between relative size of light organ and body (31.2% HL in the 67.7-mm SL holotype and 22.7% HL in the 204-mm SL specimen). McCosker (1982) noted a similar trend in *Kryptophanaron alfredi* (44.7% HL in a 25-mm SL specimen, 34.9% HL in an 89-mm SL fish).

Relationships.—*Protoblepharon* is most similar to *Parmops* in the primitive nature of the occlusion mechanism, especially the absence of a shutter knob and stalk hook. These features are important in the erection of the shutter in *Phthanophaneron, Kryptophanaron,* and *Photoblepharon* (Johnson & Rosenblatt 1988), and it is thus unclear how the shutter mechanism operates in either *Parmops* or *Protoblepharon. Protoblepharon* lacks the primary diagnostic feature of *Parmops,* expansion of the first four infraorbital bones to form a medially sloping shelf that protrudes laterally well beyond the margin of the orbit (Rosenblatt & Johnson 1991). It shares with *Parmops, Phthanophaneron, Kryptophanaron,* and *Photoblepharon* many features recognized as synapomorphies of that lineage by Johnson & Rosenblatt (1988): two supramaxillae, transverse ridges on the gular isthmus, large v-shaped lateral dentary tooth patches, over 100 lateral body scale rows, reflective lateral-line scales, an erectable (or at least elastic) shutter, and a stalk that is continuous across the snout. It lacks another derived feature of that group, a groove in the ethmomaxillary ligament (secondarily absent in *Phthanophaneron*). It is thus most parsimonious to hypothesize that *Protoblepharon* is the sister group of *Parmops* + *Phthanophaneron* + *Kryptophanaron* + *Photoblepharon.* A previously undescribed character corroborating the placement of *Protoblepharon* below *Parmops* involves the configuration of the lacrimal, nasal, and stalk. In most anomalopids, the stalk is broadly exposed at the commissure (Figs. 2B, C; 3B, C), and there is no attenuation where it joins its contralateral member. In *Protoblepharon,* the lacrimal and nasal are separated by only a small gap (least distance between them ca. 1.6% HL; Fig. 3B), and the stalk twists before passing through this gap such that the broad surface is nearly in the horizontal plane, and the narrow margin formerly in a ventral position is exposed laterally (Fig. 2B). In the *Parmops* clade, the lacrimal is separated from the nasal by a large gap (4.0% HL or more, Fig. 3C), and the broad sur-

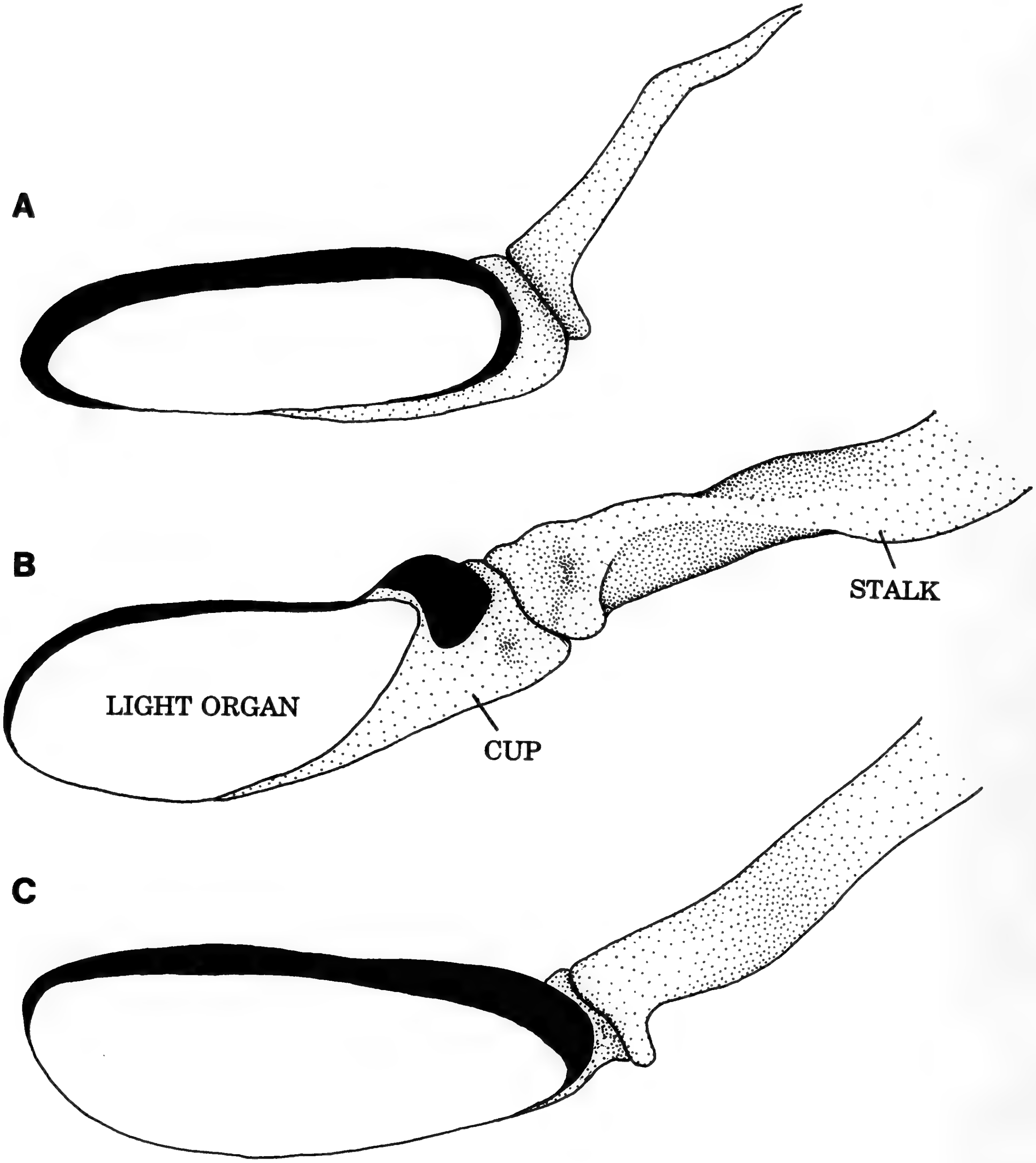

Fig. 2. Light organ and associated structures in (A) *Anomalops katoptron,* USNM 293340, (B) *Protoblepharon rosenblatti,* AMS I.24275-001, (C) *Kryptophanaron alfredi,* USNM 343635. Right side.

face of the stalk is exposed along its entire length (Figs. 2C, 3C). *Anomalops* also has a very small gap between the lacrimal and nasal (ca. 1.0% HL, Fig. 3A), and the two bones are in contact with one another in the outgroups. A large gap between the lacrimal and nasal is thus an additional synapomorphy of *Parmops, Phthanophaneron, Kryptophanaron,* and *Photoblepharon.* A small gap is autapomorphic for the Anomalopidae. Although both have small gaps, the conditions in *Anomalops* (figs. 2A, 3A) and *Protoblepharon* (figs. 2B, 3B) are different in that the stalk is never broadly exposed in *Anomalops* (it is attenuated at the commissure) and does not twist posteriorly but nearly disappears from view in the region of the

Table 1.—States in *Protoblepharon rosenblatti* of Johnson & Rosenblatt's (1988) characters not associated with the light-organ complex.

1.	Vertebrae bearing epineurals*	1, 2, 10–14
2.	Branchiostegals	spiny
3.	Openings in pars jugularis	?
4.	Parasphenoid flanges	?
5.	Swimbladder stay	—
6.	Postorbital papillae	0
7.	Cephalic sensory canal covering	Papillose
8.	Lateral-line tubes	Closed
9.	Midventral scutes	Continuous
10.	Dorsal Fin	VI-I,14
	Supraneurals	0/0/1+1/
11.	Supramaxillae	2
12.	Transverse ridges on gular isthmus	+
13.	Lateral dentary tooth patch	Large "V"
14.	Body scale rows	ca. 145
15.	Reflective or transparent lateral-line scales	+
16.	Pelvic spine	+
17.	Anal spines	II
18.	Vertebrae	14 + 16
19.	Corner of maxilla	Papillae

* Epipleurals of Johnson & Rosenblatt (1988) are epineurals (Patterson & Johnson 1995).

small lacrimal/nasal gap as it turns abruptly ventrad (Johnson & Rosenblatt 1988). The different associations between the lacrimal and nasal possibly are also reflected in the morphology of the C-shaped process of the lacrimal (Zehren 1979), which is probably smaller in *Protoblepharon* than in the *Parmops* lineage because of the closer association of the lacrimal and nasal (and hence the lateral ethmoid). Additional specimens of *Protoblepharon* that can be cleared and stained are needed to examine osteology.

A cladogram depicting relationships among the six anomalopid genera is shown in Figure 4. We constructed the tree using the Branch and Bound option of Swofford's (1991) PAUP 3.0 with the matrix in Table 4. All of the characters (Tables 1, 2) used by Johnson & Rosenblatt (1988) and Rosenblatt & Johnson (1991) initially were included in the analysis, but many are not informative and were eliminated from the matrix. Johnson & Rosenblatt (1988) and Rosenblatt & Johnson (1991) included all characters in Tables 1 and 2 on their cladograms, but noted that many features associated with the light organ could not be polarized by outgroup comparison because of the absence of comparable conditions in the outgroups. They surmised that the fully rotatable light organ of *Anomalops* and the complex shutter mechanism of the non-rotatable light organ of *Photoblepharon* represent highly specialized conditions within the family, and interpreted the less special-

Table 2.—States in *Protoblepharon rosenblatti* of Johnson & Rosenblatt's (1988) characters associated with the light organ.

I	Attachment of Ligament of Diogenes on cup	Medial
II	Attachment of Ligament of Diogenes anteriorly	Rostral Cartilage
III	Cup with medial shelf	Moderate
IV	Insertion of stalk muscle dorsally	Ligament
V	Stalk with inward flexure at cup articulation	—
VI	Rotation pad	—
VII	Postocular skin flap	—
VIIIa	Erectile shutter	+
VIIIb	Shutter knob	—
IX	Stalk hook	—
X	Stalk continuous across snout	+
XIa	Ethmomaxillary ligament with groove	—
XIb	Ethmomaxillary ligament with medial swelling	—
XII	Hook and shutter knob intimately associated	NA
XIII	Cup process attached to stalk hook by ligament	NA
XIV	Organ rotatable	+

Table 3.—Comparison of some diagnostic features of *Protoblepharon rosenblatti* among anomalopids and other trachichthyoids. Data are from the literature or specimens examined in this study (single values represent counts or measurements of a single individual). For light organ length and least distance between nasal and lacrimal, range of values given only for taxa where data from a wide range of adult sizes was available. HL = head length, ant. = anteriorly, NA = not applicable.

Taxon	Lateral-line scales	Gill rakers on 1st arch	Light organ length (% HL)	Least distance between nasal & lacrimal (% HL)	Orientation of stalk
Anomalops	57–59 (Not enlarged)	28–32[a]	35.4	1.0	Not broadly exposed
Protoblepharon	59–60 (Enlarged)	21[b]	14.5	1.6	Broadly exposed ant., twisted posteriorly
Parmops	30 (Enlarged)	30	35.6	4.8	Broadly exposed
Phthanophaneron	38 (Enlarged)	22–24[b]	22.7–31.2	4.0–4.6	Broadly exposed
Kryptophanaron	32–34[c] (Enlarged)	24–28[c]	36.3–44.7[d]	5.7	Broadly exposed
Photoblepharon	39 (Enlarged)	25–30[e]	48.6	5.6	Broadly exposed
Monocentridae	12–15[f] (Not enlarged)	19–21[f]	NA	0	NA
Trachichthyidae	25–63[g] (Enlarged in some)	15–44[h]	NA	0	NA

[a] Shimizu (1984), this study.

[b] Counts include flat plates at dorsal end of epibranchial, anterior end of ceratobranchial, or both.

[c] Colin et al. (1979), this study.

[d] McCosker (1982).

[e] Abe & Haneda (1973).

[f] Smith (1986).

[g] Gomon (1994).

[h] Kotlyar (1980).

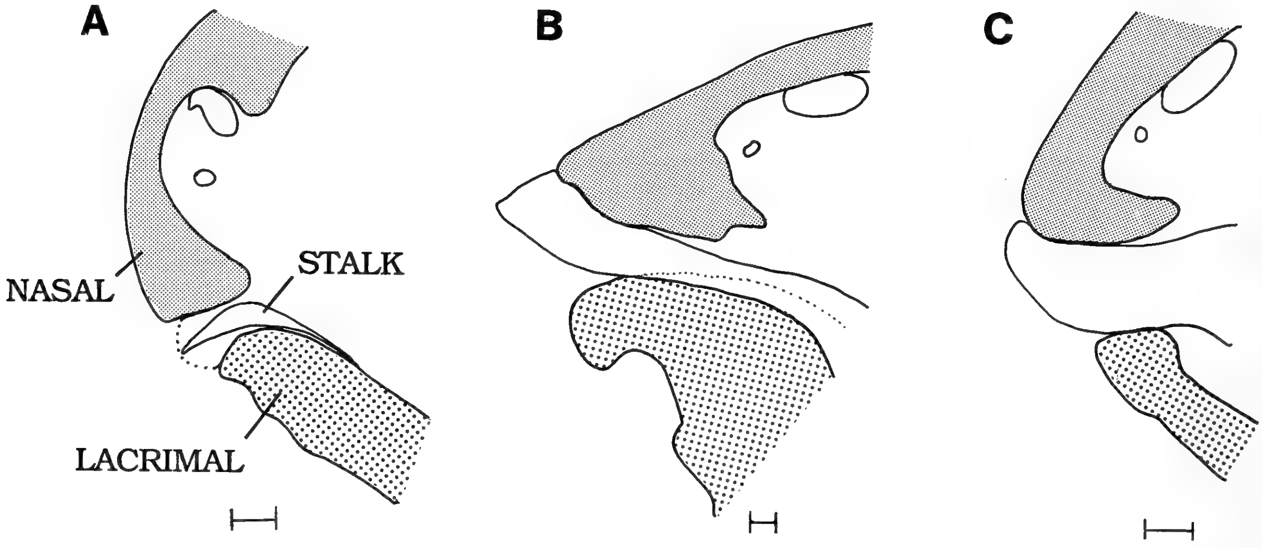

Fig. 3. Diagrammatic illustrations of the anterior snout region in three anomalopids, showing different configurations of the nasal, lacrimal, and fibrocartilaginous stalk. (A) *Anomalops katoptron,* USNM 293340, (B) *Protoblepharon rosenblatti,* AMS I.24275-001, (C) *Kryptophanaron alfredi,* USNM 343635. Dotted line in *Anomalops* shows anterior extent of skin covering stalk, that in *Protoblepharon* represents region where stalk is twisted.

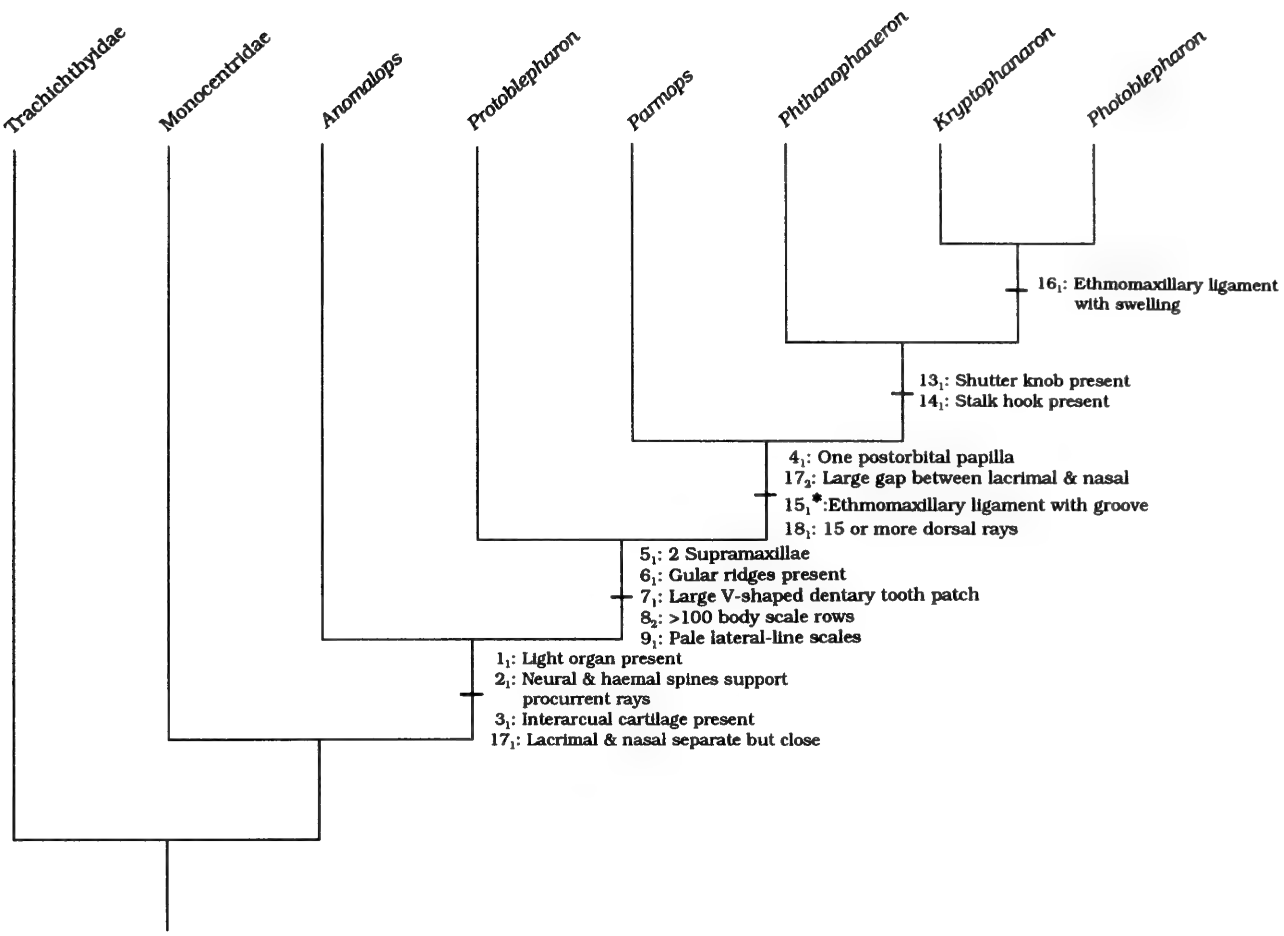

Fig. 4. Cladogram showing hypothesized relationships among anomalopid genera. * = ambiguous character resolved using ACCTRAN. Treelength = 29 CI = 0.83 RI = 0.83.

ized states in *Parmops* and *Phthanophaneron* as ancestral for the family. They polarized features of the light organ based on these assumptions.

The PAUP analysis did not make such assumptions, and recognized that the occlusion mechanisms in either *Anomalops* or cladistically primitive members of the *Protoblepharon* lineage could be ancestral for the family. Nevertheless, the phylogeny of Johnson & Rosenblatt (1988) and Rosenblatt & Johnson (1991) emerged as the single most parsimonious tree based on 18 informative characters (Table 4). We concur with Johnson & Rosenblatt (1988) that the occlusion mechanisms of *Anomalops* and *Photoblepharon* probably represent the most derived conditions within the family and that the occlusion mechanism of *Protoblepharon,* which lacks a well defined shutter knob, a stalk hook to engage the shutter knob, and a groove and swelling in the ethmomaxillary ligament, is ancestral. Relative to outgroups Monocentridae and Trachichthyidae, other features of *Protoblepharon* that might corroborate a *Protoblepharon*-like anomalopid ancestor include the small size of the light organ (14.5% HL vs. 22.7–48.6% HL in all other anomalopid genera), absence of postorbital papillae (eight in *Anomalops,* one in other anomalopids, none in the outgroups), and low number of gill rakers (21 or fewer in *Protoblepharon,* monocentrids, and some trachichthyids, 24 or more in other flashlight fishes).

Acknowledgments

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Table 4.—Character matrix used in constructing cladogram in Figure 4, followed by brief description of character states. See text and Johnson & Rosenblatt (1988) for further descriptions of characters. ? = missing data, 9 = not applicable, $^0/_1$ = polymorphism.

	1–5	6–10	11–15	16–18
Trachichthyidae	00000	00100	1$^0/_1$999	90$^0/_1$
Monocentridae	00000	00000	00999	900
Anomalops	11120	00101	11000	010
Protoblepharon	11?01	11210	00000	010
Parmops	11?11	11210	21001	021
Phthanophaneron	11?11	11210	01110	021
Kryptophanaron	11111	11210	01111	121
Photoblepharon	11111	11211	11111	121

1. Light organ absent (0), present (1).
2. Neural and haemal spines of fourth preural vertebra do not support procurrent caudal rays (0), support procurrent caudal rays (1).
3. Interarcual cartilage absent (0), present (1).
4. Postorbital papillae zero (0), one (1), eight or nine (2).
5. Supramaxillae one (0), two (1).
6. Transverse gular ridges absent (0), present (1).
7. Lateral dentary tooth patch small (0), large v-shaped (1).
8. Lateral body scale rows <50 (0), 50–100 (1), >100 (2).
9. Pale (reflective?) lateral-line scales absent (0), present (1).

*10. Pelvic-fin spine present (0), absent (1).

*11. Corner of maxilla papillose (0), with bony ornamentation (1), smooth (2).

*12. Gill rakers 21 or fewer (0), 24 or more (1).

13. Shutter knob absent (0), present (1).

14. Stalk hook absent (0), present (1).

**15. Ethmomaxillary ligament without groove (0), with groove (1).

16. Ethmomaxillary ligament without swelling (0), with discrete swelling (1).

17. Nasal connected to lacrimal (0), not connected but close (least distance between bones 1.0–1.6% headlength)—(1), separated by large space (least distance between bones >4.0% headlength)—(2).

18. Dorsal-fin rays 14 or fewer (0), 15 or more (1).

*Informative only as autapomorphy of one or more genera; ** ambiguous character.

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Literature Cited

Abe, T., & Y. Haneda. 1973. Description of a new fish of the genus *Photoblepharon* (Family Anomalopidae) from the Red Sea.—Sea Fisheries Research Station, Haifa 60:57–62.

Allen, G. R., & D. R. Robertson. 1994. Fishes of the tropical eastern Pacific. Crawford House Press, Bathurst, Australia, 332 pp.

Baldwin, C. C., & G. D. Johnson. 1995. A larva of the Atlantic flashlight fish. *Kryptophanaron alfredi* (Beryciformes: Anomalopidae), with a comparison of beryciform and stephanoberyciform larvae.—Bulletin of Marine Science 56:1–24.

Colin, P. L., D. W. Arneson, & W. F. Smith-Vaniz. 1979. Rediscovery and redescription of the Caribbean anomalopid fish *Kryptophanaron alfredi* Silvester and Fowler (Pisces: Anomalopidae).—Bulletin of Marine Science 29:312–319.

Gomon, M. F. 1994. Family Trachichthyidae. Pp. 399–410 *in* M. F. Gomon, J. C. Glover, & R. H. Kuiter, eds., The fishes of Australia's south coast. State Print, Adelaide, 992 pp.

Harvey, E. N. 1922. The production of light by the fishes *Photoblepharon* and *Anomalops.*—Carnegie Institute of Washington Publication 312: 45–60.

Haygood, M. G., & D. H. Cohn. 1986. Luciferase genes cloned from the unculturable luminous bacteriod symbiont of the Caribbean flashlight fish, *Kryptophanaron alfredi.*—Gene 45:203–209.

Johnson, G. D. 1984. Percoidei: development and relationships. Pp. 464–498 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., & S. L. Richardson, eds., Ontogeny and systematics of fishes.—American Society of Ichthyologists and Herpetologists Special Publication 1:1–760.

———, & R. H. Rosenblatt. 1988. Mechanisms of light organ occlusion in flashlight fishes, family Anomalopidae (Teleostei: Beryciformes), and the evolution of the group.—Zoological Journal of the Linnean Society 94:65–96.

Konishi, Y., & M. Okiyama. 1997. Morphological development of four trachichthyoid larvae (Pisces: Beryciformes), with comments on trachichthyoid relationships.—Bulletin of Marine Science 60:66–88.

Kotlyar, A. N. 1980. Systematics and distribution of trachichthyid fishes (Trachichthyidae, Beryciformes) of the Indian Ocean.—Transactions of the P. P. Shirshova Institute of Oceanology 110: 177–224.

McCosker, J. E. 1982. Discovery of *Kryptophanaron alfredi* (Pisces: Anomalopidae) at San Salvador, Bahamas, with notes on anomalopid light organs.—Revista De Biologia Trópical 30:97–99.

———, & R. H. Rosenblatt. 1987. Notes on the biology, taxonomy and distribution of anomalopid fishes (Anomalopidae: Beryciformes).—Japanese Journal of Ichthyology 34:157–164.

Moore, J. A. 1993. The phylogeny of the Trachichthyiformes (Teleostei: Percomorpha). Pp. 114–135 *in* G. D. Johnson & W. D. Anderson, Jr., eds., Phylogeny of the Percomorpha.—Bulletin of Marine Science 52:1–629.

Patterson, C., & G. D. Johnson. 1995. The intermuscular bones and ligaments of teleostean fishes.—Smithsonian Contributions to Zoology 559:1–83.

Roberts, C. D. 1993. Comparative morphology of spined scales and their phylogenetic significance in the teleostei.—Bulletin of Marine Science 52:60–113.

Rosenblatt, R. H., & G. D. Johnson. 1991. *Parmops coruscans,* a new genus and species of flashlight fish (Beryciformes: Anomalopidae) from the South Pacific.—Proceedings of the Biological Society of Washington 104:328–334.

———, & W. L. Montgomery. 1976. *Kryptophaneron harveyi,* a new anomalopid fish from the eastern tropical Pacific, and the evolution of the Anomalopidae.—Copeia 1976:510–515.

Shimizu, T. 1984. Order Beryciformes. Pp. 108–110 *in* H. K. Masuda, K. Amaoka, C. Araga, T. Uyeno, & T. Yoshino, eds., The fishes of the Japanese Archipelago. Tokai University Press: 1–437.

Smith, M. M. 1986. Family No. 128: Monocentridae. Pg. 413 *in* M. M. Smith and P. C. Heemstra, eds., Smiths' Sea Fishes. Macmillan South Africa (Publishers) (Pty) Ltd., Johannesburg, 1047 pp.

Swofford, D. L. 1991. PAUP: Phylogenetic analysis using parsimony, version 3.0s. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Zehren, S. J. 1979. Pisces: Teleostei. The comparative osteology and phylogeny of the Beryciformes.—Evolutionary Monographs I, 389 pp.

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Status of *Platycephalus cantori* Bleeker, 1879 (Teleostei: Platycephalidae)

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Abstract.—*Platycephalus cantori* Bleeker, 1879, *P. maculosus* Peters, 1869 and *P. bobbosok* Bleeker, 1853 are here regarded as junior synonyms of *P. carbunculus* Valenciennes *in* Cuvier & Valenciennes, 1833. Lectotypes are selected for *P. cantori* and *P. maculosus.*

With a brief description based on a specimen from Bombay, Valenciennes *in* Cuvier & Valenciennes (1833) described *Platycephalus carbunculus* (currently *Eurycephalus carbunculus* according to Imamura, 1996). Cantor (1849) identified specimens from Pinang as *Platycephalus carbunculus* and gave a more extensive description. Günther (1860) erroneously listed dried skins from Dr. Cantor's collection as types of *P. carbunculus* and synonymized *P. carbunculus* under *P. malabaricus* Cuvier, 1829. Bleeker (1879) insisted that Cantor's *P. carbunculus* was not *P. carbunculus* Va-

Table 1.—Counts and proportional measurements of holotype of *Eurycephalus carbunculus* and syntypes of *Platycephalus cantori.*

	E. carbunculus (Holotype)	*Platycephalus cantori* (Syntypes)	
Standard length (SL) mm	128.4	133.6	135.4
Head length (HL)	43.1	44.3	43.2
Counts			
Dorsal-fin rays	I-VIII-11	I-VIII-11	I-VII-?
Anal-fin rays	12	12	12
Pectoral-fin rays	19	19	19
Pelvic-fin rays	I, 5	I, 5	I, 5
Lateral line scales	54	53	53
Proportions as % SL			
Head length	33.6	33.2	31.9
Snout length	8.8	9.0	8.1
Orbital diameter	8.6	9.4	8.3
Interorbital width	1.9	1.7	?
Length of caudal peduncle	8.8	9.2	8.9
Depth of caudal peduncle	4.4	4.1	4.5
Pectoral-fin length	15.1	15.4	?
Proportions as % HL			
Snout length	26.2	27.1	25.5
Orbital diameter	25.5	28.2	25.9
Interorbital width	5.8	5.2	?
Upper jaw length	34.1	35.9	34.5
Lower jaw length	50.3	53.0	53.9

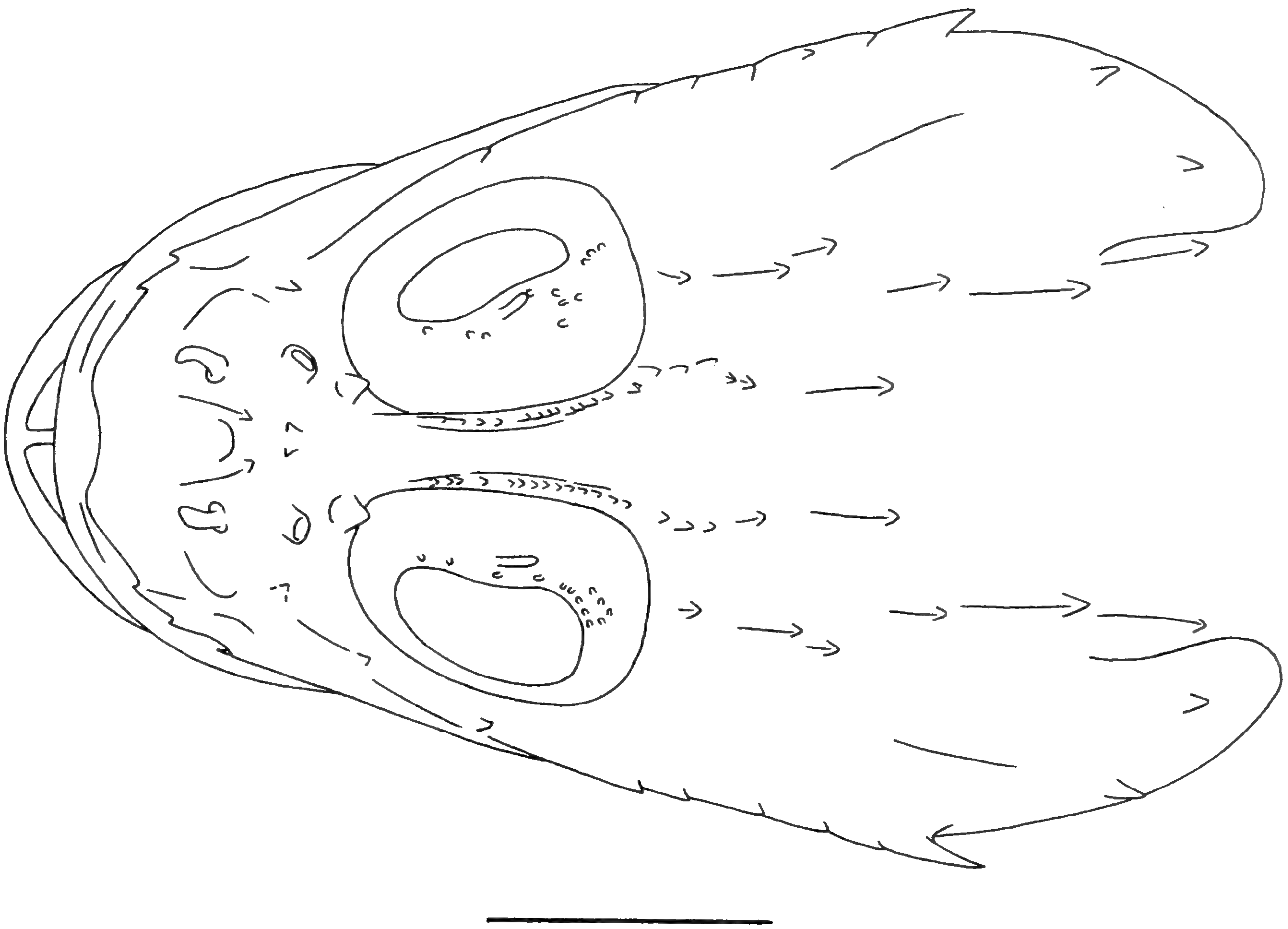

Fig. 1. Dorsal view of head of holotype of *Eurycephalus carbunculus*, MNHN 6875. Scale bar indicates 10 mm.

lenciennes and renamed it *P. cantori.* After examining the primary type specimens of *P. carbunculus* and *P. cantori,* de Beaufort & Briggs (1962) followed Bleeker in recognizing the two species. Murty (1982) listed *Thysanophrys cantori* but noted the lack of authentic records from India. We believe de Beaufort and Briggs were incorrect and we regard *P. cantori* Bleeker, 1879, *P. bobossok* Bleeker, 1860 and *P. maculosus* Peters, 1869 as junior synonyms of *P. carbunculus* Valenciennes *in* Cuvier & Valenciennes, 1833.

Counts and measurements follow Hubbs & Lagler (1958). Institutional abbreviations are taken from Leviton et al. (1985).

A characteristic series of pimple-like protuberances on the upper margin of the eye (Fig. 1), with one elongated as a simple tentacle, is present in the holotype of *Eurycephalus carbunculus* (MNHN 6875). This series is also readily visible in the putative types *P. bobossok* (RMNH 5919) and the syntypes of *P. maculosus* (ZMB 5145) but, unfortunately, cannot be seen on the dried skins (syntypes) of *P. cantori* (BMNH 1860.3.19.268–9). However, the mottled coloration on the back and sides of the body (Fig. 2), short snout, lack of any interopercular flaps, presence of a preorbital spine, supraorbital ridge well-serrated above the eye, and three or more suborbital spines confirm that the putative syntypes of *P. cantori* are identifiable as *E. carbunculus.* The same combination of characters is evident in the type specimens of *P. bobossok* and *P. maculosus.* A comparison of counts and proportional measurements of the holotype of *E. carbunculus* and the syntypes of *P. cantori* appears in Table. 1. The close agreement in proportional measurements and the combination of 11 dorsal soft rays, 12 anal-fin rays, 19 pectoral-fin rays and a

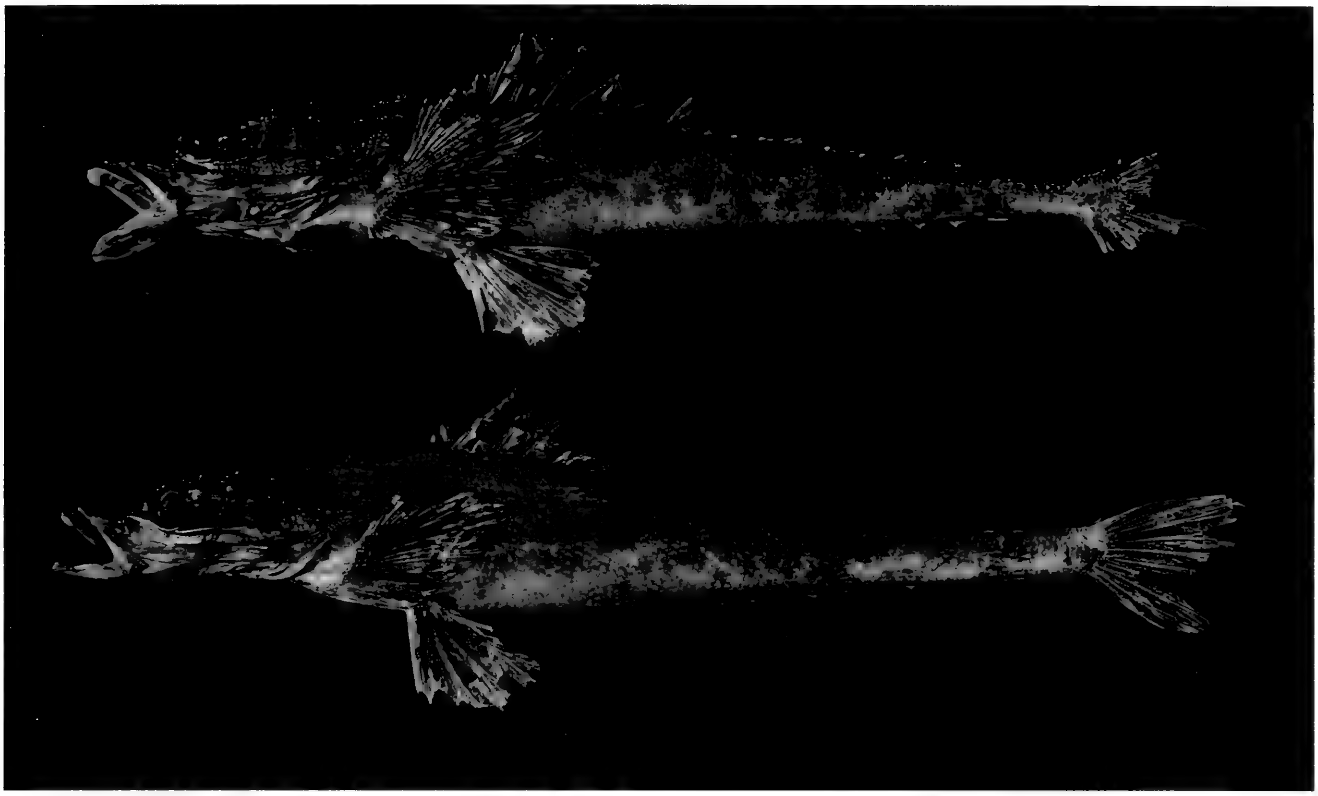

Fig. 2. Lateral view of lectotype of *Platycephalus cantori* (upper, 133.6 mm SL) BMNH 1860.3.19.268 and paralectotype (lower, 135.4 mm SL) BMNH 1860.3.19.269.

pelvic-fin ray count of 1,5 are further evidence of their strong similarity.

It seems appropriate here to designate lectotypes for *Platycephalus cantori* Bleeker and *P. maculosus* Peters. We select BMNH 1860.3.19.268 (134 mm SL, caudal fin largely broken, interorbital space entire) as the lectotype and BMNH 1860.3.19.269 (135 mm SL, caudal fin mostly complete, interorbital space truncated) as the paralectotype of *P. cantori.* ZMB 5145 (93 mm SL) is selected as the lectotype of *P. maculosus* Peters and ZMB 32760 (129 mm) as a paralectotype. As Peters (1869), in a footnote, compared several features of the above two specimens from Singapore with ZMB 724 (1, 103 mm) from the Celebes, we regard the latter to be part of the type series and, is here designated as a second paralectotype. Bleeker (1853:461) described *Platycephalus bobossok* from a single specimen (148 mm in length) from Batavia. In his later revision of *Platycephalus,* Bleeker (1879:24) listed 4 specimens of *P. bobossok* (118–180 mm in length) from Batavia and other localities. Three specimens (143, 146, 156 mm total length) are currently found in the type collection (RMNH 5919). Of these, the specimen 146 mm in total length most closely approximates Bleeker's holotype.

Acknowledgments

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Literature Cited

Bleeker, P. 1853. Diagnostische beschrijvingen van nieuwe of weinig bekende vischsoorten van Batavia. Tiental I–VI.—Natuurkundig Tijdschrift voor Nederlandsche Indie IV:451–516.

———. 1879. Revision des especes insulindiennes du genre Platycephalus.—Natuurkundige Verhandelingen Koninklijke Akademie, v. XIX (1878): 1–31.

Cantor, T. 1849. Catalogue of Malayan Fishes.—Journal of the Asiatic Society of Bengal 18(2):981–1443.

Cuvier, G., & A. Valenciennes. 1829. Histoire naturelle des poissons. F. G. Levrault, Paris, vol. 4, 518 pp.

———, & ———. 1833. Histoire Naturelle des Poissons. F. G. Levrault, Paris, v. 9:429–512.

de Beaufort, L. F., & J. C. Briggs. 1962. The fishes of the Indo-Australian Archipelago. XI. Scleroparei, Hypostomides, Pediculati, Plectognathi, Opisthomi, Discocephali, Xenoterygii. E. J. Brill, Leiden, 1–481.

Günther, A. 1860. Catalogue of the Acanthopterygian fishes in the collection of the British Museum. 2. Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Polynemidae, Sphraenidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae. London, xxi + 548 pp.

Hubbs, C. L., & K. F. Lagler. 1958. Fishes of the Great Lakes Region.—Cranbrook Institute of Science Bulletin 26:213 pp.

Imamura, Hisashi. 1966. Phylogeny of the Family Platycephalidae and Related Taxa (Pisces: Scorpaeniformes).—Species Diversity 1(2):123–233.

Leviton, A. E. et al. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985(3): 802–832.

Murty, V. S. 1982. On the fishes of the family Platycephalidae of the seas around India.—Journal of the Marine Biological Association of India (1975) 17(3):679–694.

Peters, W. (C.H.). 1869. Uber die von Hrn. Dr. F. Jagor in dem ostindischen Archipel gesammelten und dem Konigl. Zoologischen Museum uebergebenen Fische.—Monatsberichte der Koniglich-Preussische Akademie der Wissenschaften zu Berlin for 1868:254–281.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Pseudothelphusa ayutlaensis, a new species of freshwater crab (Crustacea: Brachyura: Pseudothelphusidae) from Mexico

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Abstract.—*Pseudothelphusa ayutlaensis,* new species, is described from the State of Guerrero, Mexico. The new species is placed in the genus *Pseudothelphusa* based on the presence of a first gonopod with the characteristic broadly rounded mesial process and a well developed subtriangular lateral process. The unique orientation of the mesial and lateral processes of the first gonopod distinguishes *P. ayutlaensis* from other species in the genus.

The genus *Pseudothelphusa* de Saussure, 1857, is one of the most diverse within the family Pseudothelphusidae Rathbun, 1893, with 22 species (Alvarez & Villalobos 1996, Alvarez et al. 1996), distributed exclusively in Mexico, and one, *P. puntarenas* Hobbs, 1991, from Costa Rica. The genus is distributed along the Pacific slope from Sonora to Guerrero, throughout central Mexico, and along the Gulf of Mexico slope in Veracruz (Rodríguez 1982, Alvarez 1989). Although species of *Pseudothelphusa* exhibit a great variety of gonopod morphologies, all exhibit a broadly rounded mesial process and subtriangular lateral lobe (Rodríguez 1982). In the majority of species of *Pseudothelphusa* the mesial process of the first gonopod is oriented proximally, descending from the apex towards the base of the gonopod and is reniform in shape, while the lateral process projects laterally. In *P. ayutlaensis,* new species, the mesial process is oriented distally, extending upwards from the apex; and the lateral process is projected cephalically. All the specimens are deposited in the Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (CNCR). Carapace width and carapace length are abbreviated as cw and cl, and expressed in millimeters.

Pseudothelphusa de Saussure, 1857

Pseudothelphusa ayutlaensis, new species

Figs. 1, 2

Holotype.—♂, cw 24.3 mm, cl 16.1 mm; junction of Pinela and Tonala rivers, Municipio de Ayutla de los Libres, Guerrero (16°52′N, 99°12′W), 18 Dec 1987, coll. J. P. Gallo; CNCR 8715.

Paratypes.—2 ♂, cw 23.0, 22.0 mm, cl 15.0, 14.4 mm; same locality, date, and collector as holotype; CNCR 8715. 2 ♀, cw 36.3, 28.2 mm, cl 23.5, 18.6 mm; same locality, date, and collector as holotype; CNCR 8715.

Description.—Dorsal surface of carapace covered with small papillae (Fig. 1a). Inferior frontal border continuous, thick, slightly sinuous in dorsal and frontal views, extending laterally to form superior margin of orbits (Fig. 1b). Superior frontal border formed by the folding of the carapace with an irregular row of blunt tubercles, divided by median groove, inclined towards the center (Fig. 1b). Postfrontal lobes present as two distinct elevations. Median groove deep, extending posteriorly beyond postfrontal lobes. Cervical groove wide and deep, curved slightly posteriorly, reaching anterolateral margin (Fig. 1a). Cardiac region of carapace weakly marked. Anterolateral margin between orbit and cervical

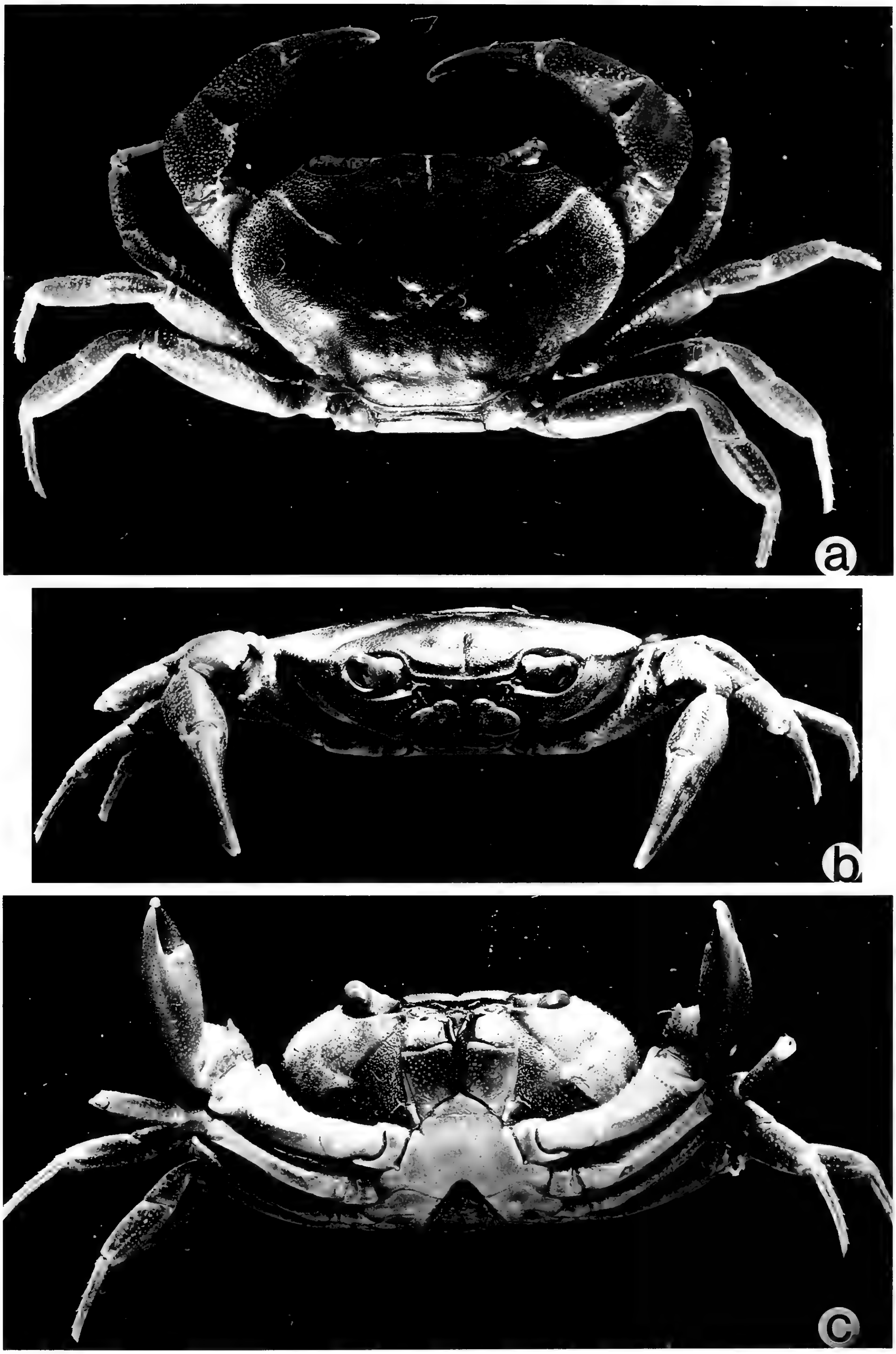

Fig. 1. *Pseudothelphusa ayutlaensis,* new species, male holotype: a, dorsal view; b, frontal view; c, ventral view. Carapace width 24.3 mm, length 16.1 mm.

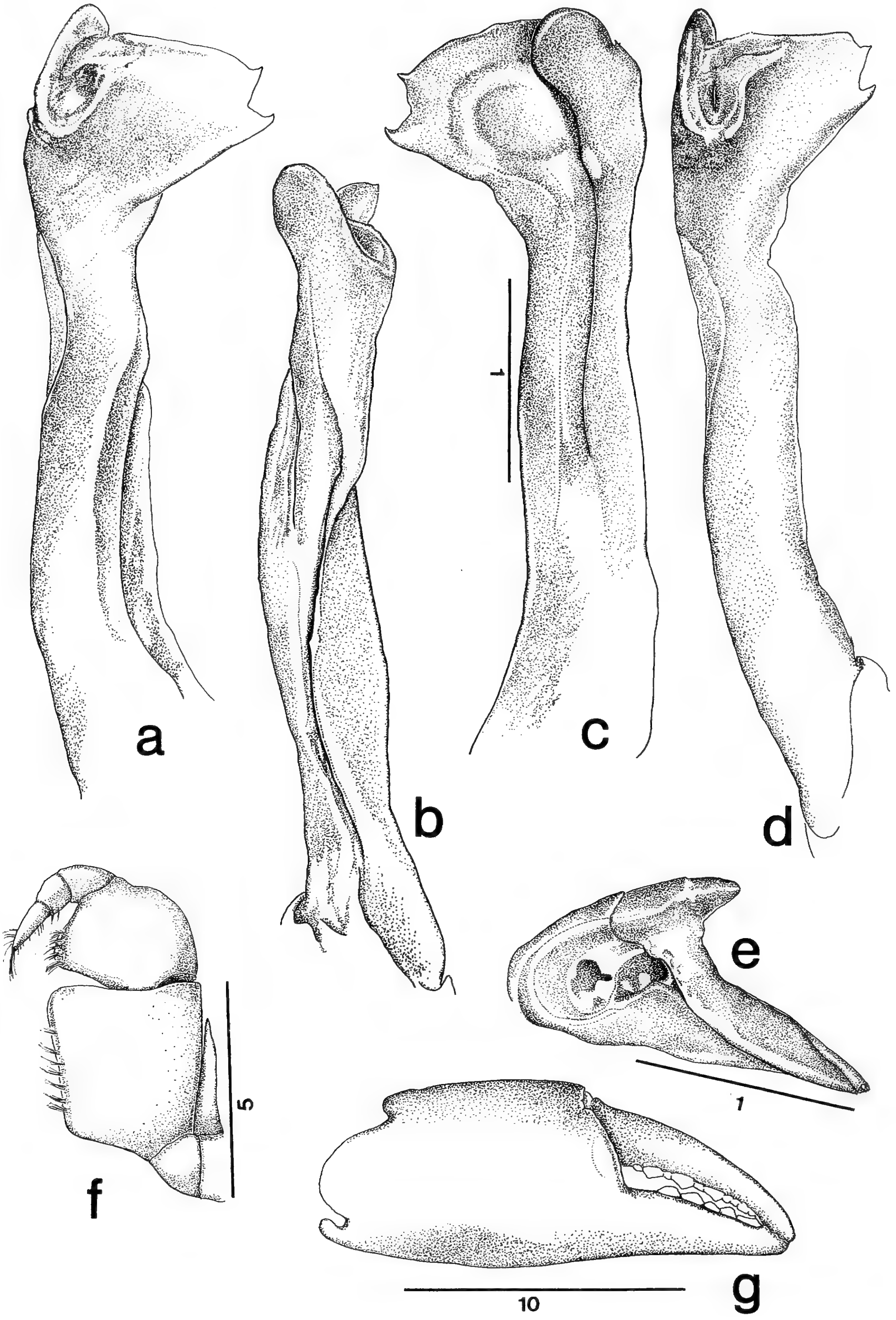

Fig. 2. *Pseudothelphusa ayutlaensis,* new species, a–e left first gonopod: a, lateral view; b, mesial view; c, cephalic view; d, caudal view; e, apical view; f, left third maxilliped; g, right chela. Scale bars: a–e = 1 mm, f = 5 mm, g = 10 mm.

groove with irregularly placed denticles, posterior to cervical groove with uniform denticles. Ratio exopod/ischium of third maxilliped 0.73. Ischium of third maxilliped trapezoidal in shape; merus narrower than ischium (Fig. 1c). Right chela the largest; fingers not gaping, teeth worn out in holotype. Both chelae with blunt denticle at base of movable finger.

First gonopod slender, with twisted sperm channel (Fig. 2a). In caudal view (Fig. 2d) with constriction at two thirds its length below cavity of apex. Marginal suture sinuous (Fig. 2b). Marginal process absent from apex of gonopod, except for one sharp tooth at base of mesial process (Fig. 2c). Mesial process rounded, oriented distally (Fig. 2b). Lateral process extending in laterocephalic direction, wide proximally, tapering distally, ending in two sharp tips (Fig. 2d). Cavity of apex oval shaped (Fig. 2e). Crest of cavity of apex low caudally, higher cephalically.

Etymology.—The specific name "ayutlaensis" makes reference to the county, Ayutla de Los Libres, in the State of Guerrero where the species is distributed.

Remarks.—The new species is placed in the genus *Pseudothelphusa* based on the torsion of the sperm channel of the first gonopod, and the presence of a typically rounded mesial process. *Pseudothelphusa ayutlaensis* is closest to those species of *Pseudothelphusa* distributed in western Mexico that lack a marginal process in the apical region of the gonopod (e.g., *P. rechingeri* Pretzmann, 1965; *P. sonorae* Rodríguez & Smalley, 1969; and *P. galloi* Alvarez & Villalobos, 1990) and to those species in which the marginal process is reduced to a series of small teeth (e.g., *P. jouyi* Rathbun, 1893; *P. lophophallus* Rodríguez & Smalley, 1969; and *P. nayaritae* Alvarez & Villalobos, 1994). The new species also resembles *P. galloi* in the shape of the lateral process of the first gonopod. Although this process is oriented differently in both species (cephalically in *P. ayutlaensis* and laterally in *P. galloi*), in both species it is roughly triangular and ends in two sharp tips. In southern Guerrero *Pseudothelphusa ayutlaensis* and *P. galloi* share the same drainage system, 10 km away from each other.

Acknowledgments

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Literature Cited

Alvarez, F. 1989. *Smalleyus tricristatus,* new genus, new species, and *Pseudothelphusa parabelliana,* new species (Brachyura: Pseudothelphusidae) from Los Tuxtlas, Veracruz, Mexico.—Proceedings of the Biological Society of Washington 102:45–49.

———, & J. L. Villalobos. 1990. *Pseudothelphusa galloi,* a new species of freshwater crab (Crustacea: Brachyura: Pseudothelphusidae) from southwestern Mexico.—Proceedings of the Biological Society of Washington 103: 103–105.

———, & ———. 1994. Two new species and one new combination of freshwater crabs from Mexico (Crustacea: Brachyura: Pseudothelphusidae).—Proceedings of the Biological Society of Washington 107:729–737.

———, & ———. 1996. Especie nueva de cangrejo de agua dulce del Género *Pseudothelphusa* (Brachyura: Pseudothelphusidae) de Guerrero, México.—Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología 67(2):297–302.

———, ———, & E. Lira. 1996. Decapoda. Pp. 103–129 *in* J. Llorente, A. N. García-Aldrete, & E. González, eds., Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una Síntesis de su Conocimiento. Instituto de Biología, Universidad Nacional Autónoma de México-CONABIO, 660 pp.

Hobbs, H. H., III. 1991. A new pseudothelphusid crab from a cave in southern Costa Rica (Decapoda: Brachyura).—Proceedings of the Biological Society of Washington 104:295–298.

Pretzmann, G. 1965. Vorlaufiger Bericht über die Familie Pseudothelphusidae.—Anzeiger der Mathematisch-Naturwissen-Schaftlichen Klasse der Österreichische Akademie der Wissenschaften 179:14–24.

Rathbun, M. J. 1893. Descriptions of new species of American freshwater crabs.—Proceedings of the United States National Museum 16:649–661.

Rodríguez, G. 1982. Les crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae.—Faune Tropicale 22:1–223.

———, & A. E. Smalley. 1969. Los cangrejos de agua dulce de México de la familia Pseudothelphusidae (Crustacea: Brachyura).—Anales del Instituto de Biología, Universidad Nacional Autónoma de México 40:69–112.

Saussure de, H. 1857. Diagnoses de quelques Crustacés nouveaux des Antilles et du Mexique.—Revue et Magazin de Zoologie Pure et Appliquée 9:304–306.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Austinixa, a new genus of pinnotherid crab (Crustacea: Decapoda: Brachyura), with the description of *A. hardyi*, a new species from Tobago, West Indies

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Abstract.—The new genus *Austinixa* is recognized for *Pinnixa cristata* Rathbun and six other species formerly assigned to *Pinnixa* White, 1846. An eighth species, *A. hardyi*, new species, is described from Tobago, West Indies. Members of *Austinixa* can be distinguished from species of *Pinnixa* sensu stricto by the transverse ridge that completely crosses the posterior surface of the carapace, the strongly deflected fingers of the chelae, and the much longer, slenderer, and smoother third walking leg. Members of *Austinixa* often are associated with callianassid shrimps. *Austinixa hardyi*, new species, found associated with a member of the callianassid genus *Callichirus* Stimpson, 1866, is the only described species of *Austinixa* having dense patches of setae on the carapace of the male.

Collections of infaunal decapods from Tobago were made by one of us (R.H.) in 1992 and 1993. One of the species collected proved to be an undescribed member of the pinnotherid genus *Pinnixa* White, 1846. It is named and it and related species are placed in a new genus below.

Abbreviations used in the accounts include: A1, antennule; cl, carapace length; Mxp3, third maxilliped; P1, cheliped; P2–5, first to fourth walking legs. Carapace size is expressed as length × width. All measurements are in millimeters (mm).

The types have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Austinixa, new genus

Diagnosis.—Carapace much wider than long, with transverse ridge extending from side to side across cardiac region. Mxp3 with palp articulated distally on merus, dactylus articulated proximally on propodus. Movable finger of chela deflected in both sexes, vertical or nearly so in males. Third walking leg (P4) much the largest. Both sexes with 7 abdominal somites. Male gonopod simple, apex often bent laterally, with corneous tip, not markedly ornate.

Type species.—*Pinnixa cristata* Rathbun, 1900, by present designation.

Included species.—*Austinixa aidae* (Righi, 1967), new combination, *Austinixa behreae* (Manning & Felder, 1989), new combination, *Austinixa chacei* (Wass, 1955), new combination, *Austinixa cristata* (Rathbun, 1900), new combination, *Austinixa felipensis* (Glassell, 1935), new combination (and its synonym *Pinnixa salvadorensis* Bott, 1955), *Austinixa gorei* (Manning & Felder, 1989), new combination, *Austinixa patagoniensis* (Rathbun, 1918), new combination, and *Austinixa hardyi*, new species.

Etymology.—We dedicate this new genus to our colleague Austin B. Williams, Systematics Laboratory, National Marine Fisheries Service, the acknowledged dean of

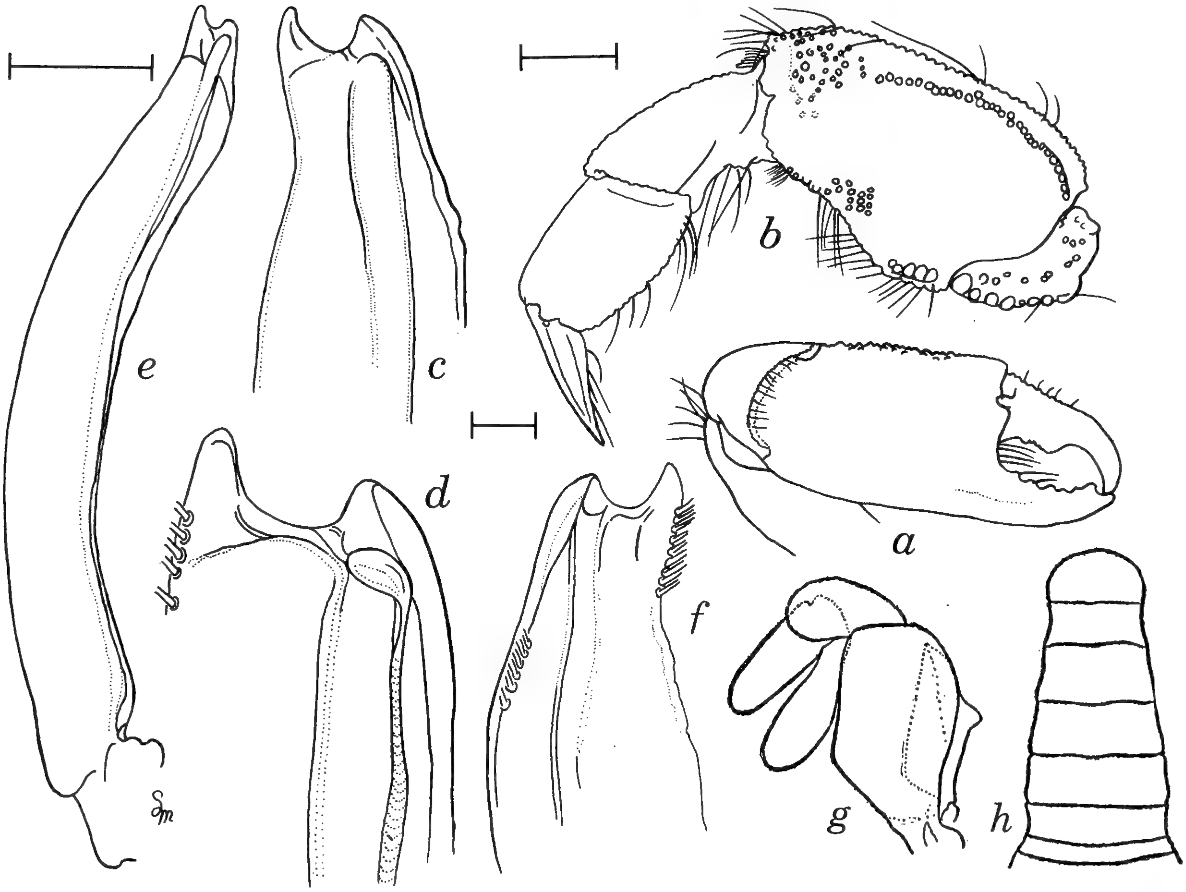

Fig. 1. *Pinnixa cylindrica* (Say). *a–f,* Chesapeake Bay, male, 7.1 by 14.7 mm, USNM 49643; *g, h,* Sarasota Bay, Florida, male, 5.6 by 11.0 mm (from Rathbun 1918: fig. 99). *a,* Right chela, outer face; *b,* Left P3, posterior face; *c,* Distal part of gonopod, abdominal view; *d,* Apex of gonopod, enlarged, abdominal view; *e,* Gonopod, abdominal view (setae omitted); *f,* Apex of gonopod, sternal view; *g,* Left Mxp3; *h,* Abdomen. Scales equal 2 mm (*a, b*), 1 mm (*c–f*), 0.1 mm (*d*).

studies on the systematics of marine decapods of the eastern United States. The name is composed of the given name Austin with the ending of the generic name *Pinnixa.* The gender is feminine.

Remarks.—The transverse ridge completely crossing the cardiac region of the carapace will serve to distinguish members of this genus from all species now placed in *Pinnixa.* The deflected movable finger in males will distinguish males of members of this genus from males of members of the type species of *Pinnixa, P. cylindrica* (Say, 1818) (Fig. 1), in which the fingers are horizontal in both sexes (Fig. 1a).

In *Pinnixa cylindrica* the third walking leg (P4) is much shorter and stouter than in members of *Austinixa,* and the surface and dorsal margin of the merus are ornamented with tubercles, some arranged in beaded carinae (Fig. 1b). In members of *Austinixa* the third walking leg is more elongate, slenderer, and the merus is smooth, not ornamented with tubercles.

The third maxilliped of *Austinixa* (Figs. 3c, 4a) is similar to that of *Pinnixa* (Fig. 1g), with the propodus and dactylus both elongate, oval, much longer than their carpus, and with the dactylus inserted basally on the propodus.

The male gonopod of members of *Austinixa* (Fig. 3o) differs from that of *Pinnixa cylindrica* (Fig. 1c–f) in having a laterally-deflected, corneous apex. The gonopod of *P. cylindrica* forms a shallow sinuous curve with the corneous apex directed along the longitudinal axis, not deflected.

The abdomen of males of *Austinixa* is similar in shape to that of *Pinnixa cylindrica,* composed of seven somites. The telson is broader than long, rounded apically, and longest of all segments.

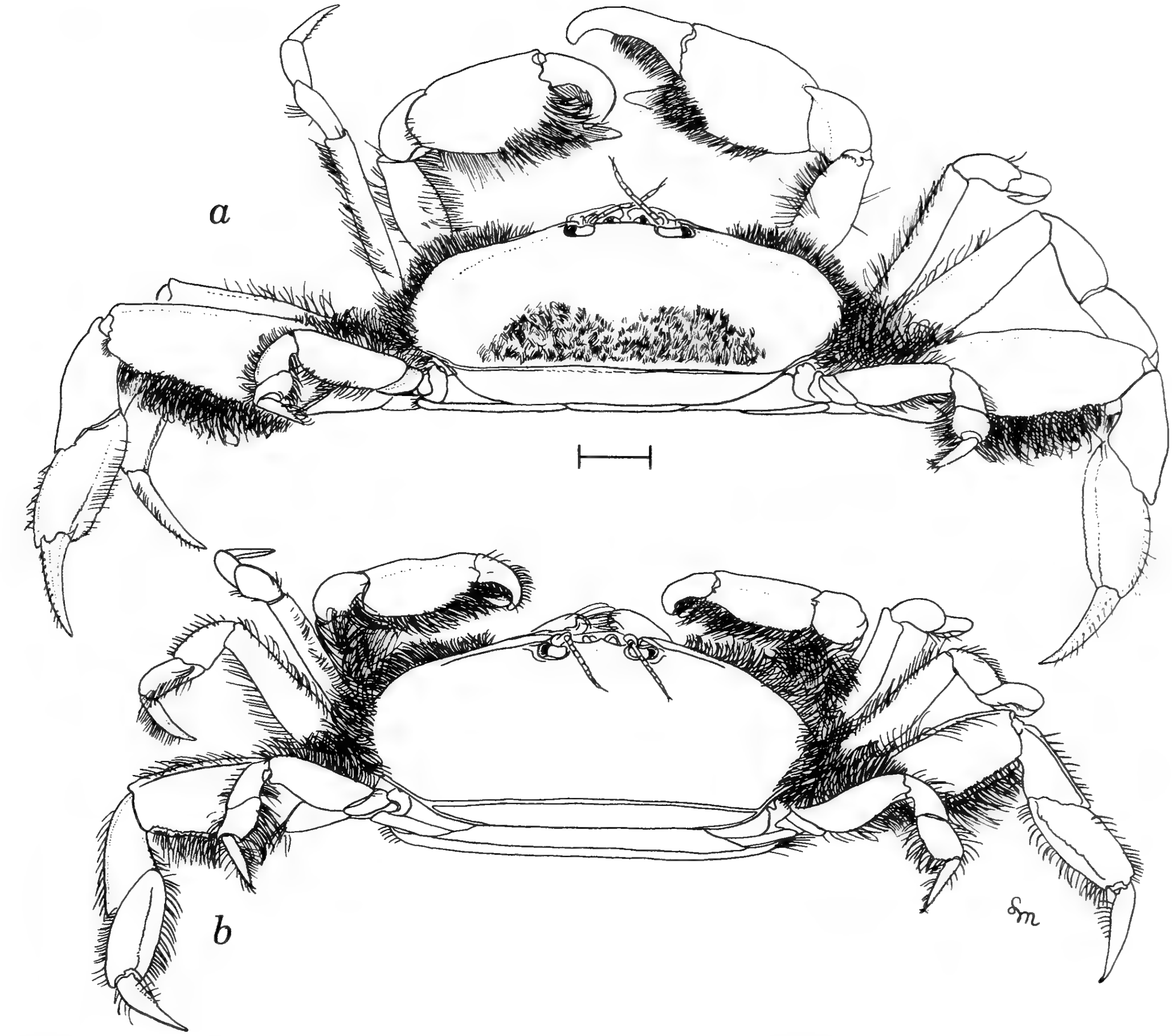

Fig. 2. *Austinixa hardyi,* new genus, new species. Dorsal view. *a,* male holotype, Tobago, 2.6 by 6.5 mm, USNM 284176; *b,* female paratype, Tobago, 2.4 by 6.5 mm, USNM 284177. Scale equals 1 mm.

Austinixa hardyi, new species
Figs. 2–4

Material.—Tobago, Bloody Bay (11°18′N, 60°38′W), beach to a depth of 1.5 m, sand bottom with some rocks, leg. R. W. Heard, sta 4, 4 Apr 1992: 16 ♂♂, 1.9 × 3.4–2.8 × 7.5, 6 non-ovigerous ♀♀, 1.9 × 5.0–2.7 × 7.3, 13 ovigerous ♀♀, 1.8 × 4.6–2.5 × 7.0. A male, 2.6 × 6.5 is holotype, USNM 284176; other specimens are paratypes, USNM 284177.

Diagnosis.—Carapace lacking branchial ridge extending laterally from orbit. Male with dorsal patch of setae on carapace anterior to cardiac crest. Propodus of P4 with bicarinate opposable (ventral) margin. Dactylus of P4 with ridge on posterior face.

Description.—Carapace smooth, 2.3–2.9 times broader than long, lacking branchial ridge on anterior surface. Male with broad patch of short setae anterior to cardiac crest, patch occasionally divided into 2 submedian patches. Carapace densely setose laterally, setae extending onto proximal segments of pereopods.

Antennular (A1) flagellum with 9 segments, third longest, ultimate more than half as long as penultimate. Basal segments with distinct movable spine.

Chelipeds (P1) of male and female dissimilar. Male chela larger, movable finger about as long as palm, strongly deflexed, almost vertical; palm height subequal to length dorsally; distal surface of palm al-

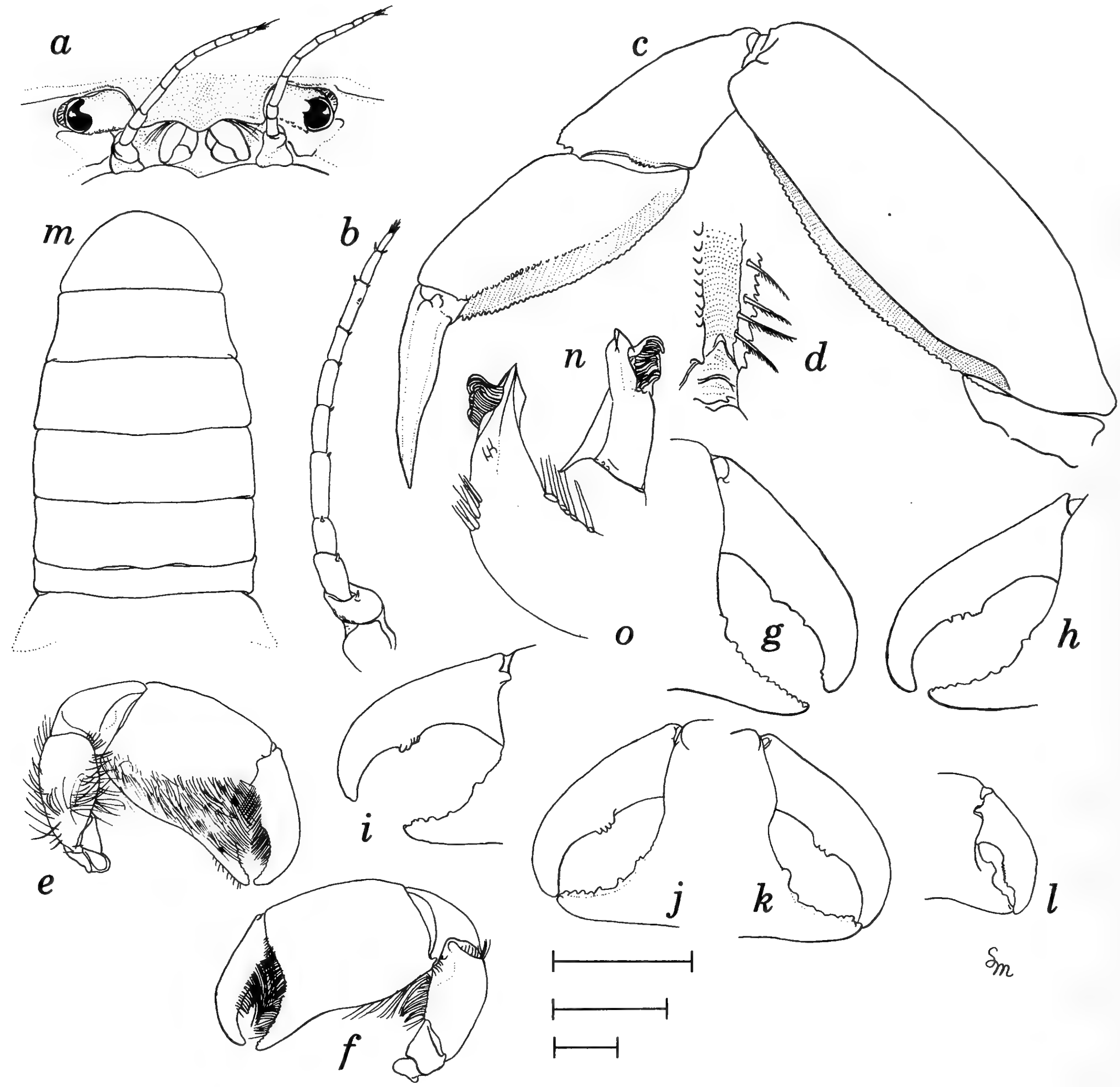

Fig. 3. *Austinixa hardyi,* new genus, new species. Male paratypes, Tobago, USNM 284177: *a–h, n–p,* 2.8 by 7.5 mm; *i,* 2.5 by 6.6 mm; *j,* 2.3 by 6.6 mm; *k,* 1, 2.4 by 6.6 mm; *m,* 1.9 by 5.0 mm. *a,* Front; *b,* Antennule; *c,* P3; *d,* Distal part of ventral margin of propodus, enlarged; *e,* Left P1, outer face; *f,* Left P1, inner face; *g,* Fingers of left chela; *h,* Fingers of left chela; *i,* Fingers of right chela; *j,* Fingers of left chela; *k,* Fingers of right chela; *l,* Fingers of left chela; *m,* Abdomen; *n,* Apex of gonopod, sternal view; *o,* Distal half of gonopod, abdominal view. Upper scale equals 1 mm (*a, c, m*), 0.5 mm (*b, g–l*); middle scale equals 1 mm (*e, f*), 2 mm (*d*); lower scale equals 0.1 mm (*n, o*).

most vertical in male; inner lower surface of palm and gape densely setose; fingers variably toothed. Female chela smaller, movable finger shorter than palm, deflexed but less so than in male, height of palm less than length; fingers variably toothed.

First and second walking legs (P2, P3) slender, largely naked except for dense patch of proximal setae, few, scattered, plumose setae on distal segments, and short setae on dactylus; setation variable.

Third walking leg (P4) much the longest, with dense patch of setae proximally and ventrally on merus, remainder of surface largely naked. Merus length about twice height in males, 2.5 times height in females. Propodus length about 1.5 times height in males, twice height in females, ventral (op-

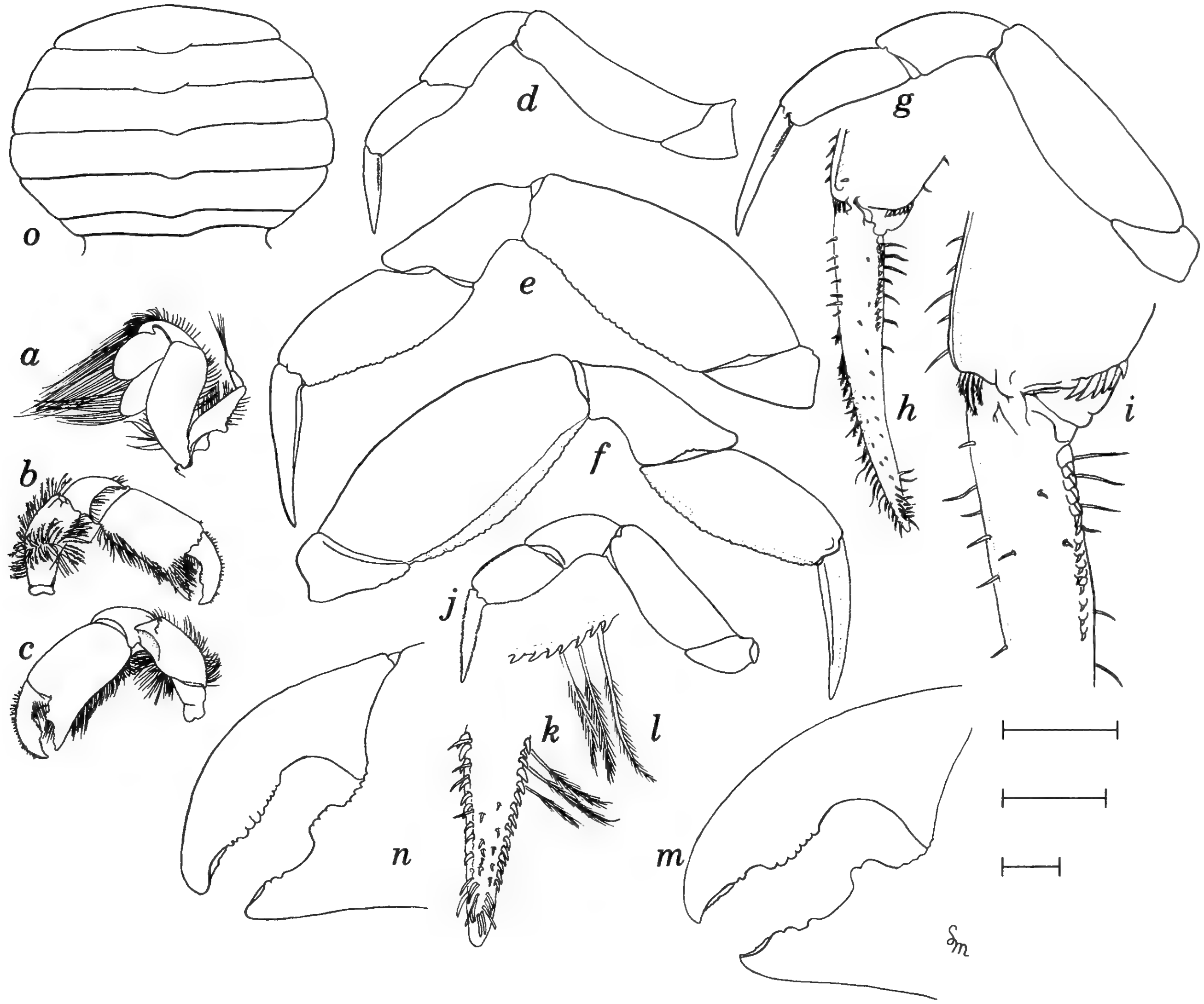

Fig. 4. *Austinixa hardyi,* new genus, new species. Female paratypes, Tobago, USNM 284177: *a–l, n, o,* 2.5 by 7.0 mm; *m,* 2.2 by 5.8 mm. *a,* Mxp3; *b,* Left P1, inner surface; *c,* Left P1, anterior surface; *d,* Right P2, anterior surface; *e,* Right P4, anterior surface; *f,* Right P4, posterior surface; *g,* Right P3, anterior surface; *h, i,* Distal part of propodus and dactylus, right P2, enlarged; *j,* Right P5, anterior surface; *k,* Dactylus of right P5, ventral view; *l,* Ventral margin of propodus, enlarged; *m,* Fingers of left chela; *n,* Fingers of left chela; *o,* Abdomen. Upper scale equals 1 mm (*a–c*); middle scale equals 1 mm (*d–g, j*); lower scale equals 0.1 mm (*h–i, k–l*), 0.5 mm (*m, n*).

posable) margin bicarinate. Dactylus with ventral ridge on posterior surface.

Fourth walking leg (P5) shortest of all walking legs, when extended reaching beyond base of carpus of P4 in females, falling short of carpus of P4 in males.

Male abdomen with sides of first 5 somites parallel, tapering at sixth somite, latter with concave lateral margins; telson broader than long, broadly rounded, longest of all somites.

Gonopod sinuous, apex sharply curved laterally, acute, surmounted by thick patch of long setae.

Size.—Males cl 1.9 mm by cb 3.4 mm to 2.8 mm by 7.5 mm; non-ovigerous females 1.9 mm by 5.0 mm to 2.7 mm by 7.3 mm; ovigerous females, 1.8 mm by 4.6 mm to 2.5 mm by 7.0 mm.

Remarks.—Austinixa hardyi differs from all known representatives of the genus in having a dense patch or patches of setae on the carapace anterior to the cardiac crest in males; the dorsal surface of the males is naked in all of the other species.

Austinixa hardyi resembles *A. aidae* and *A. gorei* in lacking the branchial ridges anteriorly on the carapace, but differs from *A.*

gorei in having a bicarinate ventral margin on the propodus of P4 and differs from both in having a posterior ridge on the dactylus of P4. *Austinixa hardyi* is a comparatively much wider species than *A. aidae* and also is much smaller, with a maximum carapace width of 7.5 mm in comparison with a width of 10 mm in *A. aidae.*

Examination under high magnification of the ventrodistal surface of the propodus as well as the proximal, ventral surface of the dactylus of the first walking leg (P2) of *A. hardyi* revealed the presence of a patch of 7–8 short but strong spines on the ventrodistal margin of the propodus and a line of 14+ short spinules proximally on the dactylus. These features need to be investigated further, as they may prove to be diagnostic characters in members of this genus. The spination of the propodus and dactylus of the last walking leg (P5) also may prove to be diagnostic.

The ornamentation of the proximal segments and relative length of all segments of the antennules (A1) also may prove to be a useful character in members of *Austinixa.* In *A. hardyi* the three proximal segments have a single movable spine and the distal segment is more than half as long as the penultimate. In *A. gorei* the proximal segments are unarmed and the distal segment is less than half as long as the penultimate. In both species the third segment is longest. These need to be surveyed throughout the genus.

Etymology.—Named for J. David Hardy, who is coordinating a survey of the fauna of Tobago for the Tobago House of Assembly.

Biology.—This species was collected as an associate of a species of *Callichirus,* a Caribbean species near *C. major* (Say, 1818).

Distribution.—Known only from Tobago.

Acknowledgments

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Literature Cited

Bott, R. 1955. Litorale Dekapoden, ausser *Uca.* Dekapoden (Crustacea) aus El Salvador, 2.—Senckenbergiana biologica 36(1/2):45–70.

Glassell, S. A. 1935. Three new species of Pinnixa from the Gulf of California.—Transactions of the San Diego Society of Natural History 8(5): 13, 14.

Manning, R. B., & D. L. Felder. 1989. The *Pinnixa cristata* complex in the western Atlantic, with descriptions of two new species (Crustacea: Decapoda: Pinnotheridae).—Smithsonian Contributions to Zoology 473:1–26, frontispiece (color).

Rathbun, M. J. 1900. The catametopous or grapsoid crabs of North America. Synopses of American invertebrates, 11.—American Naturalist 34(403): 583–592.

———. 1918. The grapsoid crabs of America.—United States National Museum Bulletin 97:461 pp.

Righi, G. 1967. Sobre alguns Decapoda do Brasil (Crustacea, Brachyura: Pinnotheridae e Parthenopidae).—Papéis Avulsos de Zoologia, São Paulo 20:99–116.

Say, T. 1817–1818. An account of the Crustacea of the United States.—Journal of the Academy of Natural Sciences of Philadelphia 1(1)[1817]: 57–63, 65–80, 97–101, 155–169; 1(2)[1818]: 235–253, 313–319, 374–401, 423–444, 445–458, pl. 4.

Stimpson, W. 1856. Descriptions of new genera and species of macrurous Crustacea from the coasts of North America.—Proceedings of the Chicago Academy of Sciences 1:46–48.

Wass, M. L. 1955. The decapod crustaceans of Alligator Harbor and adjacent inshore areas of northern Florida.—The Quarterly Journal of the Florida Academy of Sciences 18(3):129–176.

White, A. 1846. Notes on four new genera of Crustacea.—The Annals and Magazine of Natural History 18(118):176–178, pl. 2.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(3):399–411. 1997.

A new species of *Rimicaris* (Crustacea: Decapoda: Bresiliidae) from the Snake Pit hydrothermal vent field on the Mid-Atlantic Ridge

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Abstract.—A second species of the bresiliid shrimp genus *Rimicaris* Williams & Rona, 1986, *R. aurantiaca,* is described from the Snake Pit hydrothermal vent field on the Mid-Atlantic Ridge. The species possesses a highly unusual dorsal light receptive organ (the "dorsal eye") beneath the carapace, as does *R. exoculata* Williams & Rona, 1986, but is considerably smaller than that species and in many ways bridges the morphological gap between the genera *Rimicaris* (previously monotypic) and the genus *Chorocaris* Martin & Hessler, 1990. Characters in common with *R. exoculata* include the presence of the dorsal eye, lack of a well developed carpal cleaning brush on the cheliped, smooth (not notched) lateral border of the antennal scale, and brush-like pad of setae on the dactylus of the second maxilliped. Characters in common with species of *Chorocaris* include the relatively normal (not inflated) carapace, slightly produced rostrum, presence of recognizable eyestalks, and absence of a carapacial notch at the base of the antennal area that forms, with the carapace, an opercular shield such as is seen in *R. exoculata.* Previous descriptions of the dorsal eye of *R. exoculata* show that it differs from the dorsal eye of *R. aurantiaca.* The new species is also characterized by the presence of large numbers of orange-colored oil droplets visible through the dorsum of the carapace and through the thin cuticle of the abdominal sternites and, to a lesser degree, through the cuticle of the abdominal terga. The definition of *Rimicaris* is revised to accommodate the new species.

The Snake Pit hydrothermal vent fields along the Mid-Atlantic Ridge (23°20.3′N, 45°0.5′W), the ecology of which has been reviewed recently by Van Dover (1995), are known to harbor several species of bresiliid shrimps (Galkin & Moskalev 1990, Segonzac 1992, Segonzac et al. 1993, Van Dover 1995). Several visits to the site by French and American scientists beginning in 1988 have resulted in the collection of at least four species of bresiliids, only three of which, *Rimicaris exoculata* Williams & Rona, 1986, *Chorocaris chacei* (Williams & Rona, 1986), and *Alvinocaris markensis* Williams, 1988, have been described (Van Dover 1995). The fourth species, a small, previously undescribed, orange shrimp, was the subject of a recent and detailed anatomical study to investigate its retinal anatomy (Nuckley et al. 1996). The new species was referred to in that study as *Rimicaris* sp., primarily on the basis of ecological and neuroanatomical and retinal similarities between it and the previously described and co-occuring *R. exoculata.* Differences between this new species and others at the site had been noted earlier, but had been attributed to ontogenetic differences. The smaller orange shrimp were thought be be either juveniles of *R. exoculata* or members of an undescribed species of *Chorocaris.* Some of the ecological observations on these species can be found in Segonzac (1992) and Segonzac et al. (1994), as well as in Nuckley et al. (1996), and additional ones are presented here.

Cruise 129-7 of the R/V *Atlantis II* in May 1993 resulted in the return of several lots of bresiliids, including the new species described herein, collected using the DSRV *Alvin.* Some of these specimens were sent to us for identification and form the basis of the following description.

Materials and Methods

Specimens came from a single collection made by the DSRV *Alvin,* R/V *Atlantis II* cruise 129-7, 19 Jun 1993, Dive 2618, 3520 m, Snake Pit hydrothermal vent field (Moose vent [l'Elan] site), Mid-Atlantic Ridge, 23°22.1′N, 44°57.0′W (Nuckley et al. 1996). Segonzac et al. (1993) give the following coordinates for the Snake Pit hydrothermal area: 23°22′N–44°56′W (the Snake Pit "segment" extends some 40 km; Van Dover 1995). The lot contained 20 adults, 18 of which constitute the type series (holotype and 17 paratypes) and are housed in the Natural History Museum of Los Angeles County (LACM). Additional specimens mentioned by Nuckley et al. (1996) were collected on *Alvin* dives 2613 and 2623. Some of these specimens are housed at Syracuse University pending further neurological and physiological study, while others are in the possession of the Chief Dive Scientist, C. L. Van Dover. Additional specimens are undoubtedly among the extensive collections made by the French submersible *Nautile* during the *Hydrosnake* cruise in June of 1988 (see Segonzac et al. 1993) but have not been examined by us. Most specimens were initially fixed in buffered formalin and later transferred to 70% EtOH. Some specimens were kept alive and maintained for over 2 weeks at sea (see Nuckley et al. 1996) during which time behavioral observations were made; however, all specimens sent to us had been immediately preserved on board the support ship R/V *Atlantis II* and later transferred to 70% ethanol. Drawings were made with the use of a Wild M5APO dissecting stereoscope and a Nikon Labophot compound binocular microscope. SEM preparation involved dehydration through a graded ethanol series, drying via HMDS (Nation 1983), and sputter coating with gold prior to examination with a Cambridge 360 Stereoscan at the Center for Electron Microscopy and Microanalysis on the University of Southern California campus. Two specimens of nearly identical size were destroyed for SEM work (Fig. 5).

Genus *Rimicaris* Williams & Rona, 1986

Emended diagnosis.—Bresiliid with eyestalks greatly reduced or nearly absent, connected medially. Visual apparatus highly modified as bilobed organ extending posteriorly beneath transparent cuticle of carapace. Carapace spineless, greatly inflated laterally or normal (not inflated). Rostrum absent or present; if present then rounded and short, barely extending over (nonfunctional) eyestalks. Antennal scale broadly oval with margins smooth, entire, lacking distolateral notch or groove and its blunt spine. Dactylus of second maxilliped with medially-directed brush of evenly sized setae. Chelipedal carpus without well developed carpal cleaning brush. Pleurobranch gills on pereiopods 1–5, arthrobranch gills on maxilliped 3 and on pereiopods 1–4. Pereopods lacking exopods.

Type species: *Rimicaris exoculata* Williams & Rona, 1896, by monotypy.

Rimicaris aurantiaca, new species
Figs. 1–5

Chorocaris chacei (juveniles). Segonzac et al., 1993: 540 and addendum. (Not *Chorocaris chacei* Williams & Rona, 1986).

?*Chorocaris* n. sp. Van Dover 1995: 259 (table).

"Small shrimp with an orange coloration" Creasey et al. 1996: 474. (Not their *Chor-*

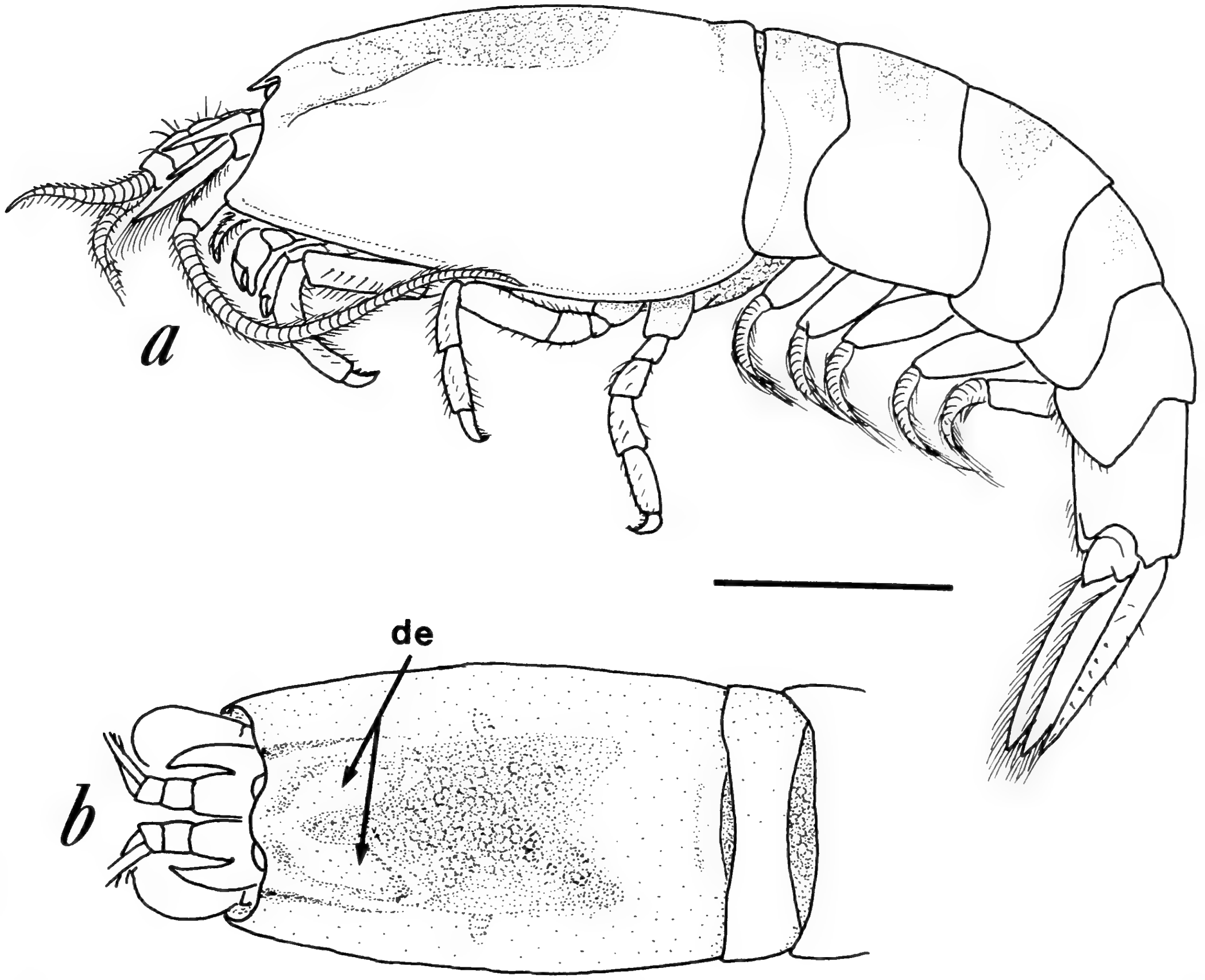

Fig. 1. *Rimicaris aurantiaca,* new species, female holotype, LACM 93-46.3, total length 24.4 mm. a, lateral view; b, paratype, 9.7 mm carapace length (23.5 mm total length), carapace and first and part of second abdominal somite, dorsal view, de, bilobed dorsal eye. Stippled areas at top of carapace and just anterior to sternite of first abdominal somite (posterior to coxa region of pereiopod 5) and dorsal regions of abdominal somites indicate regions where orange-colored oil droplets are visible through the thin and transparent cuticle. Scale bar = 5.0 mm.

ocaris sp., = *C. fortunata* Martin & Christiansen, 1995).

Rimicaris sp. Nuckley et al. 1996:98.

Material studied.—Holotype female, LACM 93-46.3, total length 24.4 mm, R/V *Atlantis II* cruise 129-7, 19 June 1993, DSRV *Alvin,* Dive 2618, 3520 m, Snake Pit hydrothermal vent field (Moose vent [l'Elan] site), Mid-Atlantic Ridge, 23°22.1′N, 44°57.0′W. Paratypes, 17 adults, same collection data, Natural History Museum of Los Angeles County, LACM 93-46.2.

Description.—Integument smooth, thin, regularly punctate, transparent on small area on dorsum of carapace (Fig. 1a, b, 2a), on swollen area just posterior to coxa of fifth pereiopods and anterior to first abdominal sternite, and to lesser degree on lateral and dorsal surfaces (terga) of abdominal somites; transparent areas appearing orange due to presence of orange-colored oil droplets below surface of cuticle.

Carapace (Fig. 1a, b, 2a, b) stout, wide, robust, with semitransparent area dorsally through which dorsal eye and many orange-colored oil droplets can be seen. Branchiostegal border produced beyond extent of rostrum. Rostrum short, wide, rounded, produced anteriorly beyond and covering central connected region of eyestalks, extending forward to point just beyond anteriormost part of antennal region of carapace. Antennal spine absent. Branchiostegal region with slight indentation continuing as sinuous indentation or groove posteriorly and dorsally.

"Normal" (frontal) eyes (Fig. 2a) reduced, not pigmented; nonfaceted externally but with internal faceting barely visible; eyestalks connected transversely to one another beneath rostrum, just visible in lateral and dorsal views, not extending anteriorly to tip of rostrum. Small spherical clear bump on each eyestalk laterally under rostrum and also single bump projecting slightly from median indentation between eyestalks (Fig. 2a).

Dorsal eyes (Fig. 1b, 2a) paired, paddle-shaped lobes, terminally (posteriorly) rounded or gently angled, extending backward perhaps 1/5 to 1/4 length of carapace, reflective, bright white in life (Nuckley et al. 1996).

Antennules (Fig. 2a–c) well developed, lengths of peduncular articles increasing in order 1 > 2 > 3; third article markedly longer on medial than lateral side. Basal article stout, bearing longitudinal row of setae and with curved setose ridge extending from base of stylocerite to groove between stylocerite and basal article. Stylocerite (Fig. 2c) strong, reaching to distal edge of second peduncular article on medial side, gently curved on lateral side but nearly straight to only slightly curved along medial border. Flagella inserted side by side but usually with lateral flagellum crossing over medial flagellum, which curves downward and backward. Peduncular and flagellar articles with setae as illustrated.

Antennae (Fig. 1a, 2b, d, e) with thick, stout peduncular articles. Flagellum usually sweeping backward, ranging in length from slightly shorter to slightly longer than carapace length. Antennal scale (Fig. 2d, e) large, broadly oval, setose only along medial and distal border, with supportive longitudinal dorsal ridge and lacking notch along distolateral border. Base of antennal scale and peduncle (Fig. 2e) not forming groove to receive leading edge of carapace border.

Mandibles (Fig. 3a, b) with 2-segmented palp; first segment with 1 long plumose seta on distodorsal border; second segment heavily setose. Cutting edge (incisor process) gently tapering, slightly produced, with 5–6 small sharp teeth giving way to row of smaller teeth along descending (ventral) border. Posterior tooth (molar process) blunt, simple, divergent from incisor process.

Maxillule (Fig. 3c) with palp well developed, incipiently bilobed, bearing 2 small distal short setae and 1 longer, plumose subterminal seta. Basal endite stout, curved strongly inward, with innermost setae in well defined row sweeping backward and inward, and with setae around distal and medial borders. Proximal endite large, narrow basally (at point where palp is attached) but expanded distally and bearing some 20 to 30 stout spines along medial border.

Maxilla (Fig. 3d) with endites reduced, nearly obsolescent. Basal endite composed of 2 roughly similar setose lobes; distal endite narrow basally and expanded distally, fringed with setae. Palp narrow, following curve of dorsal edge of distal endite. Scaphognathite large, flattened, bearing densely plumose setae on all borders, expanded distally, giving rise at posterior terminus to many long, stout, microscopically serrate setae that we presume sweep over and clean gill surfaces in life. Blade with scattered short setae.

First maxilliped (Fig. 3e) reduced, with components nearly completely fused into flattened, triangular, phylliform limb; basal and distal endites setose; palp narrow, extending beyond endites. Epipod short, stout, incipiently bilobed, with anterior dorsal bulge and posteroventral triangular terminus.

Second maxilliped (Fig. 3f) flattened but becoming pediform, composed of 5 heavily

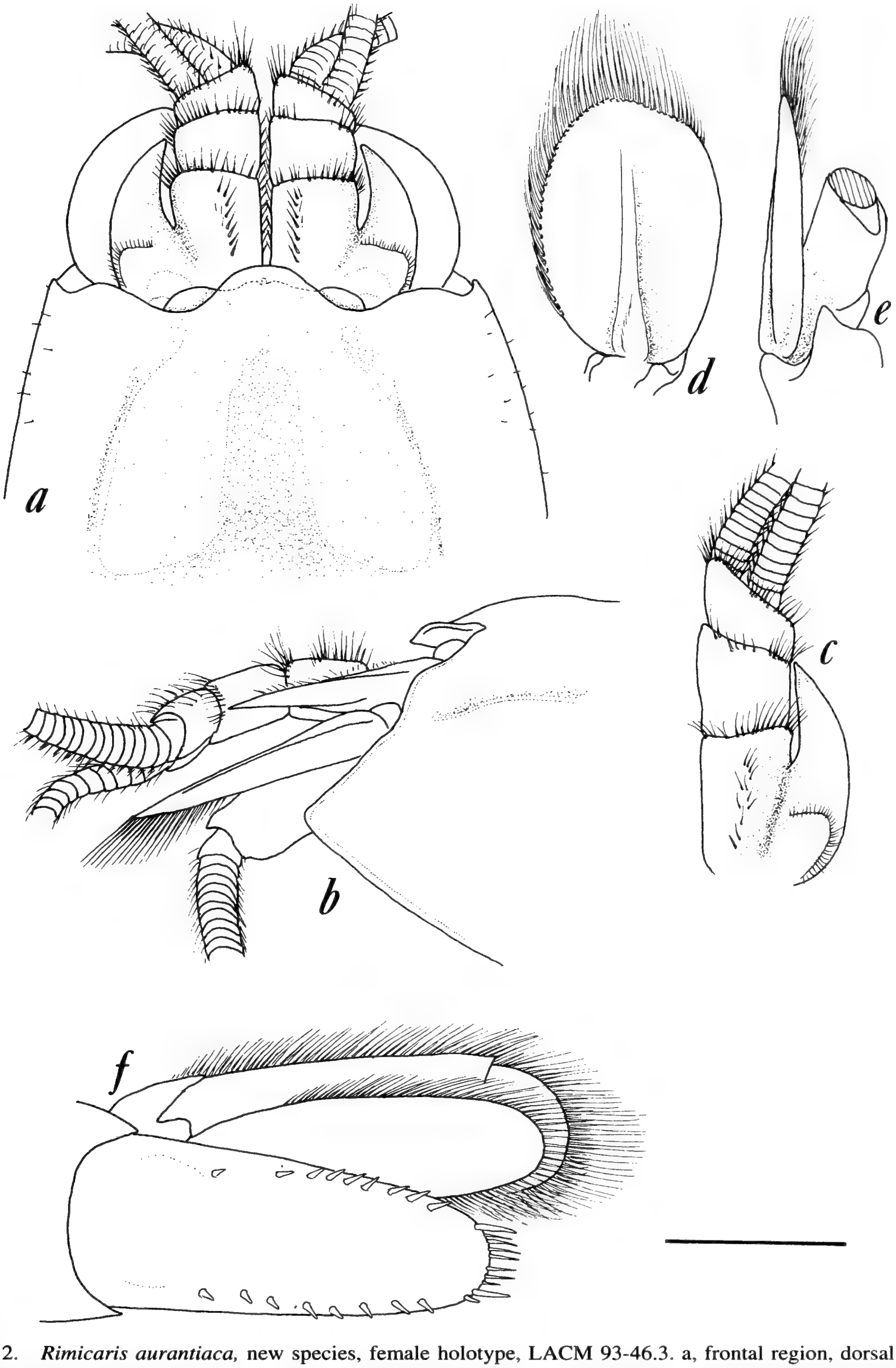

Fig. 2. *Rimicaris aurantiaca,* new species, female holotype, LACM 93-46.3. a, frontal region, dorsal view; b, left frontal region, lateral view; c, base of right antennule and its stylocerite, dorsal view; d, right antennal scale, dorsal view; e, same, lateral view; f, telson and right uropods, dorsal view. Scale bar = 2.0 mm.

Fig. 3. *Rimicaris aurantiaca,* new species, female holotype, LACM 93-46.3. a, b, right and left mandibles; c, maxillule; d, maxilla; e, first maxilliped; f, second maxilliped. Not drawn to scale.

setose articles. Dactylus with distinct row of short, evenly-sized setae forming brush along medial edge. Epipod strongly arched dorsally, with small protruberance at apex of arch.

Third maxilliped (Fig. 4a, b, 5a, b) pediform, composed of 2 short proximal articles and 3 longer more distal articles; basalmost of 2 proximal articles bearing arthrobranch and small bilobed epipod. Distal 3 articles (articles 3, 4, and 5, numbered proximal to distal) differning in length such that 3 > 5 > 4 (with 5 being distalmost article, presumably dactylus or fused dactylus + propodus). Distal 2 articles with well developed rows of stout setae (Fig. 4b); dactylus with stout spines distally. Distal spines and setae including variety of serrate, stout, plumose, and other types of spines and setae (Fig. 5a, b).

Pereiopod 1 (Fig. 4c, d) short, stout, appearing slightly twisted. Chela stout, curved downward and inward; movable finger (dactylus) approximately ¾ length of propodus, and bearing comb row of minute spines along cutting edge. Carpus expanded distally, lacking well developed cluster of cleaning spines or setae at distoventral border.

Pereiopod 2 (Fig. 4e, f, 5c) slender, approximately equal in length to pereiopod 1. Chela with row of spines on cutting edges of dactylus and propodus; these spine rows on each finger terminating in long spine directed toward opposing finger; spines overreaching opposing finger when closed (Fig. 4f, 5c). Length of dactylus approximately half that of propodus.

Pereiopods 3–5 (Fig. 4g) stout, similar to one another, slightly increasing in length from P3 to P5. Propodus with transverse rows of setae along ventral border. Dactylus short, stout, recurved, bearing numerous distal and ventral spines (Fig. 4h, 5d), and with distinct basal keel nearly obscured by protruding spines of propodus (Fig. 5e). Coxae of P5 with small, ventrally- and slightly anteriorly-directed spine between them (Fig. 4i, 5f); spine more or less straight on ventral border but bulging upward (toward body) along anterodorsal border (Fig. 4i).

Pereiopods lacking exopods.

Gill formula: pleurobranchs on pereiopods 1–5, arthrobranchs on maxilliped 3 and on pereiopods 1–4.

Abdomen (Fig. 1a) gently curving to nearly straight behind carapace. Abdominal pleura of somite 2 expanded and covering those of somites 1 and 3; posteroventral borders of pleura of somites 2–5 becoming increasingly acute from somite 2 to somite 5, but always smooth edged, lacking denticles or serrations.

Telson (Fig. 2f) with 8 or 9 spines on each side in row beginning at proximal fourth of telson and extending posteriorly and laterally; progressively more posterior spines directed more laterally than dorsally. Extremity of telson with pair of heavy spines flanking row of shorter and thinner spines and setae. Uropods elongate, oval, lower branch with well developed diaresis; both rami heavily setose.

Measurements in mm.—Total length of the 20 specimens examined (including the holotype) ranged from 21.5 to 26.8 mm.

Color.—In life the species is bright orange to reddish orange, with the ocular region reflecting light and appearing either gray or bright white (Nuckely et al. 1996: 101, figs. 2B, C), depending upon the angle of reflected light. Storage in ethanol causes these colors to fade, although a light orange color of the carapace and abdomen was still detectable some 28 months after preservation. Most obviously pigmented are the areas where the cuticle is more transparent; these include an oval region on the dorsal surface of the carapace that also contains the ocular apparatus (Fig. 1b), a slightly ventrally protruding area of the sternal cuticle just posterior to the fifth pereiopods and anterior to the first abdominal somite, and to a lesser extent the dorsal and lateral surfaces of each abdominal somite. Through each of these areas small orange-

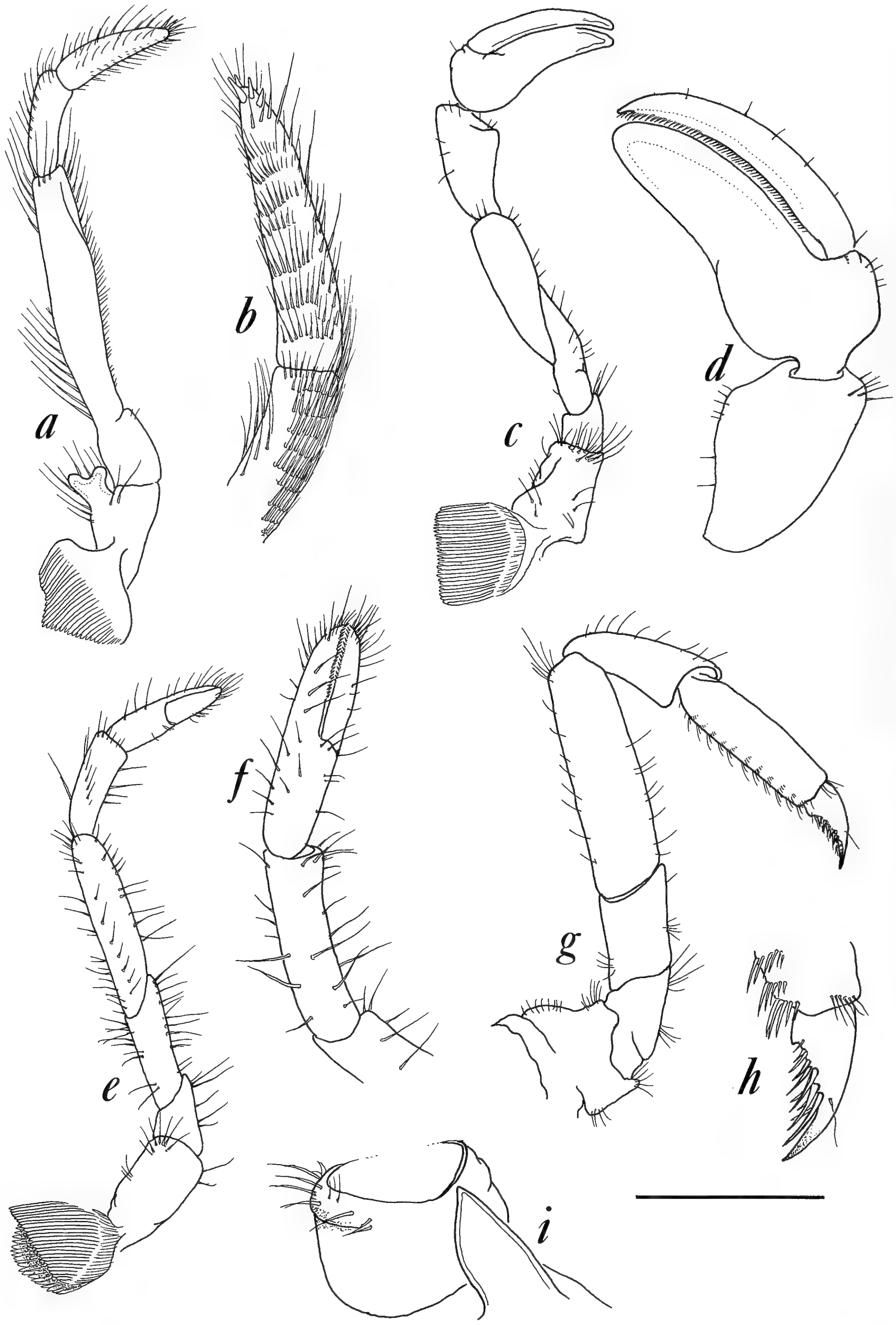

Fig. 4. *Rimicaris aurantiaca,* new species, female holotype, LACM 93-46.3. a, right third maxilliped, lateral view; b, magnified view of same, medial view; c, right pereiopod 1 (cheliped), lateral view; d, higher magnification of same, medial view; e, pereiopod 2; f, same, higher magnification of chela and carpus; g, right pereiopod 3, lateral (posterior) view; h, same, higher magnification of dactylus. Scale bar = 2.0 mm (a, c, e, g), 1.0 mm (b, d, f, h, i).

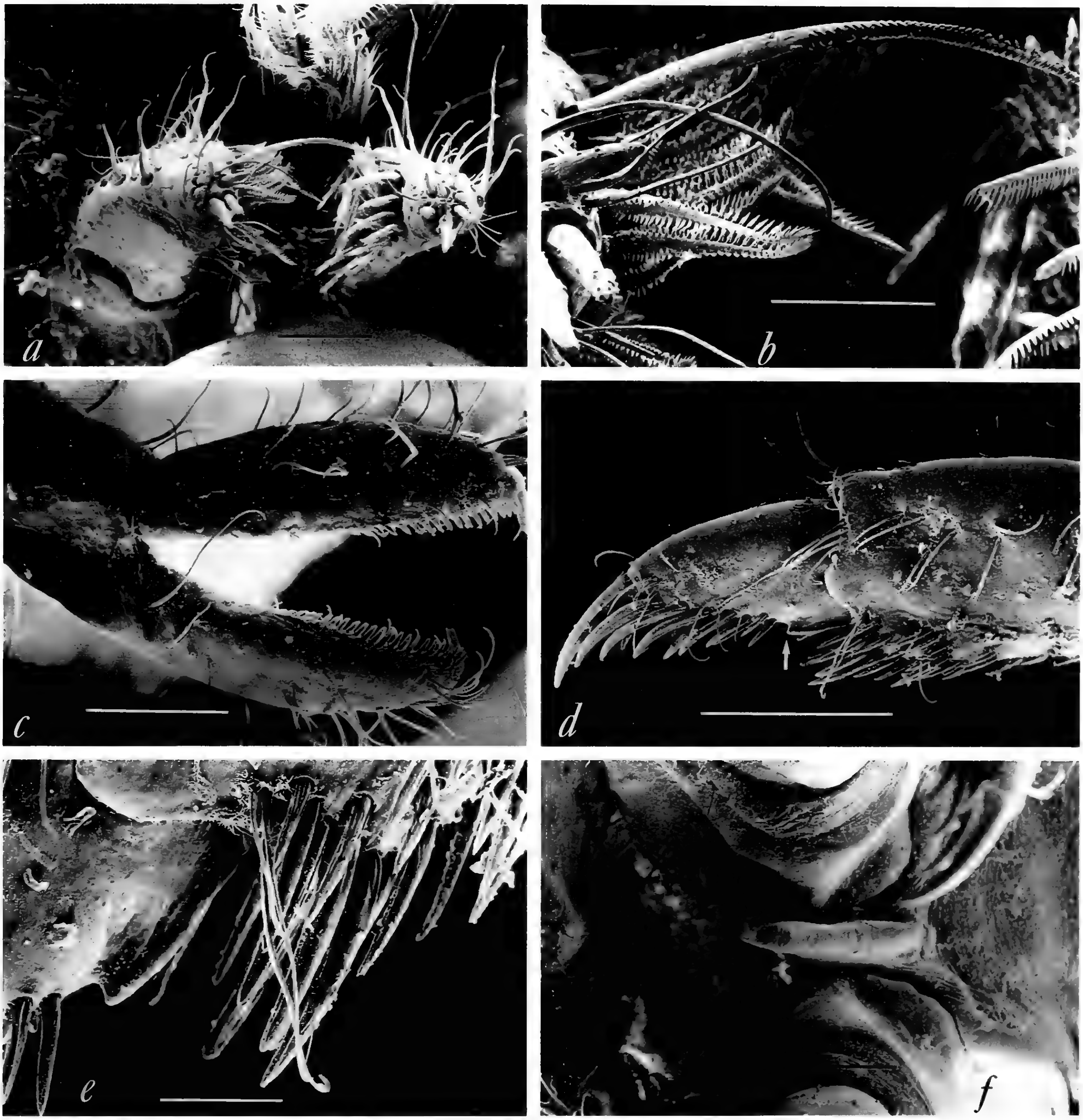

Fig. 5. *Rimicaris aurantiaca,* new species, selected SEM images. a, b, distalmost article of third maxilliped, showing diversity of setal and spine types; c, chela of right pereiopod 2 (note long spine at tip of each finger); d, dactylus and part of propodus of left pereiopod 4, lateral view; e, same, higher magnification of ventral keel (arrow in d). f, spine between coxae of pereiopod 5, anterior is toward left of photograph. Scale bars: = 200 um (a, c), 100 um (b, e), and 500 (d, f). Sizes in mm of the two specimens used in these photographs were as follows: carapace length = 10.1, total length = 26.7, carapace width = 5.4 for the larger; carapace length = 9.5, total length = 26.1, carapace width = 5.2 for the smaller.

colored oil droplets are visible even in preserved specimens.

Etymology.—The specific name is from the adjectival and feminine form of *aurantium,* a Neolatin neuter noun meaning orange (Brown 1955: 207). This choice of epithet is in reference to the distinctive coloration of this species in life. The name also honors Syracuse University, students and alumni of which are nicknamed the "Orangemen," where the original research on the fascinating visual components of the new species was completed at the Department of Bioengineering and Neuroscience and at the Institute of Sensory Research (e.g., O'Neill et al. 1995, Nuckley et al. 1996).

Remarks.—The details of the unique "enlarged dorsal eye specialized for detecting light in a very dim environment instead of the expected compound eye" possessed by this species have been presented by Nuckley et al. (1996). This organ is visible in life (see color photographs in Nuckley et al. 1996) as a branched lobe extending backward from the front of the carapace, and just below the surface of the carapace, with each lobe being paddle-shaped and posteriorly rounded. This organ in *R. aurantiaca* differs from that in *R. exoculata* in that in the latter species it is considerably more elongate (e.g., Van Dover et al. 1989).

Discussion

It is reassuring to find that previously noted differences in neuroanatomy, physiology, and ecology are in agreement with taxonomic separations based on morphological characters. Nuckley et al. (1996), based primarily on the details of the unusual visual apparatus, referred to this new species as *Rimicaris* sp., feeling that it was more similar to *R. exoculata* than to any described species of the closely related genus *Chorocaris.* They also commented on ecological differences between *Chorocaris* and *Rimicaris,* noting that *Rimicaris* sp. (now *R. aurantiaca,* new species) occurs in dense swarms at the vent site, as does *R. exoculata,* whereas no species of *Chorocaris* exhibits this behavior, or at least not to this degree. The new species shares with *R. exoculata* the highly unusual dorsal eye, with very similar retinal anatomy (O'Neill 1995, Nuckley et al. 1996, S. Chamberlain, pers. comm.). Although species of *Chorocaris* share some of the same visual components, there are important neuroanatomical differences, the most salient of which is that the visual array is always oriented anteriorly (rather than dorsally) in all species of *Chorocaris* examined to date (Kuenzler et al. 1997), whereas both *R. exoculata* and *R. aurantiaca* have a dorsally directed visual array that receives input through the cuticle of the shrimp's carapace (Kuenzler et al. 1997, and S. Chamberlain, pers. comm.). This difference may be tied to the observed differences in behavior. Shrimp capable of receiving optical input only from the anterior end, which could be blocked by swarming behavior, might be less likely to exhibit swarming than would a species with a dorsal eye, where optical input might be obstructed to a somewhat lesser degree by swarming.

The new species also shares with *R. exoculata* some small but significant external morphological details, such as an antennal scale that has a smooth (unnotched) border on its anterolateral margin, a cheliped carpus lacking a well developed cleaning brush (i.e., with at most two or three setae in the location where such a brush is found in other carideans, including all known species of *Chorocaris*; Martin et al. unpublished data), and a distinctive brush-like pad of setae on the distal segment of the second maxilliped (see also Van Dover et al. 1988). This last character, the scraping setal brush of the second maxilliped, is potentially of high interest. According to Van Dover et al. (1988) this brush in *R. exoculata* is used to scrape bacteria from the more anterior appendages (the first two pereiopods and the third maxilliped), and although the evidence to date remains somewhat equivocal, *R. exoculata* may depend mostly or even exclusively on vent bacteria for nutrition (see Van Dover et al. 1988, Casanova et al. 1993, Gebruk 1993, Segonzac et al. 1993, Van Dover 1995). Thus, this character may be an important generic character separating the two genera on morphological as well as ecological and functional grounds.

The new species differs from *R. exoculata* in ecology, coloration, and morphology. *Rimicaris aurantiaca* prefers an ambient temperature of about 10°C compared to a higher ambient temperature of 28°C preferred by *R. exoculata* (Nuckley et al. 1996); they are also less active within a swarm than are individuals of *R. exoculata* and are only rarely seen swimming singly in the water column. According to Nuckley et al. (1996), "the small orange shrimp aggregates in swarms of hundreds, probably thousands of individuals on the sides of black smoker chimneys at the Beehive Mound of the Snake Pit site at a depth of 3500 meters."

Coloration is markedly different, both from *R. exoculata* and from previously described species of *Chorocaris,* with the new species appearing bright orange compared to a drab whitish or gray color exhibited by *R. exoculata* and *Chorocaris.* The color appears to come from the numerous oil droplets visible through the cuticle of the shrimp, and indeed upon dissection the shrimp exudes some of these droplets, which remain orange-colored. Although Creasey et al. (1996) attribute the orange coloration to the presence of "an oily, lipid-rich hepatopancreas," the oil droplets obviously occur in areas where no hepatopancreas is found, as well as in the region of the hepatopancreas. Photographs in Nuckley et al. (1996: 101, fig. 2A–C) show the orange coloration and the difference in color from the sympatric and light gray colored *R. exoculata* very clearly. It is interesting to note that in the description of *Opaepele loihi* from hydrothermal vents on the Loihi Seamount of Hawaii, Williams & Dobbs (1995) refer to the color of that species as "intensely orange (astaxanthin pigment)," although in the case of *O. loihi* the color comes apparently from an accumulation of particles of iron oxyhydroxide (Williams & Dobbs 1995).

Morphological differences in the new species include a "normal" (not greatly inflated) carapace; eyestalks that, although reduced and fused medially, are closer to the original caridean eyestalk condition and are at least recognizable as such; a frontal region that does not form a protective operculum with the carapace; a third maxilliped composed of three longer and two shorter articles; and a small, blunt rostrum. All of these characters are more consistent with previous descriptions of species in the genus *Chorocaris* Martin & Hessler, 1990. Indeed, if we employ the most recent key to the genera of the Bresiliidae (Williams & Dobbs 1995) the new species keys out as a member of the genus *Chorocaris.* The characters that Martin & Hessler (1990) used to distinguish *Rimicaris* from their newly described genus *Chorocaris* seem to be, for the most part, unique to *R. exoculata.*

Rimicaris aurantiaca had been observed previously by Segonzac et al. (1993), who referred to the Beehive Mound at this site as being "densely covered with adult *Rimicaris* and juveniles identified by their red color" (English translation). At least some of these "juveniles" we now know to represent this new species, and this was in fact suspected by Segonzac et al., who noted, in an addendum to that paper, that a "new species with features intermediate between *Rimicaris exoculata* and *Chorocaris chacei*" was present at this site, and that the juvenile stages were very similar in the three species. However, there are sufficient differences between adult *R. exoculata* and *R. aurantiaca* that there can be no doubt as to their separate identity.

Special mention should be made of the recent study by Creasey et al. (1996) on genetic composition of populations of *R. exoculata.* In that paper, the following mention is made of the new species: "... Within the Snake Pit vent field, small shrimp with an orange colouration due the presence of an oily, lipid-rich hepatopancreas have been observed within swarms of *R. exoculata*" (Creasey et al. 1996: 474). In that same paragraph these authors refer to the small orange Snake Pit species (undoubtedy *R. aurantiaca*) as *Chorocaris* sp., citing Van Dover (1995). However, it should be pointed out that Creasey et al. (1996) did not use any Snake Pit specimens in their comparison, and that the specimens they refer to in the remainder of their paper as *Chorocaris* sp. were from the TAG and Broken spur sites and therefore are attributable to *Chorocaris fortunata* Martin & Christiansen, 1995. Thus their conclusion "that all morphotypes of *R. exoculata* examined, including those previously interpreted as representing separate species, are conspecific" does not apply to *R. aurantiaca,* but rather only to the two different populations of *R. exoculata* at the TAG and Broken Spur sites, the latter of which had been suggested by Murton et al. (1995) to contain a different species of *Rimicaris* based on slight morphological differences.

The somewhat intermediate assemblage of characters (i.e., some shared with *R. exoculata* and others with species of *Chorocaris*) might justify creation of yet another bresiliid shrimp genus from the hydrothermal vents. We refrain from doing so in this paper, believing that discovery of additional species is almost certainly forthcoming and will shed light on the entire assemblage, and that a conservative approach is warranted until such time that more is known. In the meantime we recognize that the generic diagnosis for *Rimicaris* as emended in this paper leaves it a rather poorly delimited genus on morphological grounds, as it must be to accommodate two shrimp species that exhibit so many morphological differences.

Unfortunately, description of the new species does not add appreciably to the body of information that would eventually lead to recognition or rejection of the family Alvinocarididae, as proposed by Christofferson (1989) and employed by Christofferson (1991) and Saint Laurent (1993, in Segonzac et al. 1993) to accommodate the genera and species of bresiliids known from hydrothermal vents and cold seeps. Thus, as have Martin & Hessler (1990), Chace (1992), Holthuis (1993), Williams & Dobbs (1995), Martin & Christiansen (1995), and Van Dover (1995), we retain the older, albeit recognized to be somewhat artificial, limits of the caridean family Bresiliidae.

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Literature Cited

Brown, R. W. 1956. Composition of scientific words. Smithsonian Institution Press, Washington, D.C., 882 pp.

Casanova, B., M. Brunet, & M. Segonzac. 1993. L'impact d'une épibiose bactérienne sur la morphologie fonotionelle de crevettes associées à l'hydrothermalisme médio-atlantique.—Cahiers de Biologie Marine 34:573–588.

Chace, F. A., Jr. 1992. On the classification of the Caridea (Decapoda).—Crustaceana 63:70–80.

Christoffersen, M. L. 1986. Phylogenetic relationships between Oplophoridae, Atyidae, Pasiphaeidae, Alvinocarididae fam. n., Bresiliidae, Psalidopodidae and Disciadidae (Crustacea Caridea Atyoidea).—Boletim de Zoologia, Universidade de Sao Paulo 10:273–281.

———. 1991. A new superfamily classification of the Caridea (Crustacea: Pleocyemata) based on phylogenetic pattern.—Zeitschrift fur Zoologische Systematik und Evolutionsforschung 28(1990):94–106.

Creasey, S., A. D. Rogers, & P. A. Taylor. Genetic comparison of two populations of the deep-sea vent shrimp *Rimicaris exoculata* (Decapoda: Bresiliidae) from the Mid-Atlantic Ridge.—Marine Biology 125:473–482.

Galkin, S. V., & L. I. Moskalev. 1990. Hydrothermal fauna of the Mid-Atlantic Ridge.—Okeanologia 30:842–847.

Gebruk, A. V., N. V. Pimenov, & A. S. Savvichev. 1993. Feeding specializations of bresiliid shrimps in the TAG site hydrothermal community.—Marine Ecology Progress Series 98:247–253.

Holthuis, L. B. 1993. The Recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda), with an appendix on the order Amphionidacea.—Nationaal Natuurhistorisch Museum, Leiden, Netherlands, 328 pp.

Kuenzler, R. O., J. T. Kwasniewski, R. N. Jinks, R. C. Lakin, B.-A. Battelle, E. D. Herzog, L. Kass, G. H. Renninger, & S. C. Chamberlain. 1997. Retinal anatomy of new bresiliid shrimp from the Lucky Strike and Broken Spur hydrothermal vent fields on the Mid-Atlantic Ridge. Journal of the Marine Biological Association (United Kingdom) (In press).

Martin, J. W., & J. C. Christiansen. 1995. A new species of the shrimp genus *Chorocaris* Martin and Hessler, 1990 (Crustacea: Decapoda: Bresiliidae) from hydrothermal vent fields along the Mid-Atlantic Ridge.—Proceedings of the Biological Society of Washington 108:220–227.

———, & R. R. Hessler. 1990. *Chorocaris vandoverae,* a new genus and species of hydrothermal vent shrimp (Crustacea, Decapoda, Bresiliidae) from the western Pacific.—Contributions in Science, Natural History Museum of Los Angeles County 417:1–11.

Murton, B. J., C. L. Van Dover, & E. Southward. 1995. Geological setting and ecology of the Broken Spur hydrothermal vent field 29°10′N on the Mid-Atlantic Ridge. Pp. 33–41 *in* L. M. Parson, C. L. Walker, & D. R. Dixon, eds., Hydrothermal vents and processes. Special Publications of the Geological Society of London, Geological Society, London, 000 pp.

Nation, J. L. 1983. A new method using hexamethyldisilazane for preparation of soft tissues for scanning electron microscopy.—Stain Technology 38:347–351.

Nuckley, D. J., R. N. Jinks, B.-A. Battelle, E. D. Herzog, L. Kass, G. H. Renninger, & S. C. Chamberlain. 1996. Retinal anatomy of a new species of bresiliid shrimp from a hydrothermal vent field on the mid-Atlantic Ridge.—Biological Bulletin 190:98–110.

O'Neill, P. J., R. N. Jinks, E. D. Herzog, B-A. Battelle, L. Kass, G. H. Renninger, & S. C. Chamberlain. 1995. The morphology of the dorsal eye of the hydrothermal vent shrimp, *Rimicaris exoculata.*—Visual Neuroscience 12:861–875.

Segonzac, M. 1992. The hydrothermal vent communities of the Snake Pit area (Mid Atlantaic Ridge; 23°N, 3480 m).—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris 314:593–600.

———, M. de Saint Laurent, & B. Casanova. 1993. L'énigme du comportement trophique des crevettes Alvinocarididae des sites hydrothermaux de la dorsale médio-atlantique.—Cahiers de Biologie Marine 34:535–571.

Van Dover, C. L. 1995. Ecology of Mid-Atlantic Ridge hydrothermal vents. Pp. 257–294 *in* L. M. Parson, C. L. Walker, & D. R. Dixon, eds., Hydrothermal Vents and Processes.—Geological Society Special Publication 87.

———, B. Fry, J. F. Grassle, S. Humphris, & P. A. Rona. 1988. Feeding biology of the shrimp *Rimicaris exoculata* at hydrothermal vents on the Mid-Atlantic Ridge.—Marine Biology 98: 209–216.

———, E. Z. Szuts, S. C. Chamberlain, & J. R. Cann. 1989. A novel eye in "eyeless" shrimp from hydrothermal vents of the Mid-Atlantic Ridge.—Nature 337:458–460.

Williams, A. B. 1988. New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine and hydrocarbon seepage.—Fisheries Bulletin 86:263–287.

———, & F. C. Dobbs. 1995. A new genus and species of caridean shrimp (Crustacea: Decapoda: Bresiliidae) from hydrothermal vents on Loihi Seamount, Hawaii.—Proceedings of the Biological Society of Washington 108:228–237.

———, & P. Rona. 1986. Two new caridean shrimps (Bresiliidae) from a hydrothermal vent on the Mid-Atlantic Ridge.—Journal of Crustacean Biology 6:446–462.

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Occurrence of three species of mud shrimps in aquiculture ponds on Caribbean coasts of Venezuela and Colombia, with a redescription of *Upogebia omissago* Williams, 1993 (Decapoda: Upogebiidae)

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Abstract.—Three species of mud shrimps, *Upogebia brasiliensis, U. omissa,* and *U. omissago,* are reported from ponds maintained for the commercial culture of penaeid shrimps on the Caribbean coasts of Venezuela and Colombia, South America. *Upogebia omissago* is redescribed and illustrated based on sexually mature individuals collected from the ponds. Catalogued lots of each species collected are listed.

Three species of mud shrimps, *Upogebia brasiliensis* Holthuis, 1956, *U. omissa* Gomes Corrêa, 1968, and *U. omissago* Williams, 1993 have been found in discrete or intermingled populations in ponds maintained for the commercial culture of penaeid shrimps on the Caribbean coasts of Venezuela and Colombia, South America. The ponds are stocked by pumping or flooding with seawater at appropriate tidal stages, and numerous organisms, including larvae and perhaps juveniles of the mud shrimps, are introduced with the incoming water. Upon attainment of the juvenile stage, the mud shrimps burrow into substrate of the ponds. Supplemental aquicultural feeding promotes growth of the cultured penaeid shrimps as well as the mud shrimps, producing sexually mature individuals of the latter in at least some cases.

The description of *Upogebia omissago* Williams, 1993 was based on only five subadult specimens from Luis Correia, Praia do Coqueiro, Piauí, northeastern Brazil. Now that larger fully mature specimens are available which exhibit features not completely developed in the originally described type series, the description can be emended. Remarks on other upogebiid species that occur in these ponds are included.

Specimens examined are deposited in the crustacean research collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., (USNM), and the University of Southwestern Louisiana Department of Zoology, Lafayette (USLZ).

Upogebia omissago Williams, 1993
Fig. 1

Material studied.—Venezuela: USNM 251468, 6 ♂, 2 ♀ ovig., shrimp farm "Siembra Mar," approximately 3 km from airport of Barcelona [Estado Anzoátegui], from R. Lemaitre, 27 Oct 1992. USLZ 3581, 1 ♂, 3 ♀ ovig., "Siembra Mar," pond 09, coll. Sergio Nates, 16 Dec 1992; USLZ 3583, 3 ♀, same, 14 Jun 1994; USLZ 3586, 5 ♂, 5 ♀, same, coll. Eduardo Viso, Apr 1993. Blanco Rambla (1995) also listed *U. omissago* from this locality.

Diagnosis.—Projections to either side of rostrum ending in acute spine. Postocular spine present. Abdominal sternites unarmed. Telson subrectangular. Carpus of cheliped with 1 long strong inferior spine and 1 short strong spine above it on mesiodistal margin. Merus of pereopod 2 bearing 1 proximal mesioventral spine and 1 subdistal dorsal spine; merus of pereopod 3 with 1 subdistal dorsal spine; merus of pereopod 4 spineless.

Description.—Rostrum triangular, short, basal width greater than median length; straight to slightly downcurved in lateral view; tip exceeding eyestalks; dorsal pair of strong subapical spines followed on each side by 2–3 remote spines and spine mesial to them at base; rostral armature merging with field of similar spines on flattened anterior cephalothoracic shield, all spines hidden in dense cover of setae anteriorly, but spines less strongly developed and setae less dense posteriorly; median area of rostrum spineless but obscured by setae; spine field abruptly ending posteriorly and followed by smooth gastric region with narrowing median extension reaching anteriorly between armed area to either side; posteriorly divergent lateral ridge bearing crest of 13–15 spines and setae, strongest on process lateral to rostrum and decreasing posteriorly. Shoulder lateral to cervical groove bearing 1–2 blunt or acute tubercles below intersection with thalassinidean line, latter continuing to posterior margin of carapace. Postocular spine present.

Abdominal sternites unarmed.

Telson subrectangular, low transverse proximal ridge confluent with inconspicuous lateral ridge at either side.

Eyestalk stout, deepest at about midlength in lateral view, slightly concave dorsally, convex ventrally, horizontal to obliquely erect in repose; prominent terminal cornea narrower than diameter of stalk; few tiny spiniform tubercles or spinules scattered on mesiodorsal aspect of stalk posterior to cornea, and ventral margin variably smooth or bearing 1–2 obsolescent spines, occasionally with single well-developed spine near cornea.

Antennular peduncle reaching to about midlength of terminal article of antennal peduncle; proximal 2 articles together longer than terminal article.

Antennal peduncle with less than ½ its length extending beyond tip of rostrum; article 2 bearing slender subdistal ventral spine; scale moderate, oval.

Maxilliped 3 bearing epipod.

Epistomial projection rather broad in lateral view, usually bearing 2 small unequal apical spines, sometimes 1 spine.

Chelipeds with ventral margin of ischium bearing 1–2 spines. Merus with row of 5–6 spines on ventral margin; single subdistal dorsal spine reaching level of postocular spine. Carpus trigonal, shallow longitudinal groove laterally, strong spine at anterior ventrolateral corner preceded by 1–2 spines; mesiodorsal crest of 6–9 crowded small spines, partly obscured by setae, in irregular row behind prominent dorsal spine on anterior margin, row flanked by 1 or 2 spines laterally and cluster of spines at proximal end mesially, and 4–6 short spines obscured by setae on anterodorsal margin mesial to articulation with propodus; 1 strong spine near middle of anteromesial margin, shorter stout spine dorsal to it, and strong slender spine at distoventral corner. Chela length about 2.6–3.2 times chela height; spineless dorsal ridge terminating anteriorly near stout subdistal spine mesial to it, ridge not always uniformly straight; mesiodorsal row of about 8–15 small spines beginning with more or less erect spines proximally that tend to cluster at either side of row and become obsolescent at about ⅔–¾ length of row; similar but more defined row of tubercles or spines below this row on upper mesial surface; distomarginal spine on mesial dactylar condyle and row of smaller spines ventral to it on distal margin; spine below lateral dactylar condyle; lower mesial surface of palm with obsolescent spines scattered or tending to form a row, and a few setae; sinuous row of crowded tubercles along proximomesial margin. Fixed finger shorter than dactyl and more slender, though stout in basal ⅔, slightly downcurved at juncture with palm and tapering abruptly to slender tip; prehensile edge with 4–5 teeth; not as well developed in female as in male. Dactyl longitudinally ridged and setose; that of male

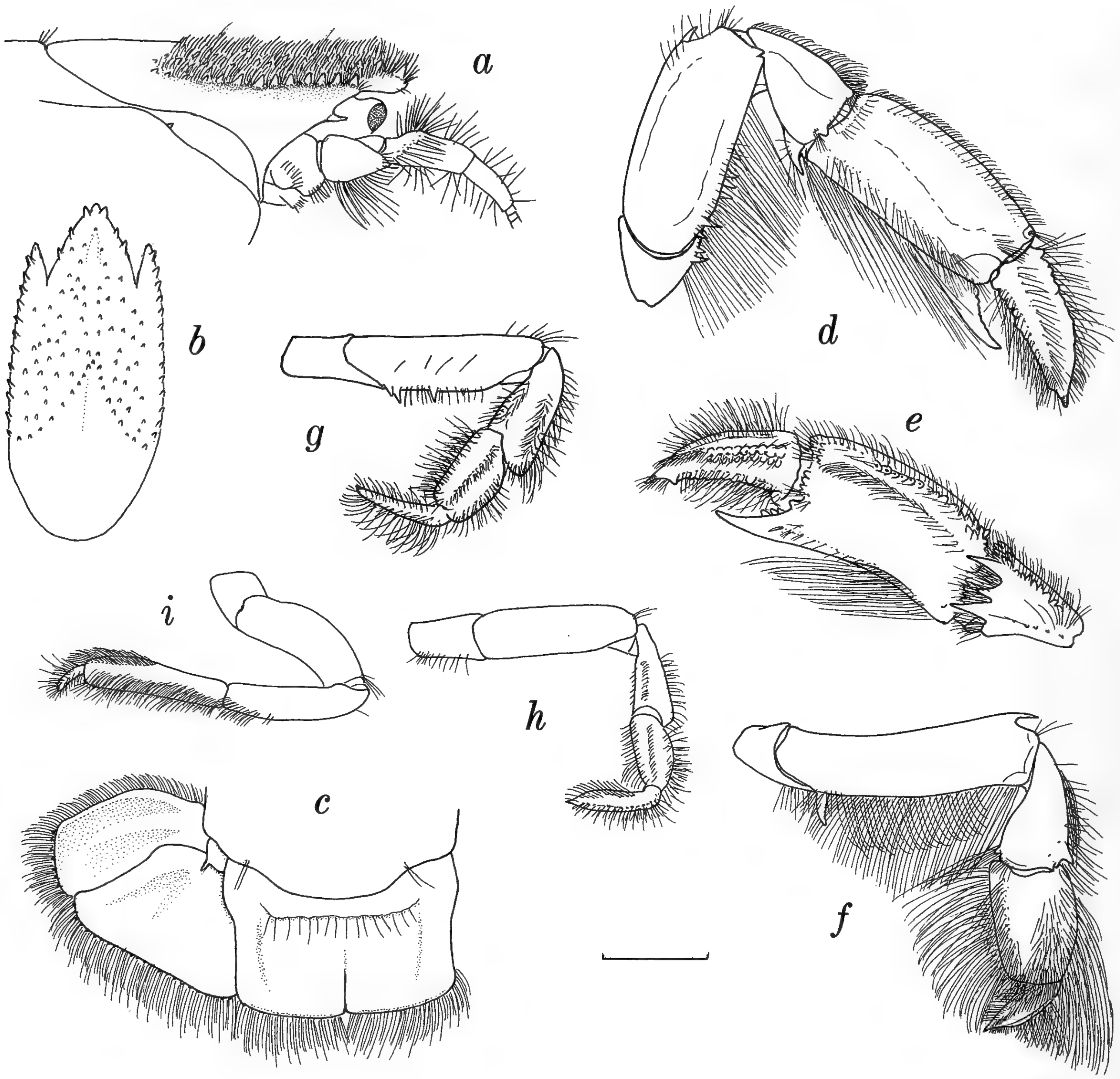

Fig. 1. *Upogebia omissago,* USNM 251468, ♀, *a,* cephalic region, lateral; *b,* anterior carapace, dorsal; *c,* parts of abdominal segment 6, telson, and uropods, dorsal; *d,* cheliped, right lateral; *e,* chela and carpus, right mesial; *f–i,* pereopods 2–5. Scale = 3 mm.

with corneous tip preceded on prehensile edge by strong tooth, followed by multidentate crest bracketed on proximal end by larger tooth, and toothless section basally; concave mesial aspect in both sexes bearing 2 unequal rows of subcircular flattened and crowded tubercles, most numerous in upper row.

Pereopod 2 reaching about to midlength of palm; carpus with acute distodorsal spine and smaller subdistal ventral spine; merus bearing slender subdistal dorsal spine and strong proximal mesioventral spine. Merus of pereopod 3 with 0–1 slender distodorsal spine and ventral spines tending to cluster near ischio-meral articulation; ischium unarmed; coxa of female with low spine lateral to gonopore, that of male with smaller gonopore, its functional status uncertain. Pereopod 4 with merus unarmed. Pereopod 5 unarmed.

Uropod with acute spine on protopod above base of mesial ramus; mesial rib of lateral ramus bearing smaller acute proximal spine, distal margin of both rami bearing close-set row of tiny spines and spiniform granules except for short mesial sector on each.

Measurements in mm.—Selected specimens larger than in type series; ♂, anterior carapace length 10.2, carapace length 14.7, chela length 8.3, chela height 3.1; ♂, same, 11.4, 16.6, 11.5, 5.1; ♀, same, 9.2, 13.7, 7.4, 2.3.

Remarks.—*Upogebia omissago* from the Venezuelan shrimp ponds attains a larger size and is more variable in morphology than specimens in the type series from a single locality in northeastern Brazil. To comparative remarks by Williams (1993), the following should be added. The species is similar to *U. vasquezi* Ngoc-Ho, 1989 (distributed from SE Florida to Brazil) in having two spines on the anteromesial margin of the carpus of the cheliped and in having spines on the lower mesial face of the chela palm, but in *U. omissago* the latter are relatively small and either scattered or in a weakly developed row compared to stronger, well aligned spines on *U. vasquezi. Upogebia omissago* resembles *U. careospina* Williams, 1993 (known from Ceará, Brazil) in having the dorsal ridge of the chela spineless, but spines or tubercles in the mesiodorsal rows are far less numerous than in *U. careospina. Upogebia omissago* differs from both of the above congeners in having the carpus of the cheliped armed with a crest of numerous dorsal spines flanked by 1 or 2 supernumerary lateral spines and a cluster of crowded mesial spines at the proximal end of the row. Each of these species has a spineless merus on pereopod 4. Rostral and adjacent dorsal spines are relatively stronger on *U. omissago* than in the others, and the spineless gastric area is far more abruptly defined, with the anterior median spineless extension being characteristic of *U. omissago.* Finally, only in *U. omissago* are there tiny mesiodorsal-ventral spinules and sharp tubercles on the eyestalks, and sharp tubercles on the shoulder of the cervical groove below its juncture with the thalassinidean line.

Notes.—Occurrence of other species of *Upogebia* taken from burrows in penaeid shrimp culture ponds on the Caribbean coasts of Venezuela and Colombia are as follows.

Upogebia brasiliensis Holthuis, 1956: USLZ 3580, 2♂, 1 ♀ ovig., shrimp farm "Siembra Mar," approximately 3 km from airport of Barcelona [Estado Anzoátegui], Venezuela, coll. Eduardo Viso, Aug. 1993; USLZ 3582, 3 ♀, same, coll. Eduardo Viso, Aug 1993; USLZ 3586, 1 ♀, same, coll. Eduardo Viso, Apr 1993 (occurring with *U. omissago*).

Upogebia omissa Gomes Corrêa, 1968: USNM 251469, 4 ♂, 1 ♀ ovig., shrimp farm: Colombiana de Acuacultura, S.A., pond P15, Bahía de Barbacoas, Cartagena, Colombia, coll. Sergio F. Nates, 4 Feb 1992, yabby pump; USLZ 3584, 1 ♂, 2 ♀ ovig., shrimp culture pond, Universidad de Oriente, Isla de Margarita, Venezuela, coll. E. Viso & O. Pichardo, 23 Jul 1994; USLZ 3588, 2 ♀ ovig., same, coll. E. Viso, O. Pichardo, S. Nates, 23 Jul 1994; USLZ 3585, 1 ♀, "Colombiana" shrimp farm, Cartagena, Colombia, coll. D. L. Felder, 26 Oct 1992; USLZ 3587, 2 ♂, 2 ♀ ovig., 1 juv., Parque Nacional Mochima, Chimana Grande, La Ensenada, Venezuela, coll. S. Nates, 26 Dec 1993.

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Literature Cited

Blanco Rambla, J. P. 1995. Additional records of ghost shrimps (Decapoda: Thalassinidea) from Venezuela.—Caribbean Marine Studies, 4:59–75.

Gomes Corrêa, M. M. 1968. Sobre as espécies de "Upogebia" Leach do litoral brasileiro, com descrição de uma espécie nova (Decapoda, Callianassidae).—Revista Brasiliera de Biologia, 28(2):97–109.

Holthuis, L. B. 1956. Three species of Crustacea Decapoda Macrura from southern Brazil, including a new species of *Upogebia*.—Zoologische Mededelingen, Leiden, 34(11):173–181.

Ngoc-Ho, N. 1989. Description de trois espècies nouvelles de la famille des Upogebiidae (Crustacea, Thalassinidea).—Bulletin du Muséum National d'Histoire Naturelle, Paris, section A, series 4, 11(4):865–878.

Williams, A. B. 1993. Mud shrimps, Upogebiidae, from the western Atlantic (Crustacea: Decapoda: Thalassinidea).—Smithsonian Contributions to Zoology, No. 544:77 pp.

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Esanpotamon namsom, a new genus and species of potamid crab (Crustacea: Decapoda: Brachyura) from a waterfall in northeastern Thailand

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Abstract.—A new genus and species of potamid crab, *Esanpotamon namsom,* is described from a waterfall in northeastern Thailand. The new genus is closest to *Demanietta* Bott, 1966, but can be distinguished by several important carapace, male abdominal and gonopodal characters.

Waterfall crabs of the family Potamidae are extremely speciose in Thailand, and about 30 species are now known (Naiyanetr 1992, Ng & Naiyanetr 1993). Several years ago, the senior author collected a number of specimens from a waterfall in northeastern Thailand which were initially referred to the genus *Demanietta* Bott, 1966. As the authors were involved in a study of all the Thai species of *Demanietta,* the specimens were kept aside for this revision.

A recent re-examination of the northeastern Thai specimens showed that they represent a new species. While the external features of this new species superficially resemble species of *Demanietta,* the male abdomen and gonopods of these northern Thai specimens differ very markedly. This observation, together with due consideration of their zoogeography (the genus *Demanietta* s. s. is known only from western and southern Thailand) has compeled the authors to establish a new genus for this new species.

The present paper describes this new genus and species, here named *Esanpotamon namsom.* The abbreviations G1 and G2 are utilized for the male first and second pleopods (gonopods) respectively. The terms used in the text follow those recommended by Ng (1988). Specimens examined are deposited in the Zoology Collection of the Department of Biology, Chulalongkorn University, Bangkok (CUMZ); and Zoological Reference Collection, School of Biological Sciences, National University of Singapore (ZRC).

Taxonomy

Family Potamidae Ortmann, 1896
Esanpotamon, new genus

Diagnosis.—Carapace much broader than long, dorsal surface flat; postorbital and epigastric cristae confluent, rugose, very low, indistinct; anterolateral margin confluent with external orbital angle. Exopod of third maxilliped with well developed flagellum which is longer than maximum width of merus. Ambulatory legs short. Male abdomen broadly triangular; tip of telson reaching to imaginary line joining midpoints of bases of chelipeds. G1 sinuous; terminal segment subcylindrical, curving upwards (towards anterior of carapace when lying in situ), distal part sharply tapering, tip appearing spine-like, subdistal dorsal surfaces with numerous long, very stiff setae, proximal dorsal part with small, swollen flap. G2 longer than G1, elongated distal segment longer than half-length of basal segment.

Type species.—*Esanpotamon namsom,* new species, by present designation.

Remarks.—Of all Indo-Chinese potamids, the external morphology of *Esanpotamon* most closely approaches that of *Demanietta* Bott, 1966 (type species *Potamon manii* Rathbun, 1904) (sensu Ng & Naiyanetr 1993), especially with regards to the broad and relatively smooth, flattened carapace, and the smooth surfaces of the chelipeds. Thus far, four species of *Demanietta* are known, i.e., *D. manii* (Rathbun 1904), *D. smalleyi* (Bott 1966), *D. merguensis* (Bott, 1966) and *D. tritrungensis* (Naiyanetr 1986); however, several additional Thai and Burmese waterfall species remain undescribed (unpublished data). All known *Demanietta* species occur along the Tenasserim Range which borders southern Thailand and southeastern Burma, and the Phuket Range in southeastern Thailand.

Esanpotamon, however, differs from *Demanietta* (sensu Ng & Naiyanetr 1993) in several key characters. The postorbital crista of *Esanpotamon* is very weak and poorly defined, whereas it is distinct and sharp in *Demanietta.* The external orbital angle and anterolateral margins are confluent without any epibranchial tooth, whereas there is a distinct epibranchial tooth and a broad external orbital angle present in *Demanietta.* Compared to known *Demanietta* species, the male abdomen of *Esanpotamon* is broadly triangular with segments 5 and 6 proportionately much broader than 9. Most significantly, the G1 is very different, with the subterminal segment gradually tapering distally, the terminal segment subcylindrical with a small proximal dorsal fold and has numerous long, stiff subdistal setae. In known *Demanietta* species, the subterminal segment has a distinct "neck", the terminal segment is conical, gently tapering, and has a broad, low dorsal fold with scattered short, soft setae (Bott 1966, 1970; Ng & Naiyanetr 1993). These differences warrant the establishment of a new genus for this new species. In addition, the distributions of *Esanpotamon* and *Demanietta* are quite distinct. *Demanietta* is known only from western and southern Thailand, whereas *Esanpotamon* occurs in northeastern Thailand.

Etymology.—The generic name is derived from an arbitrary combination of *Esan,* the name of the northeastern part of Thailand where the type species occurs, and *Potamon,* the name of the type genus of the family Potamidae. Gender neuter.

Esanpotamon namsom, new species
Figs. 1, 2

Material examined.—Holotype: male (carapace width 31.3 mm, carapace length 22.7 mm), Sam Teb Waterfall, Nam Som District, Udon Thani Province, northeastern Thailand, coll. P. Naiyanetr, 26 Oct 1991 (ZRC 1997.772). Paratypes: 1 male, 3 females (largest carapace width 23.4 mm, carapace length 18.3 mm), same data as holotype (ZRC 1997.773–776). 6 males, 4 females same data as holotype (CUMZ).

Diagnosis.—As for genus.

Description.—Carapace much broader than long; dorsal surfaces almost flat, smooth, glabrous; epigastric cristae rugose, very weak (not sharp); epigastric cristae slightly anterior of postorbital cristae; epigastric cristae separated by broad Y-shaped groove; anterolateral margin cristate, lined with small, rounded granules, strongly convex; external orbital angle small, confluent with anterolateral margin, not separated by discernible cleft (sometimes with very small notch visible in smaller specimens); anterolateral and posterolateral regions lined with oblique striae, those on anterolateral regions stronger; posterolateral margins almost straight, strongly converging towards gently sinuous posterior carapace margin; frontal margin gently sinuous, with shallow, broad cleft visible when viewed frontally; supraorbital margin lined with low, rounded granules; infraorbital margin beaded with low, rounded granules; suborbital, pterygostomial and sub-branchial regions smooth; H-shaped median carapace depression shallow but distinct, confluent

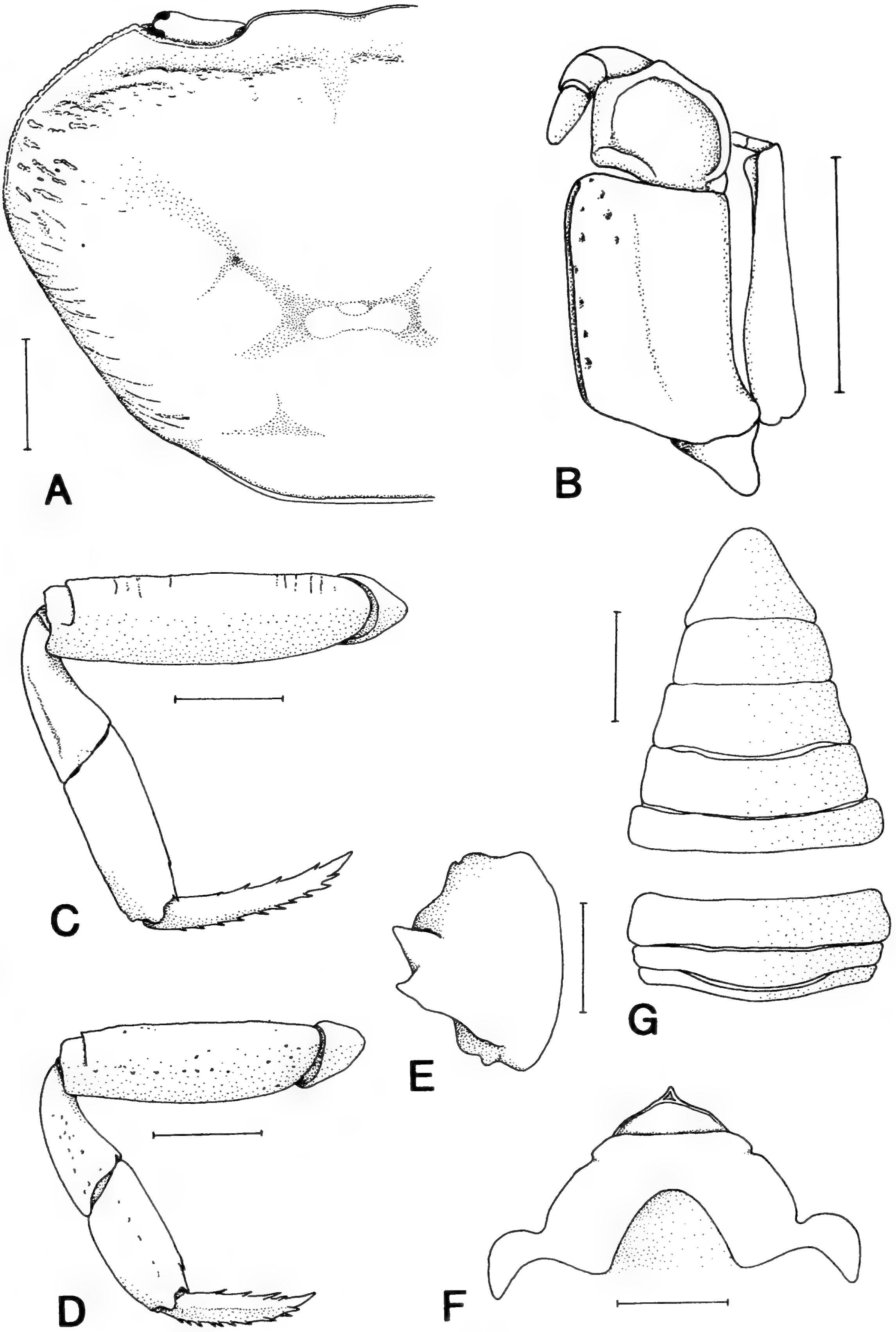

Fig. 1. *Esanpotamon namsom,* new genus and species. Holotype male (carapace width 31.3 mm, carapace length 22.7 mm) (ZRC 1997.772). A, left side of carapace; B, left third maxilliped (setae denuded); C, left third ambulatory leg (setae denuded); D, left fourth ambulatory leg (setae denuded); E, carpus of right cheliped (dorsal view); F, anterior thoracic sternites; G, abdomen (setae denuded). Scales = 5.0 mm.

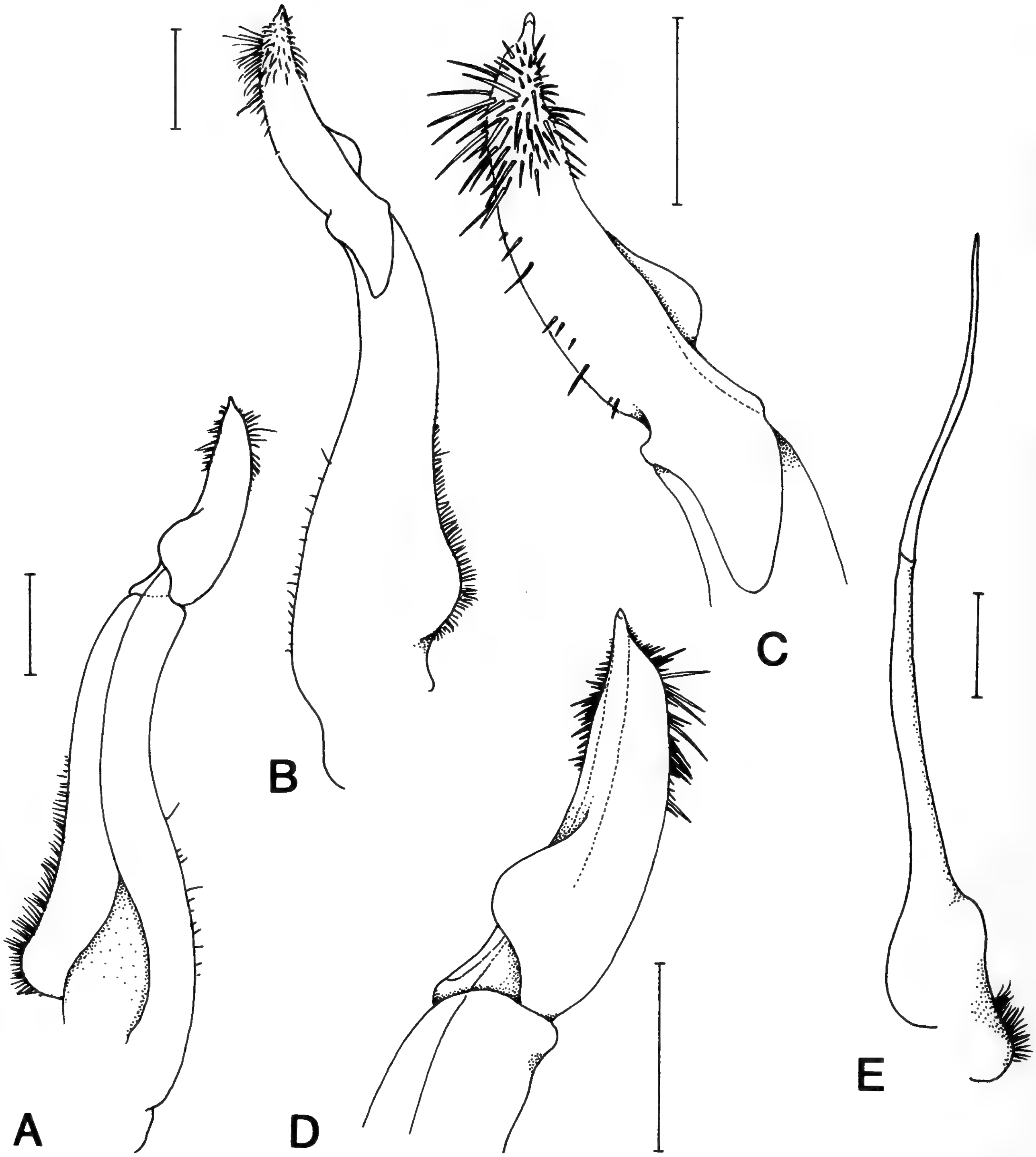

Fig. 2. *Esanpotamon namsom,* new genus and species. Holotype male (carapace width 31.3 mm, carapace length 22.7 mm) (ZRC 1997.772). A, left G1 (ventral view); B, left G1 (dorsal view); C, terminal segment of left G1 (ventral view); D, terminal segment of left G1 (dorsal view); E, left G2. Scales = 1.0 mm.

with shallow cervical grooves which reach to area between postorbital cristae and junction of antero- and posterolateral regions; shallow lateral depression present between cardiac and intestinal regions. Orbits transverse; eyes and cornea well developed. Ischium of third maxilliped rectangular, with shallow median sulcus; margins of merus cristate with median depression; exopod slender, with long flagellum.

Male chelipeds with one chela much larger than other; female chelipeds subequal; outer surfaces of palm smooth to weakly punctate; fingers gently curving, subequal in length to palm, cutting edges with numerous broad teeth and denticles;

carpus with broad, strong, sharp tooth on inner distal angle, with smaller tooth at its base positioned at approximately right angles. Ambulatory legs of normal length; fourth leg shortest; second leg longest; merus with low (usually blunt) subterminal tooth but without subterminal spine, surface lined with weak transverse striae and sometimes weakly punctate.

Male anterior thoracic sternites smooth or weakly punctate; sternites 3 and 4 completely fused without trace of sutures; suture between sternites 2 and 3 distinct, almost straight. Male abdomen with segment 3 broadest; segments 3–6 progressively narrower and less trapezoidal; lateral margins of segment 6 gently convex; telson triangular, lateral margins almost straight, tip rounded. Female abdomen broadly oval.

G1 sinuous; subterminal segment relatively slender, gradually tapering towards distal part, gently curving outwards; terminal segment, subcylindrical, approximately 0.4 times length of subterminal segment, median part broadest, gently curving upwards (towards anterior of carapace when lying in situ), distalmost part sharply tapering, tip appearing spine-like, subdistal surfaces with numerous long, very stiff setae, proximal half with small but well developed, swollen dorsal flap. G2 approximately 1.2 times length of G1, distal segment very long, approximately 0.7 times length of basal segment.

Remarks.—*Esanpotamon namsom* is the smallest known potamid crab known from Thailand (see Ng & Naiyanetr 1993), reaching carapace widths of only about 31 mm. The largest female specimen available (23.4 by 18.3 mm, ZRC 1997.774) is not fully mature, and from the shape of its abdomen, is probably only a few moults from reaching adulthood. This suggests that the holotype male has reached the adult size. In any case, the well developed G1 of the male holotype certainly indicates it is mature.

Like other waterfall crabs, *E. namsom* lives under rocks in clear, fast flowing streams (Naiyanetr 1978, 1988).

Etymology.—The name is derived from the name of the district where the species occurs, Nam Som. The name is used as a noun in apposition.

Acknowledgments

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Literature Cited

Bott, R. 1966. Potamiden aus Asien (*Potamon* Savigny und *Potamiscus* Alcock) (Crustacea, Decapoda).—Senckenbergiana Biologica 47:469–509.

———. 1970. Die Süsswasserkrabben von Europa, Asien, Australien und ihre Stammesgeschichte. Eine Revision der Potamoidea und Parathelphusoidea (Crustacea, Decapoda).—Abhandlungen Senckenbergischen Naturforschenden Gesellschaft 526:1–338.

Naiyanetr, P., 1978. The use of waterfall crabs as the evidence to indicate the relationship between the mountains of Thailand.—Abstracts of the National Conference on Agriculture and Biological Science, Animal Science Section, Kasetsart University, Bangkok, 1 pg.

———. 1986. Crab of Tenasserim Range Part II.—Abstracts of a Seminar on Wildlife of Thailand, Faculty of Forestry, Kasetsart University, Bangkok 7:11.1–11.3.

———. 1988. Freshwater crabs in Thailand.—In Book published in memory of the Royal Cremation of Associate Professor Dr. Praphun Chitachumnong, Chulalongkorn University, Phaisalsilpa Press, Bangkok, 15 pp.

———. 1992. Validation of five new species of Thai potamid crabs (Crustacea: Decapoda: Brachyura).—Raffles Bulletin of Zoology 40(1):1–7.

Ng, P. K. L. 1988. The freshwater crabs of Peninsular Malaysia and Singapore. Department of Zoology, National University of Singapore, Shinglee Press, Singapore, 156 pp.

———, & P. Naiyanetr. 1993. New and recently described freshwater crabs (Crustacea: Decapoda: Brachyura: Potamidae, Gecarcinucidae and Parathelphusidae) from Thailand.—Zoologische Verhandelingen 284:1–117.

Ortmann, A. 1896. Das system der Decapoden-Krebse.—Zoologische Jahrbuchner (Systematics) 9:409–453.

Rathbun, M. J. 1904. Les crabes d'eau douce.—Nouvelles Archives du Muséum d'Histoire Naturelle, Paris (4)6:225–312, pls. 9–18.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Tridentella ornata (Richardson 1911), new combination: records of hosts and localities (Crustacea: Isopoda: Tridentellidae)

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Abstract.—*Tridentella williamsi* Delaney, 1990, is shown to be a junior synonym of *Aega ornata* Richardson, 1911. As *Tridentella ornata,* the species is recorded from five different host fish species, from the Gulf of Mexico and the Caribbean. The presence of pleotelsonic pits is documented and briefly discussed. The distribution and host information of the 14 known species of *Tridentella* are provided.

Over a period of several years, isopods taken from the nasal cavities of groupers from the Gulf of Mexico were accumulated, and eventually made available to us for study. A review of literature on the family Aegidae from the Atlantic showed that our material was conspecific with a Richardson (1911) species, and also with a recently described Caribbean species of *Tridentella.* This note clarifies the taxonomy of the species, and records new localities and fish hosts.

Family Tridentellidae Bruce, 1984
Tridentella Richardson, 1905
Tridentella ornata (Richardson, 1911)
Fig. 1

Aega ornata Richardson, 1911:624, figs. 1–4.

Tridentella williamsi Delaney, 1990:643, figs. 1–3.

Type material examined.—Holotype of *Aega ornata,* USNM 42377, ♂ tl 8.0 mm, from *Pagrus pagrus,* southern United States, coll. R/V *Albatross,* 1885.—Holotype of *Tridentella williamsi,* USNM 239198, ♂ tl 8.5 mm, from *Epinephelus mystacinus,* British Virgin Islands.—Paratype of *Tridentella williamsi,* USNM 239199, ♂ tl 8.5 mm, from *Epinephelus flavolimbatus,* British Virgin Islands.

Non-type material examined.—USNM 253284, 1 ♂ tl 7.3 mm, 1 ovigerous ♀ tl 9.2 mm, 2 non-ovigerous ♀ tl 9.1 mm, 10 mm, from nasal cavity of *Mycteroperca microlepis,* 85–100 miles WNW of Clearwater, Florida, 10 Mar 1984.—USNM 253285, ♂ tl 11.2 mm, from *Mycteroperca phenax,* Big Elbow, Florida, 132 m, 30 May 1978.—USNM 253286, 1 ovigerous ♀ tl 12.7 mm, from *Epinephelus flavolimbatus,* Gulf of Mexico, 26°00′N, 84°20′W, 157–168 m, Feb 1984.—USNM 253287, 1 ♀ tl 8.5 mm, from nasal cavity of *Mycteroperca microlepis,* SW of Panama City, Florida, 25 m, 10 July 1977.—USNM 253288, 1 ♂ tl 7.2 mm, 1 juvenile 5.0 mm, from nasal cavity of *Mycteroperca phenax,* 36 miles SW of Panama City, Florida, 53 m, 17 May 1971.—USNM 253289, 1 ♀ tl 9.3 mm, from nasal cavity of *Mycteroperca phenax,* north–east Gulf of Mexico, 13 Feb 1977.

Diagnosis.—Eyes large, well pigmented, not contiguous. Frontal lamina elongate, five-sided, apically acute, apex meeting acute rostrum, 2 long sides slightly concave. Pereonites 4–7, and pleonites 1–5 with row of small tubercles along posterior margin; pleonites 3 and 4 with additional short median row of tubercles; pleonite 5

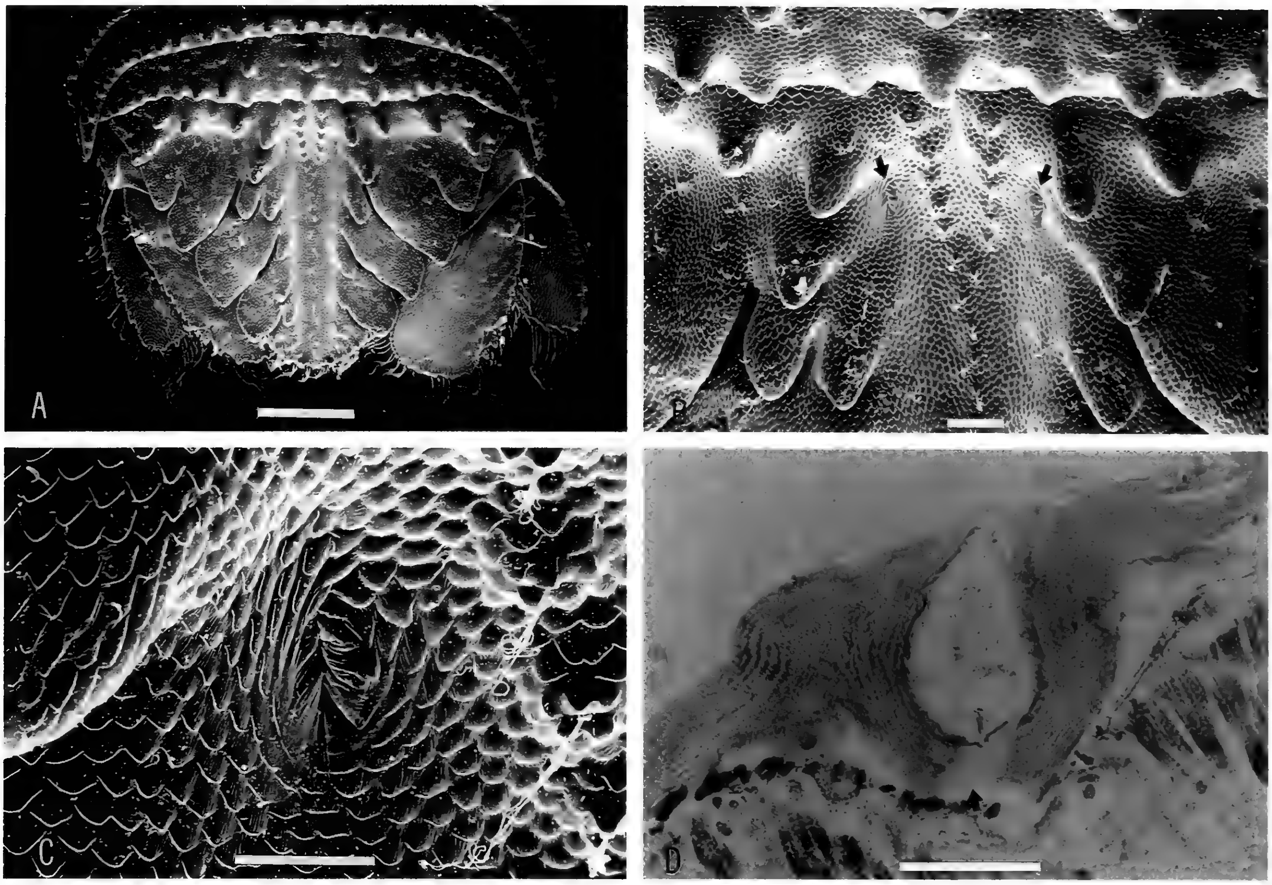

Fig. 1. *Tridentella ornata:* A, pleonite 6 and pleotelson, scale = 500 μ; B, pleotelson enlarged, arrows indicate pits, scale = 100 μ; C, pleotelsonic pit opening enlarged, scale = 50 μ; D, cross-section through pleotelsonic pit, arrow indicates unsclerotised section of wall, scale = 50 μ.

with 2 additional rows of tubercles. Pleotelson triangular, basal width about 1.3 times middorsal length, with irregular row of large tubercles across base; shallow median longitudinal groove running from base to apex, flanked by row of large tubercles on each side, with invaginated pit on each side near base; lateral parts of pleotelson incised into 4 broad flattened sections; posterior margin rounded, crenulate.

Remarks.—The locality for the single specimen of *Aega ornata* described by Richardson (1911) is given as "southern United States". Comparison of this specimen with the type material and figures of *Tridentella williamsi* from the British Virgin Islands (Delaney 1990), and our material from the Gulf of Mexico reveal no differences in the very characteristic pereonal and pleonal ornamentation. Equally, no differences in appendage structure could be detected. (In Richardson's description, the captions for figures 3 and 4 of the first and second maxillae are reversed). Females of the genus *Aega* Leach, 1815, lack the narrow, twisted, and strongly spined maxilliped that characterizes the males of the genus.

The pair of basal pits on the pleotelson are each marked on the surface by a puckered slit-like opening, which leads to a small flask-shaped chamber, whose walls are formed by the invaginated exoskeleton. At the base of the chamber is a non-sclerotized region of the exoskeleton. No other structure is visible, and there was no sign of a statolithic inclusion in the specimen sectioned. The pits are sited in the same position as the paired pleotelsonic statocysts of anthurid isopods (see Barnard 1925), and although this feature might tempt one to speculate on a link between the Flabellifera and Anthuridea, these pits should be seen as one possible stage in the development of the type of innervated statocysts seen in the anthurids.

Of the 14 species of *Tridentella* described, only five have been recorded as associated with fish. These involve five different fish families. In the case of *T. ornata* under discussion here, the species has been taken from five different host fishes belonging to two separate fish families. These facts support the thesis proposed by Delaney & Brusca (1985:730), that these isopods should be regarded as micropredators, rather than parasites. Tridentellids are thought to lurk in the benthos, and pounce on almost any passing fish, to take a meal of blood and drop off again.

The following is a list of the described species of *Tridentella,* with localities, depth and host records:

Tridentella acheronae Bruce, 1988. New Zealand, Kermadec Is., 424–1006 m. Host not recorded.

Tridentella cornuta Kussakin, 1979. Northwest Pacific, 20–50 m. Host: *Hemitripterus villosus* (Cottidae).

Tridentella glutacantha Delaney & Brusca, 1985. North Farallon Islands, Santa Catalina Islands, off Los Angeles, 128–360 m. No host recorded.

Tridentella japonica Thielemann, 1910. Off Tokyo, Japan. No host recorded.

Tridentella laevicephalax Menzies, 1962. Southern Chile, 24 m. No host recorded.

Tridentella ornamenta (Menzies & George, 1972). Peru-Chile Trench, 907–935 m. No host recorded.

Tridentella ornata (Richardson, 1911). South–eastern United States, Gulf of Mexico, Caribbean Sea, 25–168 m. Hosts: red porgy, *Pagrus pagrus* (Sparidae); yellowedge grouper, *Epinephelus flavolimbatus,* misty grouper, *E. mystacinus,* gag grouper, *Mycteroperca microlepis,* scamp, *M. phenax* (Serranidae).

Tridentella quinicornis Delaney & Brusca, 1985. Off Santa Barbara Islands and Farnsworth Bank, California, 53 m. No host recorded.

Tridentella recava Bowman, 1986. New York Bight, 100–300 m. In burrows of tilefish, *Lopholatilus chamaeleonticeps* (Malacanthidae).

Tridentella saxicola (Hale, 1925). New South Wales, Queensland, Australia, 11–146 m. No host recorded.

Tridentella sculpturata Kussakin, 1955. Northwest Pacific, 70–96 m. Hosts: *Enophris diceraus* and *Alchichthys elongatus* (Cottidae).

Tridentella tangaroae Bruce, 1988. New Zealand, 90–94 m. No host recorded.

Tridentella virginiana (Richardson, 1900). Nova Scotia to Florida; Gulf Stream off Florida, 220–550 m. No host recorded.

Tridentella vitae Bruce, 1984. Fiji, 360 m. Host: *Pristipomoides flavipinnis* (Lutjanidae).

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Literature Cited

Barnard, K. H. 1925. A revision of the family Anthuridae (Crustacea Isopoda), with remarks on certain morphological peculiarities.—Journal of the Linnean Society of London, Zoology 36: 109–160.

Bowman, T. E. 1986. *Tridentella recava,* a new isopod from tilefish burrows in the New York Bight (Flabellifera: Tridentellidae).—Proceedings of the Biological Society of Washington 99:269–273.

Bruce, N. L. 1984. A new family for the isopod crustacean genus *Tridentella* Richardson, 1905, with description of a new species from Fiji.—Zoological Journal of the Linnean Society 80: 447–455.

———. 1988. Two new species of *Tridentella* (Crustacea, Isopoda, Tridentellidae) from New Zealand.—Records of the National Museum of New Zealand 3(7):71–79.

Delaney, P. M. 1990. *Tridentella williamsi,* a new species of isopod crustacean from the British Virgin Islands, Western Atlantic (Flabellifera: Tridentellidae).—Proceedings of the Biological Society of Washington 103:643–648.

———, & R. C. Brusca. 1985. Two new species of *Tridentella* Richardson, 1905 (Isopoda: Flabellifera: Tridentellidae) from California, with a rediagnosis and comments on the family, and a key to the genera of Tridentellidae and Corallanidae.—Journal of Crustacean Biology 5:728–742.

Hale, H. M. 1925. Review of the Australian isopods of the cymothoid group. Part I.—Transactions of the Royal Society of South Australia 49:128–185.

Kussakin, O. 1955. New for far-eastern waters of the U.S.S.R.—the warm water families of Isopoda.—Travaux Trudy Zoologicheskogo Instituta, Akademiya NAUK USSR 18:228–234.

———. 1979. On the isopod crustaceans (Isopoda) of the Sea of Okhotsk.—Transactions, Academiya NAUK CCCP [Investigations of Pelagic and Bottom Organisms from the Far-Eastern Seas] 15:106–122.

Leach, W. E. 1815. A tabular view of the external characters of four classes of animals, which Linné arranged under Insecta; with the description of the genera comprising three of these classes into order, etc., and descriptions of several new genera and species.—Transactions of the Linnean Society of London 2:306–400.

Menzies, R. J. 1962. The zoogeography, ecology, and systematics of the Chilean marine isopods.—Lunds Universitets Arsskrift, N. F. (2)57(11):1–162.

———, & R. Y. George. 1972. Isopod Crustacea of the Peru–Chile Trench.—Anton Bruun Report 9:1–124.

Richardson, H. 1900. Synopses of North American invertebrates. 7. The Isopoda.—American Naturalist 34:207–230.

———. 1905. A monograph on the isopods of North America.—Bulletin of the United States National Museum 54:1–727.

———. 1911. Description of a new species of *Aega* from the Atlantic coast of the United States.—Proceedings of the United States National Museum 40:623–624.

Schioedte, J. C., & F. Meinert. 1879. Symbolae ad Monographiam Cymothoarum Crustaceorum Isopodum Familiae 1. Aegidae.—Natur-historisk Tidsskrift (3)13:281–378.

Thielemann, M. 1910. Beiträge zur Kenntnis der Isopodenfauna Ostasiens.—Münchens Abhandlungen der Akademie Wissenschaft math.-phys. Kl. suppl.-bd 2, 3:1–109.

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Doxomysis acanthina, a new leptomysinid (Crustacea: Mysidacea) from the northern Great Barrier Reef, Australia, with extensions to the known distributions of *D. australiensis* W. M. Tattersall, 1940 and *D. spinata* Murano, 1990, and a key to the genus *Doxomysis*

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Abstract.—*Doxomysis acanthina* is described from the lagoon at Lizard Island, northern Great Barrier Reef, Queensland, Australia. The spines on the palp of its maxillary endopod are distinctive in having 2 types of secondary spinule, long and slender and small and thorn-like. *D. spinata,* previously found only in the Northern Territory, is provisionally identified from Lizard Island, and the known range of *D. australiensis* is extended into northern Queensland waters. The telson of all three species exhibit sexual dimorphism. A key to the genus *Doxomysis* is given.

Nine species belonging to the genus *Doxomysis,* tribe Leptomysini, have been taken in the Australian region. W. M. Tattersall (1936) recorded *D. littoralis* Tattersall, 1922 from the vicinity of Low Isles, Great Barrier Reef. Some of the specimens were faintly spinulose and Pillai (1973) tentatively referred these to *D. longiura* Pillai, 1963. *D. australiensis* was described under the name of *Afromysis australiensis* from Broken Bay, New South Wales by Tattersall (1940). It was recorded from Morton Bay, southern Queensland by Bacescu & Udrescu (1982), who also described *D. proxima* from the same area. Panampunnayil (1986) described *D. johnsoni* from Western Australia in the coastal waters of the extreme southwest and Murano (1990) described *D. brucei* and *D. spinata* from Port Essington, Northern Territory. Pillai (1973) recorded the occurrence of 9 specimens of *D. quadrispinosa* in the North Australian Basin. They were taken individually on 4 different cruises and were found mostly to the east of Christmas Island or off the North West Cape of Western Australia.

Three species of *Doxomysis, D. spinata* (identified provisionally), *D. australiensis* and the new species *D. acanthina* described here, were found in a survey of the mysid fauna of the Lizard Island region of the Great Barrier Reef during the years 1975–1980. These records extend the known distributions of *D. spinata* and *D. australiensis* eastwards and northwards respectively into the waters of northeastern Queensland. Murano's (1990) description of *D. spinata* was made from a single adult male. The females of this species from Lizard Island reveal that it exhibits the same type of sexual dimorphism in the structure of the telson as that found in *D. longiura* by Pillai (1973) and as is also seen in *D. australiensis* (Bacescu & Udrescu 1982, fig. 5) and in *D. acanthina.*

The genus *Doxomysis* is one of a group of 9 allied genera in the tribe Leptomysini. Although full descriptions are not available for many of the 48 species that belong to these genera, an affinity among them is suggested by resemblances in the following characters: the enlargement and elaboration of the palp on the endopod of the maxilla; the similarity in the structure of the modified terminal and subterminal setae of the exopod of the fourth male pleopod; the well-defined cleft in the telson and the overall resemblance in the structure and pattern of distribution of telson spines. The genera are listed below:

Afromysis Zimmer, 1916 (6 species)
Australomysis W. M. Tattersall, 1927 (5 species)
Bathymysis W. M. Tattersall, 1907 (2 species)
Doxomysis Hansen, 1912 (15 species)
Hyperiimysis Nouvel, 1966 (1 species)
Iimysis Nouvel, 1966 (2 species)
Nouvelia Bacescu & Vasilescu, 1973 (3 species)
Pseudoxomysis Nouvel, 1973 (1 species)
Tenagomysis Thomson, 1900 (13 species)

Fenton (1991) pointed out the need to reassess the status of this group of genera and discussed problems arising from the lack of information on diagnostic features in many of the species. Members of the genus *Afromysis* are characterised by the markedly crescentic form of the maxillary palp, a feature that distinguishes them from members of the other genera in the group. In the genera *Doxomysis, Hyperiimysis* and *Pseudoxomysis* (the doxomysid sub-group), the palp is broader than long and typically fan-like in appearance, while in the genera *Tenagomysis, Iimysis, Australomysis, Bathymysis* and *Nouvelia* (the tenagomysid sub-group), it is longer than broad and usually obovate in shape. *Nouvelia* also contains a single species in which the palp is broader than long and resembles that of the doxomysid sub-group.

The doxomysid sub-group may be further divided on the basis of the structure of the marsupium of the female, which is formed of only two pairs of oostegites in the genus *Doxomysis,* while in both *Hyperiimysis* and *Pseudoxomysis* it is made up of three pairs and in both, there is also a small projection at the base of the fifth pair of thoracic limbs, which, in the case of *Pseudoxomysis,* has been interpreted as a rudimentary forth pair of oostegites. Although smaller, the basal projection in *Hyperiimysis* could be given the same interpretation. This feature is probably indicative of a close affinity between the two genera, as are others they have in common, such as a spine on the anterior border of the labrum and secondary spinules on the distal spines of the maxillary palp. Such similarities suggest that the species concerned should be placed in the same genus. However, differences in the structure of their thoracic limbs may mitigate against doing so, as the carpopropodus is made up of 3 articles in *Pseudoxomysis* and two articles in *Hyperiimysis.* Additionally, in the the latter genus the carpo-propodus of the eighth thoracic limb is enlarged and modified to form a prehensile structure.

Among the members of the tenagomysid sub-group, *Australomysis* and *Bathymysis* both lack the pair of plumose setae present in the telson cleft of all the other genera. They both contain species with dorso-ventrally flattened eyes and they are not clearly distinguished from each other anatomically, apart from the fact that the distal spines of the maxillary palp are barbed in *Bathymysis* and simple in *Australomysis.* They also have widely separate distributions and contrasting habitats. *Australomysis* has been found in shallow inshore waters along the south-west, south and east coasts of Australia and in the surf zone on the Pacific coast of central Japan (Fukuoka & Murano 1994), while both species of *Bathymysis* were taken at depth in the Atlantic (W. M. Tattersall 1907, 1951).

The genus *Iimysis* was erected to accommodate those *Tenagomysis* species that had an anterior spine on the labrum and a tarsus made up of four articles (Nouvel 1966). As indicated by Fenton, 1991, *T. tanzaniana* (Bacescu 1975) should probably be transferred to this genus. Its tarsus is made up of only three articles, but it has a spine on the anterior border of the labrum.

The genus *Nouvelia* is distinguished by a tarsus consisting of only three articles and a gap in the row of lateral spines on the telson. It includes *N. nigeriensis* (O. Tattersall, 1957), a species in which the palp on the maxilla is broader than long and which might, therefore, be better placed in the genus *Doxomysis.*

At least 10 species are known to have secondary spinules on the spines that border the distal margin of the maxillary palp. In the descriptions of 3 of these, the spinules are shown in figures of the maxillae, but not mentioned in the text. They are present in the members of the genus *Bathymysis* and in 3 species of *Tenagomysis, T. australis, T. tasmaniae* and *T. bruniensis* (Fenton 1991), in *Hyperiimysis madagascariensis* (Nouvel 1966, fig. 10), in *Pseudoxomysis caudaensis* (Nouvel 1973, fig. 10) and in 3 species of *Doxomysis, D. spinata,* where they are long and slender (Murano 1990, fig), *D. rinkaiensis,* which has small spinules on the expanded tips of some of the spines (Valbonesi & Murano 1980, fig 3D) and *D. acanthina,* described below, in which there are 2 distinct sets of spinules, one, long and slender, towards the bases of the spines and the second, short and close- set nearer the tips. Among the species under discussion, *D. acanthina* is the only one so far found with more than 1 type of secondary spinule.

As *D. murariui* was described from 1 damaged female and *D. sanuriensis* from two damaged specimens, the status of these two species is difficult to ascertain. The illustrations of both show secondary spinules on the spines of the maxillary palps (Bacescu 1993, figs. 1E, maxillule (sic) and 2B, maxillule (sic)). This does not correspond with the account of the spines in the description of *D. sanuriensis,* however, while in the description of *D. murariui,* the spines are not discussed. The elongate shape of the maxillary palp of the latter species suggests that it may have a greater affinity with the tenagomysid group of species than with the doxomysid group.

Doxomysis acanthina, new species

Figs. 1–3

Material examined.—179 specimens were taken from the Lizard Island lagoon, during 1975–1980. Of these 113 were caught in nets and traps deployed close to the sandy floor, 60 in plankton hauls made in the lagoon center at night and 3 in traps placed above living coral. 3 additional specimens were taken in a night haul in the open channel between Lizard Island and Eagle Cay.

Size range.—Length, measured from anterior border of eyes to end of telson; 55 adult males, 3.7–6.5 mm.; 27 immature males, 2.5–3.8 mm.; 4 brooding females (up to 8 larvae in marsupium), 5.0–5.5 mm.; 12 adult females, marsupium empty, 4.5–5.5 mm.; 32 immature females, 2.8–5.0 mm.; 49 juveniles, 1.5–3.5 mm.

Type series.—Type specimens deposited in the Australian Museum, Sydney, paratypes deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C. Types and Paratypes all collected in the Lizard Island lagoon, 14°40′S, 145°27′E.

Holotype: adult male and slide preparation of right maxilla, AM P42693, light trap, sandy lagoon floor, depth 11 m, 28 May 1975, 1922–1927 hrs (Sta. #STL-75-L10).

Allotype: adult female, AM P42694, plankton net pushed above lagoon floor, depth 9 m, 31 May 1975, 1600 hrs (Sta #STL-75-P8).

Paratypes: 2 adult males, AM P43138, 3 adult males, USNM 259765, light trap light, sandy lagoon floor, depth 11 m, 28 May 1975, 1922–1927 hrs (Sta. #STL-75-L10), 1 adult female, USNM 259766, light trap on living *Porites* coral, E of Palfrey Island, depth 1 m, 4 Jan 1975, 2228–2233 hrs (Sta. #STL-75-T11).

Description.—Body slender. Integument spiny, small scale-like spinules conspicuously dense on carapace, less dense on abdomen, eyestalks, sparse on bases of antennae, pleopods. Carapace small, rounded, exposing last 2 thoracic segments. Rostrum short, bluntly pointed, reaching base of eyestalks (Figs. 1A, B).

Eyes prominent, fairly dark, hemispheri-

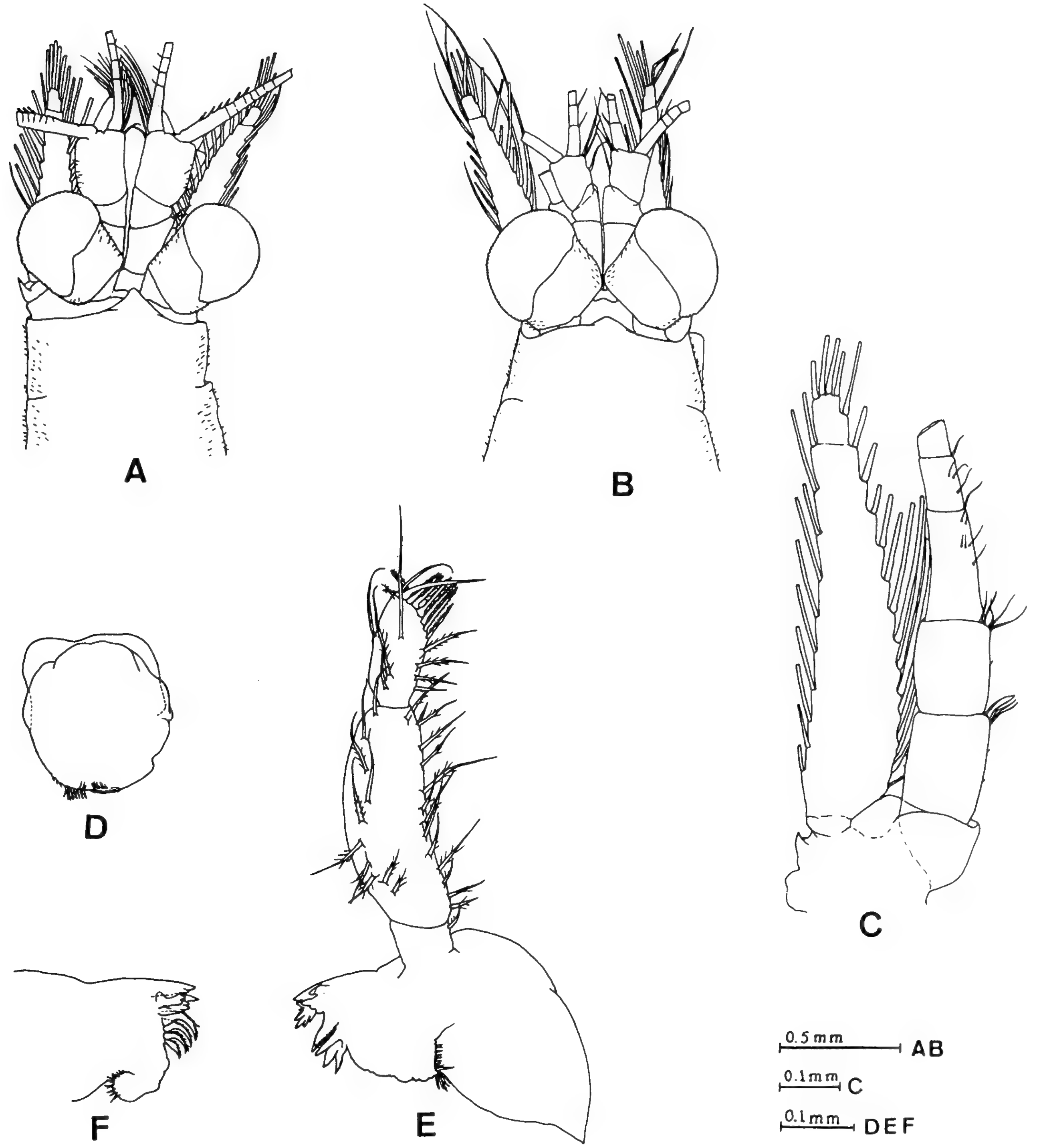

Fig. 1. *Doxomysis acanthina.* A, Anterior end of male. B, Anterior end of female. C, Left antenna. D, Labrum. E, Right mandible and palp. F, Left mandible.

cal, greater in diameter than width of eyestalks.

Antennular peduncle of male stout, first article less than 0.5 total length, third article expanded, appendix masculina conical with prominent sensory bristles (Fig. 1A). Antennular peduncle of female slender, first segment 0.5 total length (Fig. 1B).

Antennal scale narrow, overreaching antennular peduncle by about 0.25 of its length, distal segment present, suture inconspicuous (Fig. 1C).

Labrum rounded, without anterior spine (Fig. 1D).

Mandible with well-developed incisor process, lacinia mobilis, spine row and spinulose molar process, palp typical of genus,

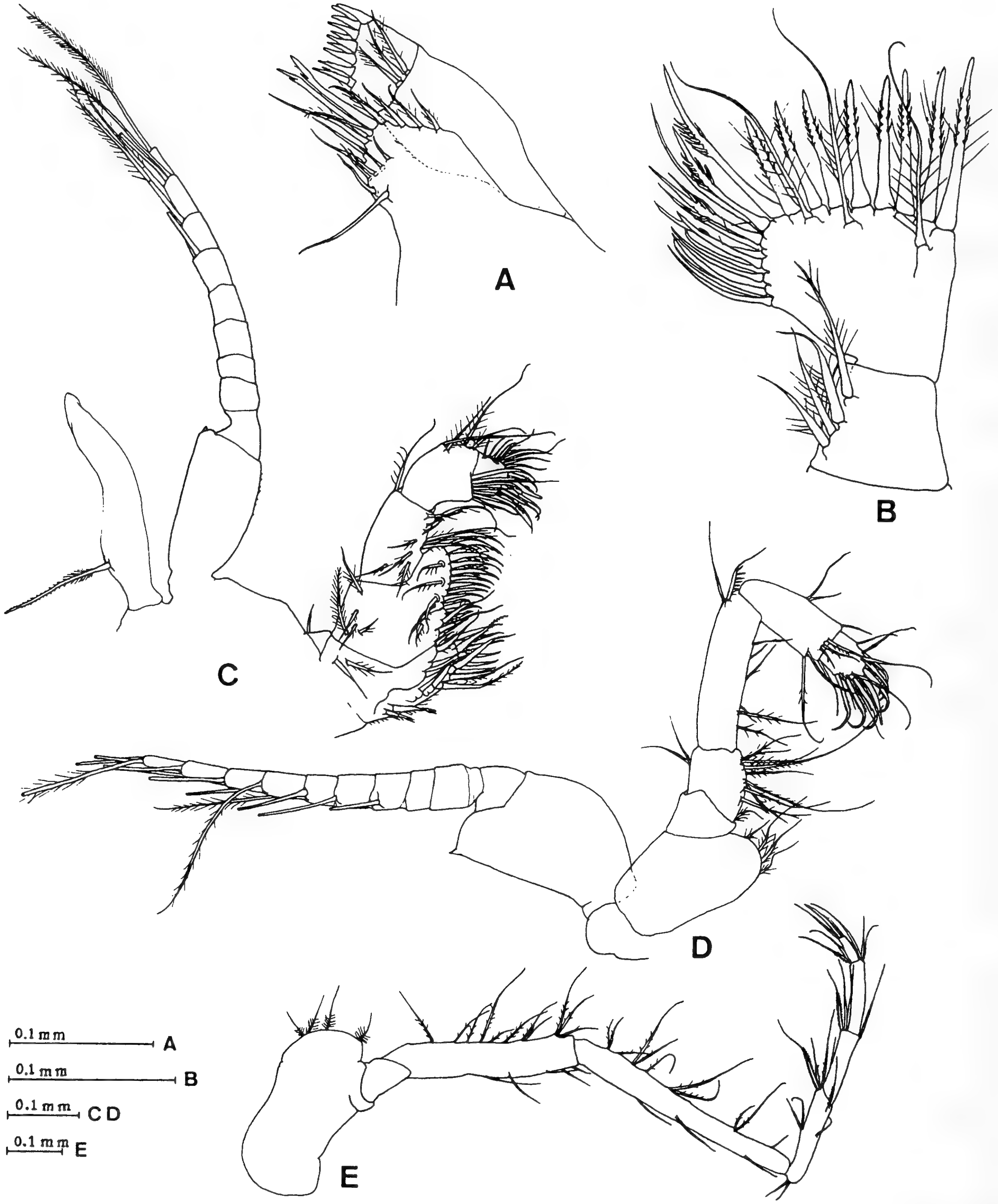

Fig. 2. *Doxomysis acanthina.* A, Maxillule. B, Segment 2 of endopod of maxilla. C, Thoracic limb 1. D, Thoracic limb 2. E, Endopod of thoracic limb 4.

apart from relatively slender second article (Figs. 1E, F).

Maxillule with inner lobe of segment 1 ending in 2 prominent notched spines, segment 3 armed with 10 short straight spines (Fig. 2A).

Palp of maxillary endopod expanded to form characteristic plate, bordered by 7–8 stout spines, each carrying a few long slender secondary spinules and 3–6 small, thorn-like, closely spaced spinules, in 2 lateral rows on distal part of each spine (Fig. 2B).

Thoracic limb 1 with robust endopod, row of 10 strong curved setae on masticatory endite of merus, epipod with a long seta near base (Fig. 2C). Dactylus of thoracic limb 2 armed with 7 prominent serrate spines (Fig. 2D). Thoracic endopods 3–8 with oblique articulation between carpus and propodus, propodus made up of 2 subequal subsegments, dactylus slender, ending in long sharp nail (Fig. 2E).

Marsupium of female formed of 2 pairs of oostegites borne on thoracic limbs 7 and 8.

Segment 6 of abdomen elongate, almost twice as long as segment 5.

Pleopods of male biramous, sympod slightly spinulose, exopods with 7 segments. Endopod of pleopod 1 short, unsegmented with single distal seta, 5 lateral setae, pseudobranchial lobe ending in 4 setae with bulbous bases (Fig. 3A). Pleopods 2–5 with 6-segmented endopods. Exopod of pleopod 4 modified: basal segment with shallow keel on inner edge; 4th segment with small, naked seta on inner distal margin; 5th segment with large, robust, curved spine, extending from outer distal margin to reach almost 0.6 length of terminal spines, distal 0.3 with outer row of close-set, secondary spinules; 6th segment with slender, naked distal seta on outer border, adjacent to strong, slightly curved spine, extending beyond terminal setae, row of sharp, slender secondary spinules on distal 0.6 of outer margin; 7th segment small, ending in 2 long subequal setae (Figs. 3B, C). Pleopod 5 with prominent conical distolateral process on basal segment of endopod (Fig. 3D).

Uropod slender, all margins setose, exopod almost twice as long as telson, endopod slightly more than 0.75 length of exopod, spine row of endopod with 22–23 spines, closely-set, alternately small and large in proximal part near statocyst, grading distally to larger, more widely-spaced spines near apex (Fig. 3E).

Telson about equal in length to pleonite 6, cleft slightly more than 0.25 total telson length. Telson of male strongly tapering, width at apex 0.5 width at base, apical lobes narrow, margins slightly concave, 11–12 lateral spines, terminating in 4 prominent apical spines, the second being the longest, cleft with 8–9 small spines on each side, 2 plumose setae projecting from base (Fig. 3F). Telson of female with less pronounced taper than that of male, width at apex 0.6 that of base, apical lobes broad, margins markedly concave, 12 lateral spines, grading into 5 large, somewhat spatulate apical spines, central apical spines subequal, 9–10 cleft spines on each side (Fig. 3G).

Chromatophore pattern.—Observed in 2 females hand-netted above the pale sandy lagoon floor. Eyestalk; 1 white chromatophore and 1 red chromatophore. Cephalothorax; 1 large, highly branched white chromatophore and 1 red chromatophore mid-dorsally above proventriculus, 1 white mid-lateral chromatophore on each side, 1 red mid-ventral chromatophore. Marsupium; 1 white dorso-lateral chromatophore on each oostegite, 1 red ventro-lateral chromatophore on anterior part of each posterior oostegite. Abdomen; 1 white mid-dorsal chromatophore on each segment, that of last segment large and highly branched, situated above sixth abdominal ganglia, 1 white and 1 red mid-ventral chromatophore on each segment. Telson; 1 red dorsal chromatophore.

Note on habitat.—The major portion of the *D. acanthina* catch was made up of 113 specimens found living just above the sandy floor of the lagoon, while 60 were caught in plankton tows taken in the lagoon at night, an indication that this species migrates into the water column during the hours of darkness. Only 3 specimens were caught above living coral and 3 in offshore plankton tows made at night

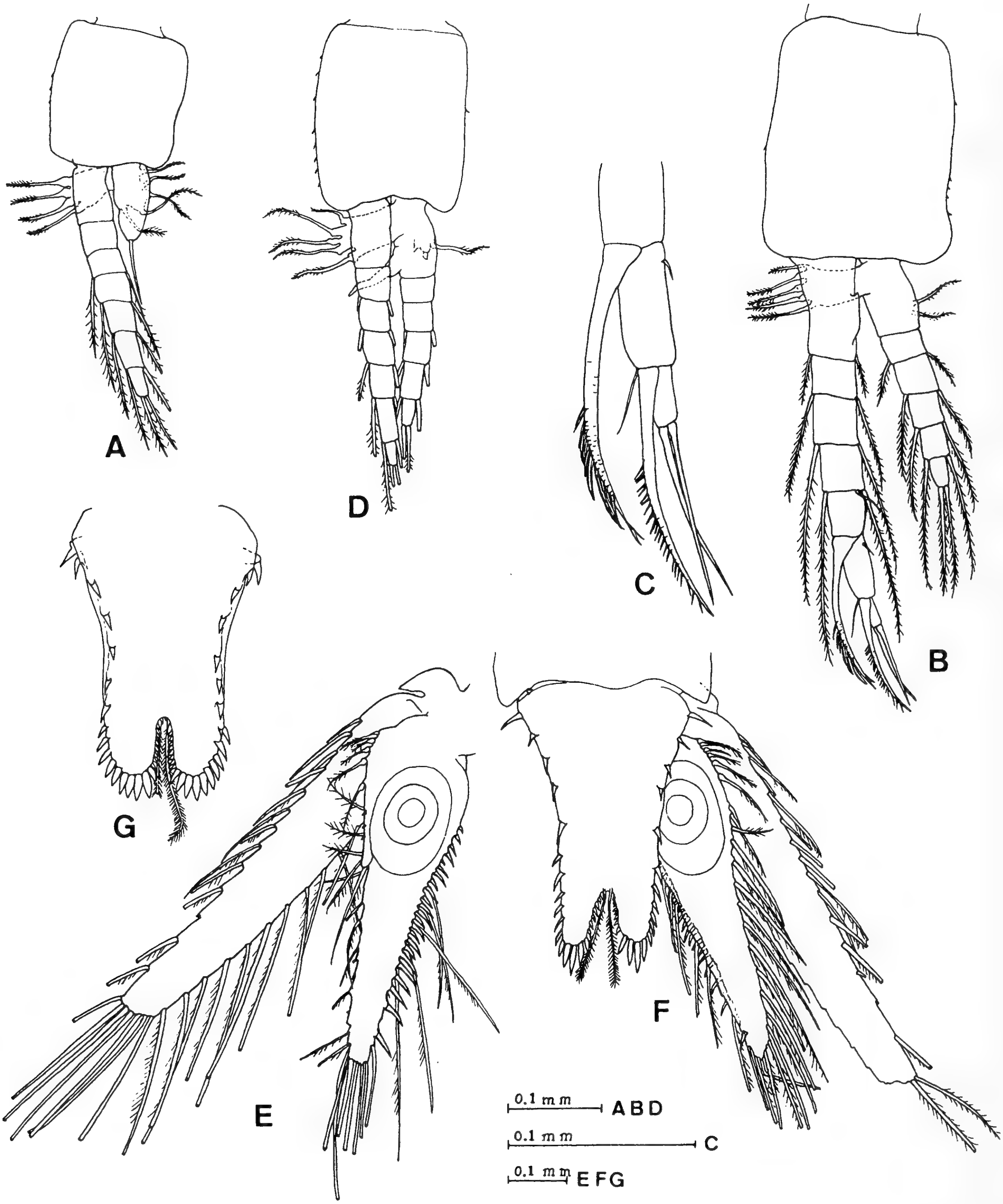

Fig. 3. *Doxomysis acanthina.* A, Pleopod 1. B, Pleopod 4. C, Terminal 3 segments of exopod of pleopod 4. D, Pleopod 5. E, Left uropod of male. F, Right uropod and telson of male. G, Telson of female.

in the channel between Lizard Island and Eagle Cay.

Etymology.—From the Greek "akanthinos", thorny, referring to the lateral rows of small, thorn-like secondary spinules on the spines of the maxillary palp.

Doxomysis spinata Murano, 1990
Fig. 4.

Material examined.—326 specimens, provisionally assigned to this species, were caught at Lizard Island, 308 in a light trap

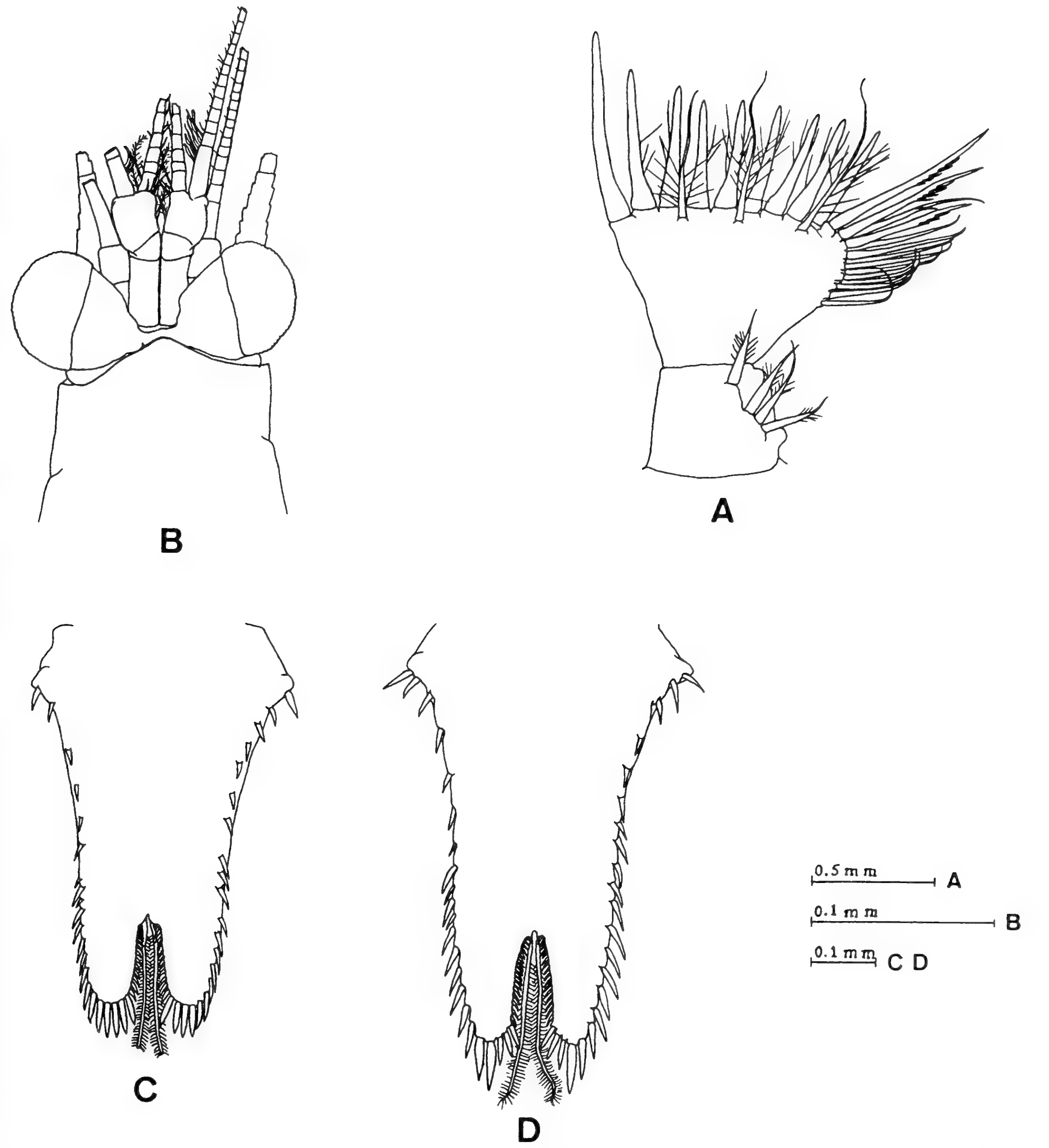

Fig. 4. *Doxomysis spinata.* A, Segment 2 of endopod of maxilla. B, Anterior end of female. C, Telson of female. D, Telson of male.

on the reef flat, 17 in a light trap on living *Acropora formosa* and a single female in a hand-net just above the sandy lagoon floor.

Size range.—Length, measured from anterior border of eyes to end of telson, 93 adult males, 3.5–5.7 mm; 36 immature males, 2.8–4.0 mm; 38 brooding females (up to 9 larvae in marsupium), 4.5–6.0 mm; 17 adult females, marsupium empty, 4.5–5.5 mm; 141 immature females, 3.0–5.2 mm; 1 juvenile, 1.7 mm.

Description of Lizard Island specimens.—These correspond in most features with Murano's (1990) description of *D. spinata,* which was made from a single male, 5.8 mm in length, taken in Port Essington, Northern Territory. Their integument is smooth and they have the long slender secondary spinules on the spines of the maxillary palp, noted in *D. spinata* (Fig. 4A). The secondary sexual characters of the males resemble those of the type specimen. They have a similarly robust antennular peduncle with a prominent appendix masculina and the exopod of pleopod 4 is modified in the same way as in the type specimen, although mature individuals have a slightly longer inner seta on segment 7 than is shown in Murano's Fig. 4C.

It is possible, however, that in spite of their similarity to *D. spinata,* the specimens from Lizard Island will prove to belong to a separate species, because they differ from the type specimen in the number of spines on the endite on the merus of the endopod of thoracic limb 1, in the number in the spine row on the endopod of the uropod and in the number of spines on the telson. The counts were made on 10 of the Lizard Island males, varying in length from 4.2–6.8 mm, with the smaller specimens tending to have a smaller number of spines than the larger. The spine counts were as follows:

	L.I. specimens	Holotype
Endite on thoracic limb 1—	8–10	7
Endopod of uropod—	21–33	37
Each side of telson,		
lateral spines—	14–20	12
apical spines—	5	3
cleft spines—	10–16	9

These differences suggest that the Lizard Island specimens may be distinct from *D. spinata,* but since the range of variation in specimens from the type locality cannot as yet be assessed, they have been relegated to the same species provisionally, pending the collection of further material in the Northern Territory. An examination of the type specimen of *D. spinata* has confirmed that it corresponds with the Lizard Island specimens, except in the features detailed above.

In the females from Lizard Island the antennule has a slender basal segment equal in length to the combined lengths of the second and third segments (Fig. 4B). The marsupium is formed of 2 pairs of oostegites. The telson is moderately tapered and has 16 lateral spines, 5 subequal apical spines and 12 cleft spines on each side (Fig. 4C). It differs from the male telson (Fig. 4D) in being slightly less tapered, in lacking a large posterior apical spine and in having a shorter cleft with fewer cleft spines.

Note on habitat.—325 of the Lizard Island specimens of *D. spinata* were trapped in the vicinity of coral, while only 1 was netted above the sandy lagoon floor.

Doxomysis australiensis
(W. Tattersall, 1940)

Material examined.—During May 1976, 4 specimens of *D. australiensis* were taken at Lizard Island. They included a single female, caught in a net pushed above the lagoon floor and an immature male and 2 juveniles caught in 2 plankton tows made at night in the channel between Lizard Island and Eagle Cay. Its smooth integument distinguishes it from *D. acanthina* and its lack of secondary spinules on the maxillary palp separates it from *D. spinata* (Table 1).

Size range.—Length, measured from the anterior border of the eyes to the end of the telson, 1 immature male, 4.0 mm; 1 brooding female (12 larvae in marsupium), 6.5 mm; 2 juveniles, 1.5 and 2.4 mm.

Note on distribution.—This species was described from Broken Bay, New South Wales, and has been recorded from Moreton Bay, southern Queensland (Bacescu & Udrescu 1982). The Lizard Island material extends its known range into the waters of northern Queensland.

The 4 specimens of *D. australiensis* in the Lizard Island samples were taken on 2 days in mid-May 1976, one in association with *D. acanthina* near the lagoon floor and the other three at night in offshore plankton

Table 1.—Comparison between *D. acanthina, D. spinata* and *D. australiensis.*

	D. acanthina	*D. spinata*	*D. australiensis*
Integument			
Carapace	spiny	smooth	smooth
Abdomen	spiny	smooth	smooth
Max. palp			
Spine no.	7–8	8–10	10
Secondary spinules	2 types	1 type	absent
1st type	long, slender	long, slender	
2nd type	close-set	absent	
Male pleop. 4			
Exop. seg. 7			
Distal setae	both long, stout	1 long, 1 small	both curved, moderate
Exop. seg. 6			
Length	greater than 2 × seg. 7	2 × seg. 7	6 × seg. 7
Exop. seg. 5			
Distal seta length	greater than distal seta	less than distal seta	greater than 2 × distal seta
Exop. seg. 1			
Keel	present on inner margin	absent	keel not recorded
Uropod			
Endop. spines	22–23	type, 37 L. Is., 21–33	42–45
Telson			
Lat. spines	11–12	type, 12 L. Is., 14–20	19–21
Apic. spines	4	type, 3 L. Is., 5	4
Cleft spines	9–10	type, 9 L. Is., 10–16	23
Sexual dimorphism			
Male telson:			
Apic. lobes	tapered	tapered	tapered
Apic. spines	pointed	pointed	pointed
Fem. telson:			
Apic. lobes	rounded	less rounded	tapered
Apic. spines	spatulate	more pointed	pointed

tows. *Doxomysis australiensis* occurs in the coastal waters of central New South Wales and southern Queensland, where it was the second most abundant mysid in samples from Moreton Bay examined by Bacescu & Udrescu (1982). It may be reaching the northern limit of its range in the region of Lizard Island. The small number of specimens taken and the fact that strong south-easterly trade winds were blowing at the time, raise the possibility that it is carried into the area intermittently, when trade winds dominate the weather pattern and enhance the northward flow of the coastal current.

The species of Doxomysis.—The genus *Doxomysis* is made up of the following 15 species:

D. acanthina n. sp.—Lizard Island, Queensland, Australia.

D. anomala W. M. Tattersall, 1922—Andaman Islands, India.

D. australiensis (W. M. Tattersall, 1940)—E. coast, Australia; Mossel Bay, South Africa.

D. brucei Murano, 1990—Port Essington, N.T., Australia.

D. hanseni Colosi, 1920—Malay Archipelago.

D. johnsoni Panampunnayil, 1986—W. coast, Australia.
D. littoralis W. M. Tattersall, 1922—Andaman Islands, India; Great Barrier Reef, Australia.
D. longiura Pillai, 1963—Kerala, India.
D. microps Colosi, 1920—Galapagos Is., Ecuador.
D. murariui Bacescu, 1993—Bali, Indonesia.
D. proxima Bacescu & Udrescu, 1982—Moreton Bay, Australia.
D. quadrispinosa (Illig, 1906)—Tropical Indo-Pacific.
D. rinkaiensis Valbonesi & Murano, 1980—Tanabe Bay, Japan.
D. sanuriensis Bacescu, 1993—Bali, Indonesia.
D. spinata Murano 1990—Port Essington, N.T., Australia.

Doxomysis zimmeri Colosi, 1920 has been omitted from the above list, as it was considered to be a synonym of *D. quadrispinosa* (Illig 1906) when reviewed by W. Tattersall (1922, 1951) and Pillai (1973). They argued that its description lacked characters distinguishing it from the latter species. Sri Lanka, the type locality of *D. zimmeri,* is also within the known distribution range of *D. quadrispinosa.*

Key to the Species of *Doxomysis*

1a. Integument of carapace and abdomen smooth 2
b. Integument of carapace and abdomen spiny 12
2a. Median dorsal tubercle on posterior surface of carapace . . . . *D. johnsoni*
b. Dorsal surface of carapace lacking projections 3
3a. Telson with 1 stout and 2 small terminal spines on each apical lobe, cleft wide and shallow . . . . *D. anomala*
b. Telson with 3–8 stout terminal spines on each apical lobe, cleft narrow and deep 4
4a. Row of spines on lateral margin of telson with large gap, at least half as long as telson 5
b. Spine row on lateral margin of telson without gap, or with small gap, 1 quarter telson length, or less 6
5a. Telson with 6 spines on each lateral margin, a large gap between the 3 proximal spines and the 3 distal spines . . . . *D. murariui*
b. Telson with set of 8–9 small, evenly spaced spines on distal extremity of each lateral margin . . . . *D. hanseni*
6a. Telson with 9 spines on each lateral margin, a gap between the 4 proximal and the 5 distal spines, endopod of uropod with row of 29 spines . . . . *D. sanuriensis*
b. At least 12 spines on each lateral margin of telson, 32–50 spines on endopod of uropod 7
7a. Telson with rounded apical lobes, about 8 broad, spatulate terminal spines on each lobe . . . . *D. brucei*
b. Telson with tapered apical lobes, 3–4 long, pointed terminal spines on each lobe 8
8a. Spines on distal margin of maxillary palp with secondary spinules 9
b. Spines on distal margin of maxillary palp without secondary spinules . . . 10
9a. Spines on maxillary palp expanded towards tip, small secondary spinules located distally on expanded part, 48–50 spines on endopod of uropod . . . . *D. rinkaiensis*
b. Spines on maxillary palp taper to a point, long slender secondary spinules more proximally located, fewer than 40 spines on endopod of uropod . . . . *D. spinata*
10a. Lateral and terminal spines total about 17 on each side of telson, maxillary palp with 9 blunt spines . . . *D. littoralis*
b. Lateral and terminal spines total 25–29 on each side of telson, maxillary palp with 10 or 12 sharp spines . . . 11
11a. Maxillary palp with 10 spines, about 47 spines on endopod of uropod . . . . *D. australiensis*
b. Maxillary palp with 12 spines, about 32 spines on endopod of uropod . . . . *D. proxima*
12a. Gap in lateral spine row of telson, or spines confined to distal part of margin 13

b. Lateral spine row of telson without gap 14
13a. Eyes large, rounded, diameter approximately twice that of eyestalk .... *D. quadrispinosa*
b. Eyes small, flattened, diameter similar to that of eyestalk .... *D. microps*
14a. Antennal scale reaches end of antennular peduncle, maxillary palp with 9 simple spines .... *D. longiura*
b. Antennal scale extends beyond antennular peduncle by 1 third of its length, maxillary palp with 7–8 spines bearing both long slender and short thornlike secondary spinules ... *D. acanthina*

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Literature Cited

Bacescu, M. 1975. Contributions to the knowledge of the mysids (Crustacea) from the Tanzanian waters.—Science Journal, University of Dar es Salaam 1(2):39–61.

———. 1993. New contributions to the Mysidacea (Crustacea, Peracarida) of Indonesia: *Doxomysis genus.*—Travaux du Muséum d'Histoire naturelle Grigore Antipa 33:285–290.

———, & A. Udrescu. 1982. New contribution to the knowledge of the Mysidacea from Australia.—Travaux du Muséum d'Histoire naturelle Grigore Antipa 24:79–96.

———, & Vasilescu. 1973. New benthic mysids from the littoral waters of Kenya: *Mysidopsis kenyana* n.sp. and *Nouvelia natalensis mombasae* n.g., n.sp.—Revue Roumaine de Biologie, Serie de Zoology 18:249–256.

Colosi, G. 1920. Raccolte planctoniche fatte dalla R. Nave "Liguria" del 1903–1905, Crostacei—4—Misidacei 2(9):229–260.

Fenton, G. E. 1991. Three new species of *Tenagomysis* from the coastal waters of south-eastern Tasmania (Crustacea: Mysidacea: Mysinae: Leptomysini).—Memoirs of the Museum of Victoria 52:325–335.

Fukuoka, K., & M. Murano. 1994. A new species of the Genus *Australomysis* (Crustacea, Mysidacea) from Japan.—Proceedings of the Japanese Society of Systematic Zoology 51:18–24.

Hansen, H. S. 1912. Report on the scientific results of the Expedition to the tropical Pacific—Steamer "Albatross" The Schizopoda.—Memoirs of the Museum of Comparative Zoology Harvard 35(4):173–296.

Illig, G. 1906. Bericht über die neuen Schizopodengattungen und Arten der Deutchen Tiefsee-Expedition 1898–1899, 1, Mysiden.—Zoologischer Anzeiger 30:194–211.

Murano, M. 1990. Three new leptomysids (Mysidacea) from northern Australia.—Crustaceana 59(3):231–244.

Nouvel, H. 1966. Mysidaces recoltes par S. Frontier a Nosy-be 3. *Hyperiimysis madagascariensis* n. gen., n.sp., Leptomysini.—Bulletin de la Société d'Histoire Naturelle de Toulouse 102(2–3):493–505.

———. 1973. *Pseudoxomysis caudaensis* n. gen., n. sp., crustace, mysidace (Leptomysini) de la Mer de Chine meridionale.—Bulletin de la Société d'Histoire Naturelle de Toulouse 109:131–141.

Panampunnayil, S. U. 1986. New mysids from the South Australian coastal waters: *Paranchialina secunda* sp. nov.; *Leptomysis longisquama* sp.nov. and *Doxomysis johnsoni* sp.nov.—Journal of Plankton Research 8(6):1183–1195.

Pillai, N. K. 1963. On a new mysid from the inshore waters of the Kerala coast.—Journal of the Marine Biological Association of India 5:258–262.

———. 1973. Mysidacea of the Indian Ocean. Papers on the Zooplankton Collections of the IIOE.—Handbook to the International Zooplankton Collections 4:1–125.

Tattersall, O. S. 1957. Report on a small collection of mysidacea from the Sierra Leone estuary together with a survey of the genus *Rhopalopthalmus* Illig and a description of a new species of *Tenagomysis* from Lagos, Nigeria.—Proceedings of the Zoological Society of London 129:181–128.

Tattersall, W. M. 1907. Preliminary diagnosis of six new Mysidae from the west coast of Ireland.—Annals and Magazine of Natural History 7(19): 106–118.

———. 1922. Indian Mysidacea.—Records of the Indian Museum 24:445–504.

———. 1927. Australian opossum shrimps (Mysidacea).—Records of the South Australian Museum 3(3)235–257.

———. 1936. Mysidacea and Euphausiacea.—Scientific Reports of the Great Barrier Reef Expedition 5:143–176.

———. 1940. Report on a small collection of Mysidacea from the coastal waters of New South Wales.—Records of the Australian Museum 20: 327–340.

———. 1951. A review of the Mysidacea of the United States National Musem.—Bulletin of the United States National Museum 201:1–292.

Valbonesi, A., & M. Murano. 1980. Mysidae of shallow water in Tanabe Bay.—Publications of the Seto Marine Biological Laboratory 25(1/4): 211–226.

Zimmer, C. 1916. Beitrage zur Kenntnis der Meeresfauna Westafricas. Crustacea, 4: Cumacea und Schizopoden.—Hambourgh 2(1):55–66.

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Acanthomysis bowmani, a new species, and *A. aspera* Ii, Mysidacea newly reported from the Sacramento-San Joaquin Estuary, California (Crustacea: Mysidae)

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Abstract.—*Acanthomysis bowmani,* a new species is described and named. Geographical range is extended for *A. aspera* Ii (1964) to include the Sacramento-San Joaquin Estuary. Evidence indicates that both species were recently introduced into this estuarine system.

W. M. Tattersall (1932) reported five species of Mysidacea in San Francisco and San Pablo Bays. Distribution of one of these species, *Neomysis mercedis* Holmes, 1897 extends upstream into the Sacramento-San Joaquin Delta. *Neomysis mercedis,* an epibenthic species, shares this Delta with a recently described species, *Deltamysis holmquistae* Bowman & Orsi (1992). This paper discusses two species of *Acanthomysis* that have begun to appear in plankton samples collected since 1992, *A. bowmani,* a new species, first caught 8 July 1993, and *A. aspera* Ii (1964), first caught 5 August 1992.

Methods.—All samples were collected with a tow-net mounted in a frame constructed of steel pipe and towed for 10 minutes from the bottom to the surface in several steps depending on water depth. The mouth of the net was 0.3 m in diameter, bag length equaled 1.5 m, and mesh size was 505 μm.

Acanthomysis bowmani, new species
Figs. 2–4

Material examined.—All specimens from Suisun Bay, California (Fig. 1), J. J. Orsi, 11 Apr 1996. Holotype male, 11.6 mm total length (USNM 282745); Allotype, female, 12.5 mm (USNM 282746); Paratypes (USNM 282747) 7 males and 1 dissected male (7.7–11.8 mm), 4 females (10.5–11.8 mm), and 12 juveniles (3.5–8.1 mm).

Description.—Body slender, elongate. Carapace (Fig. 2A, B) with anterior margin produced into sharp triangular rostrum ventrally supported with distinct keel and 2 struts at base, posterior margin emarginate exposing somites 7 and 8, anterio- and posteriolateral lobes rounded. Narrow, nearly inconspicuous furrow encircles carapace about ⅓ the distance posterior from rostrum. Eyes prominent, stalked; short pigmented stripe near base of stalk dorsomedially; cornea large, kidney-shaped, dorsal margin scalloped, conspicuous ocular tooth on anterosuperior edge (Fig. 2A, B).

Antennular peduncle (Fig. 2C) stout, 3-segmented; combined length of segments 1 and 2 equal length of segment 3; segment 1 with group of 4 pinnate setae distolaterally; segments 2 and 3 without conspicuous setae; ventrolateral male lobe on segment 3 conspicuous, heavily setose with fine simple setae.

Antennal peduncle (Fig. 3A) 3-segmented; segments 1 and 3 subequal in length; segment 2 about 1.5 times longer than segment 1 or 3, with 3 stout naked and 1 pinnate setae distolaterally; segment 3 with 4

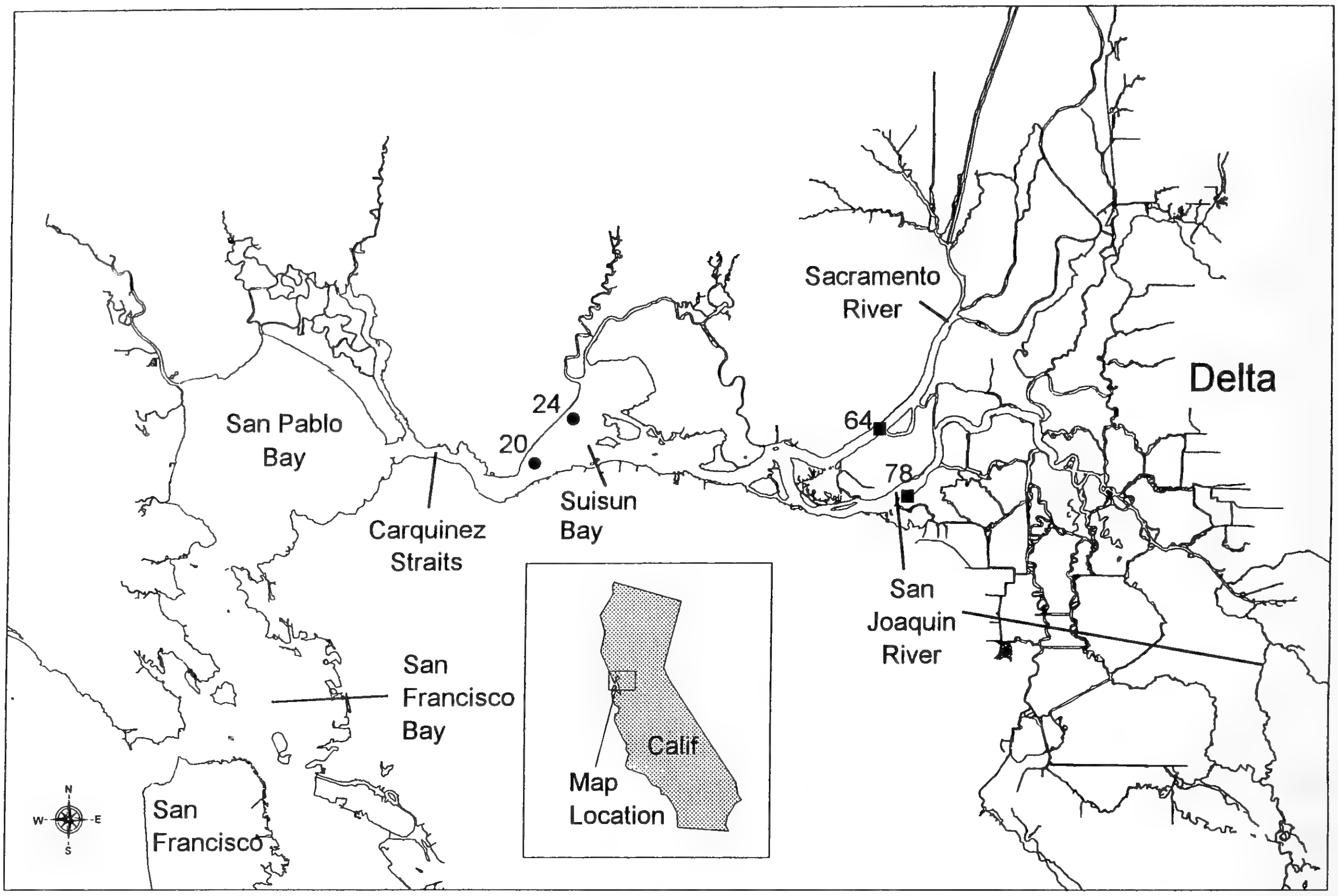

Fig. 1. Sacramento-San Joaquin Esturary with sampling stations of the California Department of Fish and Game. Stations 20 and 24 in Suisun Bay are where specimens of *Acanthomysis aspera* were first collected and stations 64 and 78 are where *A. bowmani* was first obtained.

stout naked and 2 pinnate setae distolaterally, 2 small pinnate setae ventrally. Antennal scale blade-like, setose all around, about 1.8 times longer than peduncle, lateral margin nearly straight, medial margin slighty convex near base, 8.4 times as long as wide near base, rounded articulated tip 0.05 times scale length.

Right and left mandibles (Fig. 3B) with bicuspid incisors, left lacinia mobilis with 3 robust cusps, right monocuspid; each mandible with 3 robust setose accessory blades; left molar with medial surface slightly papillose, base heavily papillose and armed with clump of short, stout setae; right molar basal surface armed with row of strong, tooth-like projections and clump of short, stout setae. Mandibular palp (Fig. 3C) 3-segmented, segment 1, inconspicuous; second proximal segment robust, triangular in cross section, 1.5 times longer than distal segment, lateral margin with stout, naked setae, medial margin with 4 widely separated, stout setae; distal segment lateral margin armed with spines furnished with lateral rows of spinules, medial margin with 6 widely spaced naked setae, terminating in single robust, naked spine.

Maxillule (Fig. 3D) typical of genus, outer lobe with hump-like process on anterior margin, posterior margin naked. Maxilla (Fig. 3E) exopod blade-like, 4 times as long as broad at greatest width; endopod 2-segmented, proximal segment with rectangular patch of minute papillae near lateral margin, distal segment margins setose. Labrum (Fig. 3F) and paragnaths (Fig. 3G) typical of genus.

Endopod of first (Fig. 3H) and second (Fig. 3I) thoracic limbs typical of genus. Endopod of third thoracic limb (Fig. 4A) with ischium 1.8 times longer than merus, ischium as long as carpo-propodus, carpopropodus 9-segmented, dactylus small

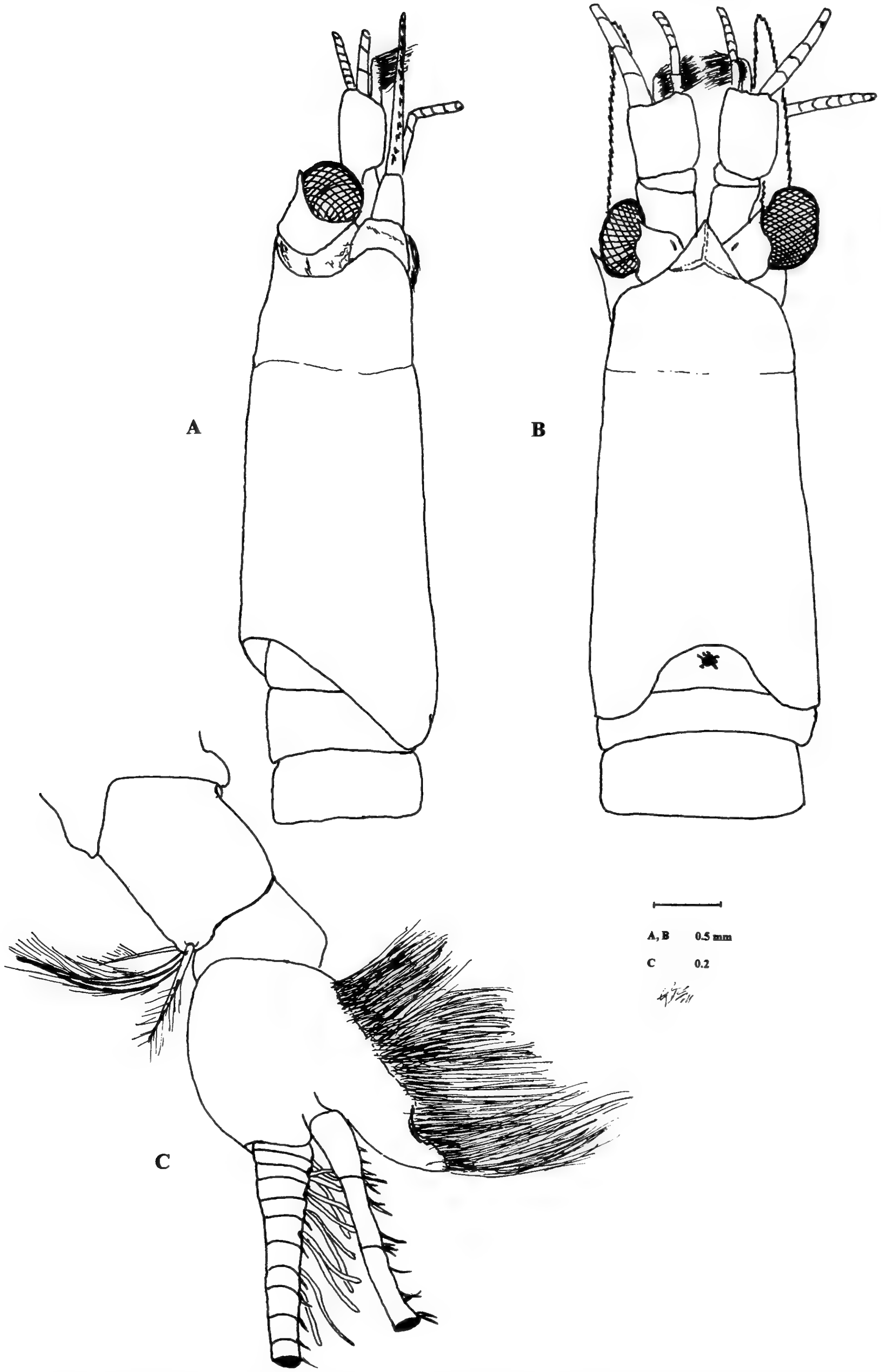

Fig. 2. *Acanthomysis bowmani,* new species: A. Anterior profile; B. Dorsal view; C. Antennule peduncle. Male, 11.6 mm.

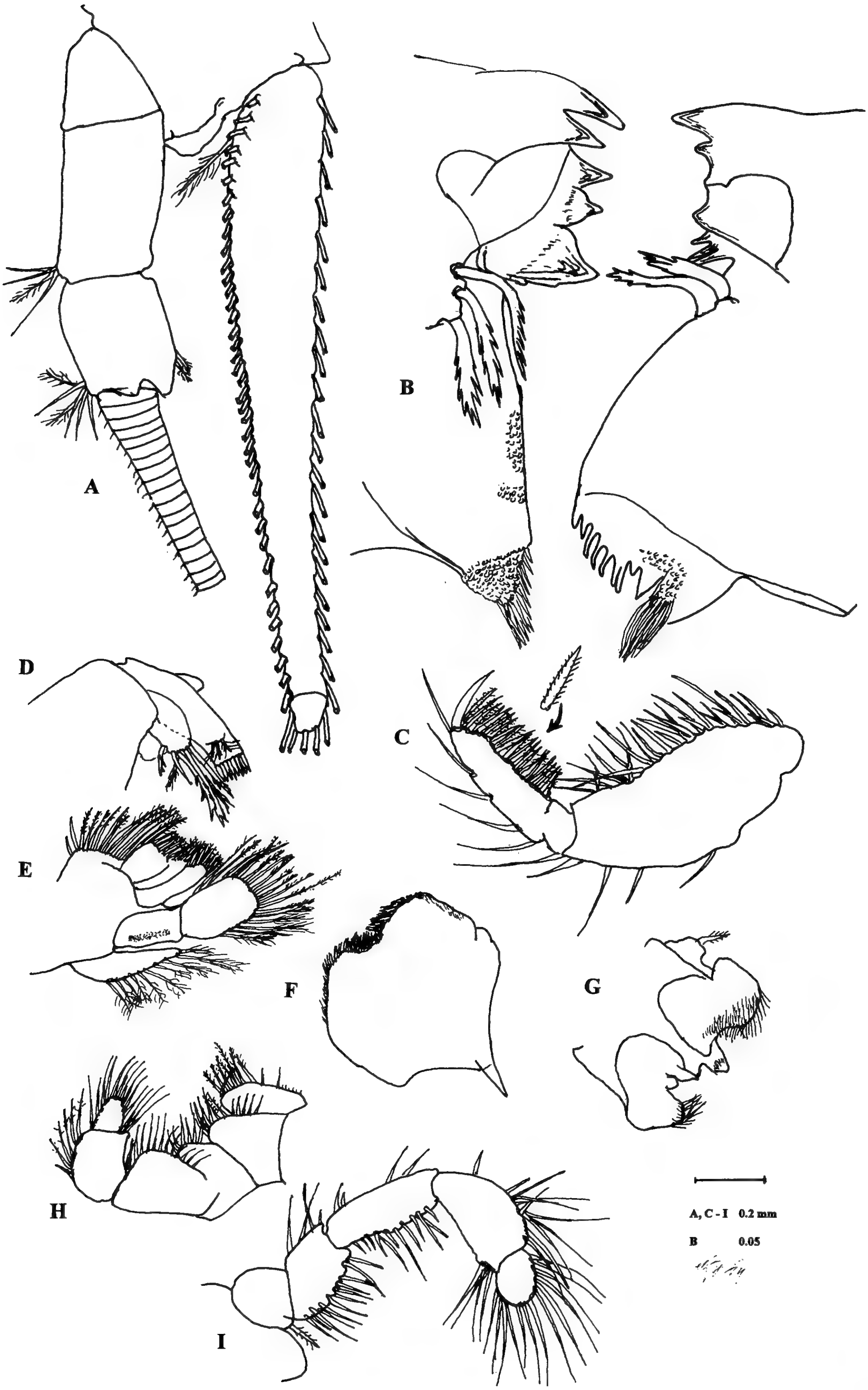

Fig. 3. *Acanthomysis bowmani,* new species: A. Antenna and antennal scale; B. Right and left mandibles; C. Mandibular palp; D. Maxillule; E. Maxilla; F. Labrum; G. Paragnaths; H. Endopod of 1st thoracic limb; I. Endopod of 2nd thoracic limb. Male, 11.6 mm.

about 0.2 times length of strong terminal claw; exopod (Fig. 4B) about 2/3 length of endopod, 9-segmented. Structure of endopods and exopods of thoracic limbs 4 to 8 similar to 3.

Penis (Fig. 4C) robust, length about 1.7 times width, each with pair of terminal lobes containing an aggregate of naked setae, posterior margin with 7 naked setae around edge of an articulation and small plumose setae near base, anterior margin with 1 naked and 3 pinnate setae.

Male pleopods 1 to 3 and 5 rudimentary, unjointed; pleopod 1 smallest (Fig. 4D) and 5 longest (Fig. 4F); pleopod 4 biramous (Fig. 4E), endopod unjointed, exopod long, 2-segmented, segment 1 about 1.5 times longer than endopod and 1.2 times longer than segment 2 which terminates in 2 long, robust, spinulose nails, a long, robust seta and 1 minute spine.

Uropod (Fig. 4G) exopod blade-like, lateral margin slightly concave, medial margin slightly convex, about 1.4 times longer than endopod; endopod margins tapering distally, 2 distally directed spines along medial margin near statocyst ventrally.

Telson (Fig. 4H) linguiform, 2.4 times longer than width at base, each lateral margin with 3–4 spines near base, a space and 18–19 spines of equal length along distal 2/3, ultimate marginal spines 3.3 times longer than other marginal spines and as long as pair of terminal spines.

Remarks.—Close resemblance exists between *A. bowmani,* n. sp., and two species reported from the western Pacific Ocean by Ii (1964), *A. sinensis* and *A. longirostris* (Table 1). In addition to two subtle character variations, e.g., arrangement of the long spines on or near the apex of the telson and the difference in the number of distal telsonal marginal spines, the near equal length of the two segments that comprise the exopod of male fourth pleopod and a longer antennal scale separates *A. bowmani* from the other two species (Table 1). Presently *A. sinensis* is known only from the East China Sea off the mouth of the Yangtze River, while *A. longirostris* has a more cosmopolitan distribution in oriental waters. It has been reported from Ariake Bay, Japan, Port Kusan and Haejun Bay, Korea (Ii 1964, Jo & Ma 1996), and waters off the North China Coast (Shen et al. 1989).

To provide an additional taxonomic character and to ease total length measurements, the relationship between carapace length of *A. bowmani* (measured along the dorsal midline from rostral tip to posterior margin) and its total length (measured from rostral tip to posterior margin of telson) was determined using a least square linear regression. This relationship is described by the equation, total length = 3.69 (carapace length) − 0.07; with a sample size of 28 specimens, the correlation coefficient equaled 0.98.

Ecological notes.—*Acanthomysis bowmani* is most abundant in June and July in Suisun Bay (Fig. 1) at about 2.0‰S. Water temperature at which type specimens were collected was 16° C, specific conductivity equaled 340 μS/cm, <0.5‰S.

Etymology.—Named in honor of the late Dr. Thomas E. Bowman, curator of Crustacea U.S. National Museum of Natural History and our close colleague, who contributed greatly to the systematic knowledge of the Mysidacea.

Acanthomysis aspera Ii, 1964

Acanthomysis aspera, reported from coastal waters around Japan (Mauchline & Murano 1977), China (Shen et al. 1989) and Korea (Jo & Ma 1996) has begun to appear in collections from the western end of Suisun Bay, downstream of *A. bowmani* sampling locations (Fig. 1). This is the first record of the occurrence of this species in the eastern Pacific. Dr. Tom Bowman verified the identification of the specimens.

Synanthropic introductions.—Historical and biogeographic evidences strongly suggest that *A. bowmani* and *A. aspera* were introduced to the Sacramento-San Joaquin Estuary with the flushing of ship ballast wa-

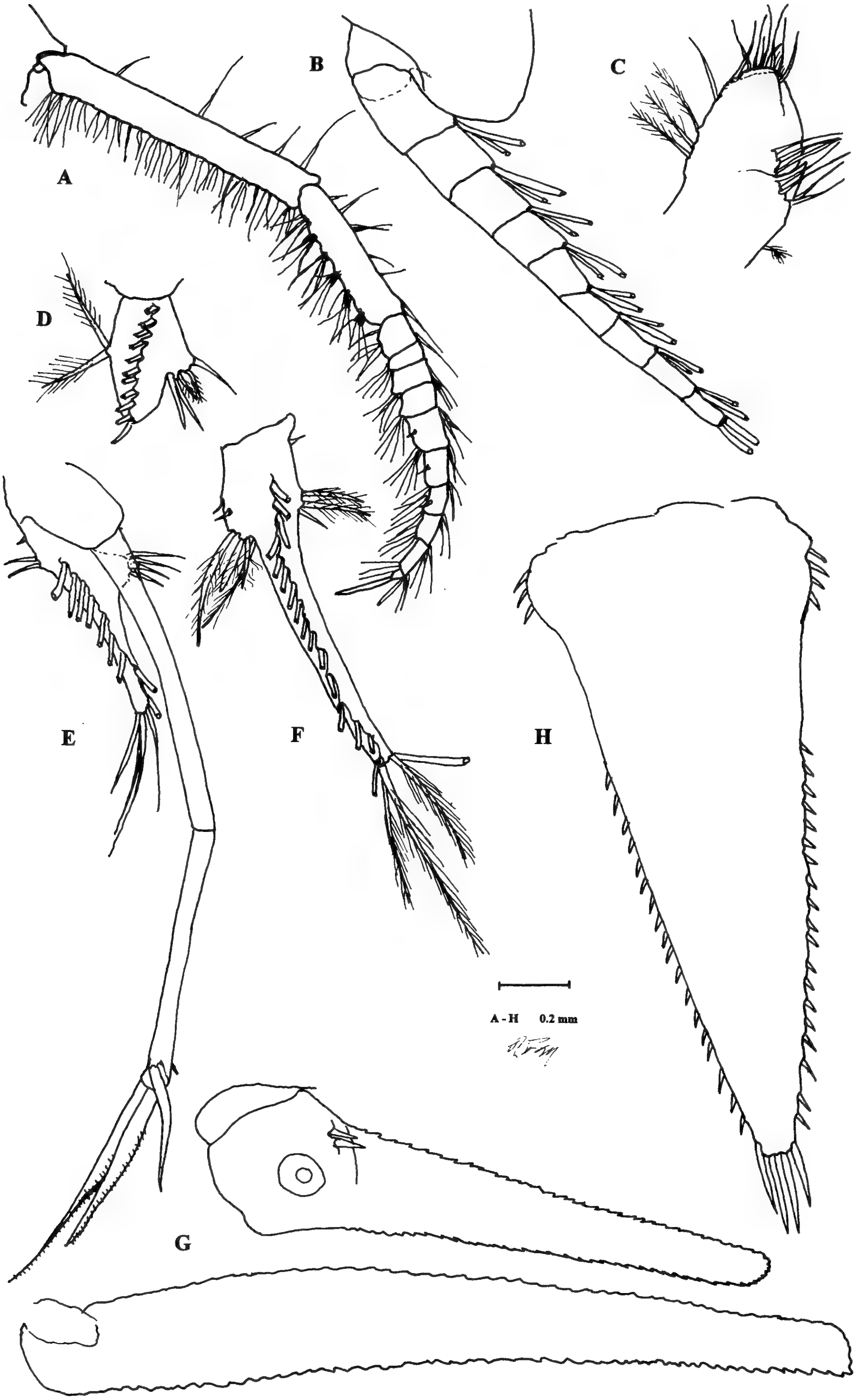

Fig. 4. *Acanthomysis bowmani,* new species, A. Endopod of 3rd thoracic limb; B. Exopod of 3rd thoracic limb; C. Penis; D. Pleopod 1; E. Pleopod 4; F. Pleopod 5; G. Uropod endopod (upper), exopod (lower); H. Telson. Male, 11.6 mm.

Table 1.—Comparison of diagnostic characteristics of *Acanthomysis bowmani,* n. sp., taken from the waters of the Sacramento-San Joaquin Estuary, California, with those noted by Ii (1964) for *A. sinensis,* and *A. longirostris* from waters off the western Pacific Ocean.

Characters	*A. bowmani*	*A. sinensis*	*A. longirostris*
Rostrum	Reaches middle of antennular peduncle first segment	Reaches middle of antennular peduncle first segment	Long, reaches second joint of antennular peduncle
Eye stalk	Proximal half without spinules	Proximal half without spinules	Proximal half with spinules
Antennal scale	8.4× as long as broad	5.0× as long as broad	7.0× as long as broad
Carpopropodus	9 segments	10 segments	9–11 segments
4th pleopod of male	2-segmented, 1st 1.2× longer than 2nd	2-segmented, 1st 30× longer than 2nd	2-segmented, 1st 22× longer than 2nd
Uropod	Endopod with 2 spines near statocyst	Endopod with 2 spines near statocyst	Endopod with 2–3 spines near statocyst
Telson	3–4 basal marginal spines, 18–19 distal marginal spines	4 basal marginal spines, 13–14 distal marginal spines	3 basal marginal spines, 20 distal marginal spines
Apex of telson	Narrowly truncated, with 2 terminal spines and 2 long ultimate marginal spines	Broadly truncated, with 4 terminal spines	Narrowly truncated with 2 terminal spines
Distribution	Coastal	Offshore	Coastal

ter (Carlton 1979). *Acanthomysis aspera* has been reported from coastal regions of Japan (Ii 1964), China (Shen et al. 1989) and Korea (Jo & Ma 1996), while morphological characteristics of *A. bowmani* show very close affinity with congeneric species that also have only been reported from the western Pacific. Although the Sacramento-San Joaquin Estuary has been continuously and systematically surveyed for the past 25 years, neither species occurred in any samples taken at the same collecting sites and at similar times prior to 5 August 1992.

Other crustaceans foreign to the Sacramento-San Joaquin Estuary have been reported. Ferrari & Orsi (1984) found a copepod, *Limnoithona sinensis* Burckhardt, previously reported from the Yangtze River delta and described a new species, *Oithona davisae,* which is also common in the Western Pacific. Likewise, Bowman and Orsi (1992) suggest that *Deltamysis holmquistae* may also have been introduced.

A possible site of introduction of the *Acanthomysis* spp. is the Port of Oakland, since it receives a considerable amount of shipping from the Far East. Research on these exotic species is currently underway because they may have a detrimental affect on the endemic Mysidacea.

Acknowledgments

We would like to thank all those from the California Department of Fish and Game that assisted in the collection and processing of the field material. Sally Skelton first detected *A. bowmani* in the samples being processed from Suisun Bay. The Interagency Ecological Program provided support for the sampling work.

Literature Cited

Bowman, T. E., & J. J. Orsi. 1992. *Deltamysis holmquistae,* a new genus and species of Mysidacea from the Sacramento-San Joaquin Estuary of California (Mysidae: Mysinae: Heteromysini).—Proceedings of the Biological Society of Washington 105:733–742.

Carlton, J. 1979. Introduced invertebrates of San Francisco Bay. Pp. 427–444 *in* T. Conomos, ed., San Francisco Bay: the urbanized estuary. Pacific Division, American Association for the

Advancement of Science, San Francisco, California, 493 pp.

Ferrari, F. D., & J. Orsi. 1984. *Oithona davisae,* new species, and *Limnoithona sinensis* (Burckhardt, 1912) (Copepoda: Oithonidae) from the Sacramento-San Joaquin Estuary, California.—Journal of Crustacean Biology, 4:106–126.

Ii, N. 1964. Fauna Japonica, Mysidacea (Crustacea). Biogeographical Society of Japan, Tokyo, 610 pp.

Jo, S.-G., & C.-W. Ma. 1996. Mysidacea (Crustacea from the West Coast of Korea.—Journal of the Korean Fishery Society, 29:805–827.

Mauchline, J., & M. Murano. 1977. World list of the Mysidacea, Crustacea.—Journal of the Tokyo University of Fisheries 64:39–88.

Shen, C. J., J. Y. Liu, & W. Shaowu. 1989. Mysidacea in waters off the North China Coast.—Studia Marina Sinica 30:189–227.

Tattersall, W. M. 1932. Contribution to a knowledge of the Mysidacea of California. II: the Mysidacea collected during the survey of San Francisco Bay by the U.S.S. *Albatross* in 1914.—University of California Publications in Zoology 37:315–347.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Lamellibrachia satsuma, a new species of vestimentiferan worms (Annelida: Pogonophora) from a shallow hydrothermal vent in Kagoshima Bay, Japan

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Abstract.—Vestimentiferan tube worms were found forming clumps in 82–110 m in Kagoshima Bay, southern Japan, during a series of surveys exploring the biological community associated with shallow hydrothermal vents in 1993. The newly found tube worm is described here as *Lamellibrachia satsuma,* a new species. It differs from other congeneric species in having a short vestimentum, a short obturaculum, up to 4 pairs of lamellar sheaths and up to 19 pairs of branchial lamellar sheaths. About 20 living worms were maintained in a laboratory for more than 400 days. Release of eggs from the opening of the tube was observed at the beginning of the maintenance experiment. Trochophore-like larvae were also examined and photographed.

Kagoshima Bay is characterized by two gigantic calderas, the Aira and the Ata, which form the northern and the southern areas of the bay, respectively. The northern bay-head area is about 18 km long and 20 km wide and is separated from the southern area by an active volcano, Mt. Sakurajima, but connected by a shallow and narrow strait (40 m deep and 2 km wide). The eruption forming the Aira Caldera that is the present bay-head area is thought to have occurred about 22,000 years ago (Aramaki & Ui 1966). In the east part of the head area, two hydrothermal vent sites at depths of about 80 m and 200 m are recognized by the appearance of gas bubbles that reach the surface and are called "Tagiri" by local fishermen (Oki & Hayasaka 1978). The word "Tagiri" originates from a Japanese word meaning 'boil and bubble'. Although "Tagiri" sites are quite shallow when compared with other hydrothermal vents, the chemical characteristics of these sites are believed to be the same or close to those of hydrothermal vents where associated biological communities are found. In 1993, during a series of surveys exploring the community associated with submarine fumaroles in Kagoshima Bay, we discovered a world of vestimentiferan worms forming clumps at depths of 82–110 m and collected a batch of living worms by means of a small dredge attached to a deep towed camera system (Hashimoto et al. 1993).

The first vestimentiferan species, *Lamellibrachia barhami,* was described as a unique pogonophoran worm from the Northeast Pacific at a depth of 1125 m (Webb 1969). In a study of *L. luymesi* collected at 500 m depth off Guyana, the class Vestimentifera was placed in the phylum Annelida (van der Land & Nørrevang 1975). Jones (1985) proposed, however, a new phylum, Vestimentifera, for the vestimentiferan tube worms in working on above species and various other species from deep-sea vents and seeps. Mañe-Garzón & Montero (1985) also proposed a separate phylum under the name Mesoneurophora with the description of a new species of *Lamellibrachia.* Describing two new vestimentiferan species, Southward (1991) reclassified the vestimentiferan worms as a subclass of the class Pogonophora within the phylum Annelida. The affiliation of vestimentiferans to Annelida is also suggested by the hemoglobin structure (Suzuki et al. 1989) and by the amino acid sequence of Elongation Factor-1α (Kojima et al. 1993), the analysis of 28S ribosomal DNA demonstrated that the Vestimentifera form a monophyletic group to the exclusion of the polychaete *Melinna* and the periviate pogonophore *Siboglinum* used for comparison (Williams et al. 1993). Rouse & Fauchald (1995) recently proposed that the name Articulata be used to include the Vestimentifera and Pogonophora as well as the Clitelata, the Polychaeta, and the Euarthropoda and Onychophora. In this study, we follow the classification proposed by Southward (1991) and place the vestimentiferan worms in the phylum Annelida.

To date, eight genera and 13 species of vestimentiferans have been described from hydrothermal vents, cold seeps, and other deep-sea bottoms (Jones 1985, Southward 1991, Southward & Galkin 1997). Two of them were amalgamated into a single species on the basis of careful examination of morphology and allozymes (Southward et al. 1995). Vestimentiferans are known from depths of 300–3270 m, in the eastern Pacific and the Gulf of Mexico (Jones 1985), the Lau Basin (Southward 1991), the Manus Basin (Southward & Galkin 1997), off Guyana (van der Land & Nørrevang 1975), off Uruguay (Mañe-Garzón & Montero 1986), and from the eastern Atlantic (Dando et al. 1992). Around Japan, several types of vestimentiferans have been also observed by manned or unmanned deep-sea submersibles and captured from deep-sea chemosynthetic communities in Sagami Bay (Hashimoto et al. 1989) and the mid-Okinawa Trough (Hashimoto et al. 1995) between depths of 690–1370 m in tectonically active zones. The vestimentiferans in Kagoshima Bay represent the shallowest occurrence of the group in the world. Recently, partial nucleotide sequences of mitochondrial DNA were analyzed from several local populations of Japanese vestimentiferans (Kojima et al. 1995). This analysis suggested the presence of more than one genetically distinguishable populations of *Lamellibrachia* species-complex around Japan. The authors also suggested that the populations differed in their vertical distribution. In this study, a shallow water species from Kagoshima Bay is described.

Material and Methods

More than a hundred vestimentiferan specimens were collected by a small dredge 40 cm wide × 10 cm high × 50 cm deep, attached about 1 m beneath the bottom of a deep towed color television camera system operated by R/V *Kaiyo,* in the northern semi-closed area of Kagoshima Bay in February, 1993. Other additional specimens were collected by an unmanned deep-sea research vehicle *Dolphin 3K* seven months later, at the same site.

Specimens for taxonomic study were fixed in 10% formalin and transferred to 70% ethanol. Some dozens of worms were dissected from their tubes on the vessel and the remainder were kept intact. Specimens for chemical analysis were frozen at −80°C, a part of which were used in this study to calculate the dry/wet weight ratio of the soft body. Living worms were washed very carefully by using a brush to eliminate sediments and to examine newly settled larvae that might attach on the adult tubes. Every ten to twenty cleaned specimens were transferred into a 10-liter bottle and kept in the refrigerator of the research vessel at about 5°C. The living animals were transported to the laboratory of the Faculty of Fisheries at Kagoshima University within a week after the sampling. The worms were maintained in a glass tank 30 cm wide × 18 cm long × 24 cm deep filled with 10 l of filtered seawater (Millipore 1.2 μm filter). The tank was maintained at 16°C in an incubator because the temperature of the bottom seawater at the collecting site is constant throughout the year at about this value. The water was changed for every 7–14 days to maintain a salinity of about 34 parts per thousand and a pH value of about 8.2, even though this last value altered by the addition of sodium sulfide. The worms were provided on average with 1.6 g of sodium sulfide ($Na_2S{\cdot}9H_2O$) as a source of hydrogen sulfide twice a day. The maximum concentration of hydrogen sulfide was calculated to be about 0.7 mM per 1 of sea water (not analyzed). The concentration in culture was, therefore, about 35 times higher than the concentration of hydrogen sulfide in the field, where only 0.02 mM per 1 was recorded.

The types are deposited in the National Science Museum, Tokyo (NSMT), Japan Marine Science and Technology Center (JAMSTEC), the National Museum of Natural History, Smithsonian Institution (USNM), the Los Angeles County Museum of Natural History (LACM-AHF), the Museum National d'Histoire Naturelle de Paris (MNHN), and the Australian Museum, Sydney (AM).

Family Lamellibrachiidae Webb, 1969
Genus *Lamellibrachia* Webb, 1969
Lamellibrachia satsuma, new species
Figs. 1–5

Material examined.—Holotype (NSMT-Pc-H3), 15 paratypes (5: NSMT-Pc-P4, P5, P6, P7, P8; 10: USNM 175102–175111), Kagoshima Bay, Deep Tow Camera Observation DT-13, 6 Feb 1993, 31°39.55′N, 130°48.07′E, 98 m; 13 paratypes (5: MNHN UE798–UE802, 8: JAMSTEC Ves-0270-77-93), DT-15, same site, 6 Feb 1993, 102 m; 6 paratypes (3: MNHN UE803–UE805, 3: JAMSTEC Ves-0278-80-93), *Dolphin 3K* Dive 154, 12 Sep 1993, 31°39.83′N, 130°48.97′E, 101 m; 40 paratypes (10: USNM 175092–175101; 10: LACM-AHF POLY 1873–POLY 1882; 10: AM W23599–W235608; 10: JAMSTEC Ves-0281-90-93), *Dolphin 3K* Dive 157, 12 Sep 1993, 31°39.80′N, 130°48.05′E, 122 m; 7 paratypes (JAMSTEC Ves-0291-97-93), *Dolphin 3K* Dive 164, 16 Sep 1993, 31°39.70′N, 130°48.02′E, 110 m.

Measurements.—Tube length 60–1000 mm ($\bar{X}$ 317 mm, $n = 71$); opening width of top collar 2.5–8.7 mm ($\bar{X}$ 5.6 mm, $n = 78$), bottom width of top collar 1.7–7.2 mm ($\bar{X}$ 3.9 mm, $n = 81$), width of basal end 0.5–2.4 mm ($\bar{X}$ 1.1 mm, $n = 53$); tube wet weight 0.18–4.16 g ($\bar{X}$ 1.35 g, $n = 53$). Body length 45–443 mm ($\bar{X}$ 219 mm, $n = 53$); body wet weight 0.08–1.57 g ($\bar{X}$ 0.68 g, $n = 53$) (dry/wet weight ratio 0.06–0.28, $\bar{X}$ 0.23, $n = 37$, measured differently using materials for chemical analysis). Obturacular length 1.8–9.8 mm ($\bar{X}$ 5.2 mm, $n = 64$); obturacular width 1.0–5.6 mm ($\bar{X}$ 4.1 mm, $n = 53$). Vestimental length 7.2–24.0 mm ($\bar{X}$ 17.2 mm, $n = 64$). Vestimental length/Obturacular length ratio 2.1–8.3 ($\bar{X}$ 3.5, $n = 64$); Vestimental length/obturacular width ratio 2.3–9.7 ($\bar{X}$ 4.5, $n = 53$). Obturacular lamellar sheaths 0–4 pairs ($\bar{X}$ 2.77, $n = 57$). Sex ratio 1.39:1 (32 males: 23 females).

Description.—Anterior face of obturaculum of adult bare, lacking secreted structures (Figs. 1a, b, 2a); with up to 19 pairs of branchial lamellae (Figs. 1a, b, 2a, b); each lamella formed by a single series of fused branchial filaments with pinnules; branchial lamellae hidden by up to four pairs of peripheral lamellar sheaths (Figs. 1a, b, 2a, b); sheaths composed of fused fine filaments, with only extreme distal tips of filaments free (Figs. 1a, b, 2a, b); obturaculum lenticular in transverse section (Fig. 2b), lacking dorsal groove, with ventral ridge, distally; with single, medial excretory pore opening in groove at base of obturaculum. Anterior margin of vestimentum forming short sheath or collar extending around base of obturaculum; central dorsal surface of vestimentum of male (holotype) with paired ciliated grooves, diverging at anterior ends (Fig. 1a); postero-ventral margin of vestimentum broadly incised (Fig. 1a, b); ventral surface with numerous small papillae topped by cuticular plaques 35–63

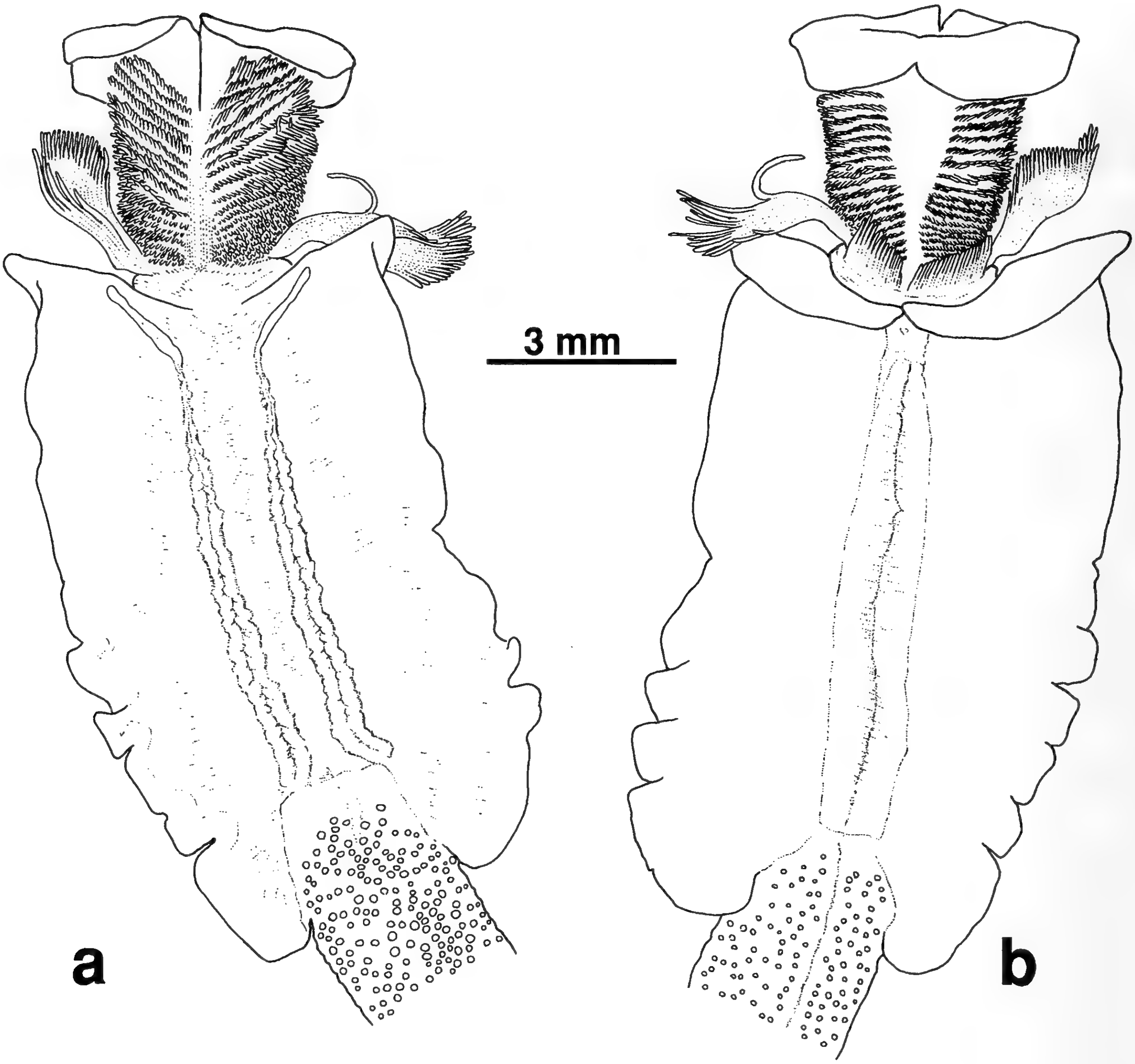

Fig. 1. *Lamellibrachia satsuma,* new species.—Holotype. a, Anterior end, in dorsal view; b, Same, in ventral view. Body fixed after removed from the tube. Scale = 3 mm.

µm in diameter. Trophosome very long, with numerous small papillae topped by cuticular plaques 51–82 µm in diameter. Opisthosome of selected specimen with 33 segments (Fig. 3a–c), anterior 27 with a single row of setae (Fig. 3b, d–f); most setae with two groups of denticles, anterior group bearing 6–9 denticles, posterior group with 10–15 denticles in 3–4 rows (Fig. 3e–f). Tube with obvious growth collars and irregularly placed light and dark bands (Figs. 2a, 4). Anterior parts of tubes more straight than posterior in large specimens; posterior parts coiled in general. Tubes tangled together in tight clusters, making large hemispherical clumps on thick sediments; clumps sometimes more than 10 m in diameter.

Etymology.—The specific epithet *satsuma,* a noun in apposition, refers to the old province on Kyushu island. Japanese name of the species, "satsuma-haorimushi" is also composed of the provincial name and the group name of vestimentiferan worms.

Remarks.—Among the five described species of the genus *Lamellibrachia, L. satsuma* and *L. barhami* Webb, 1969 differ from the other three by the number of peripheral lamellar sheaths, i.e. up to four pairs in the first two species, six pairs in *L.*

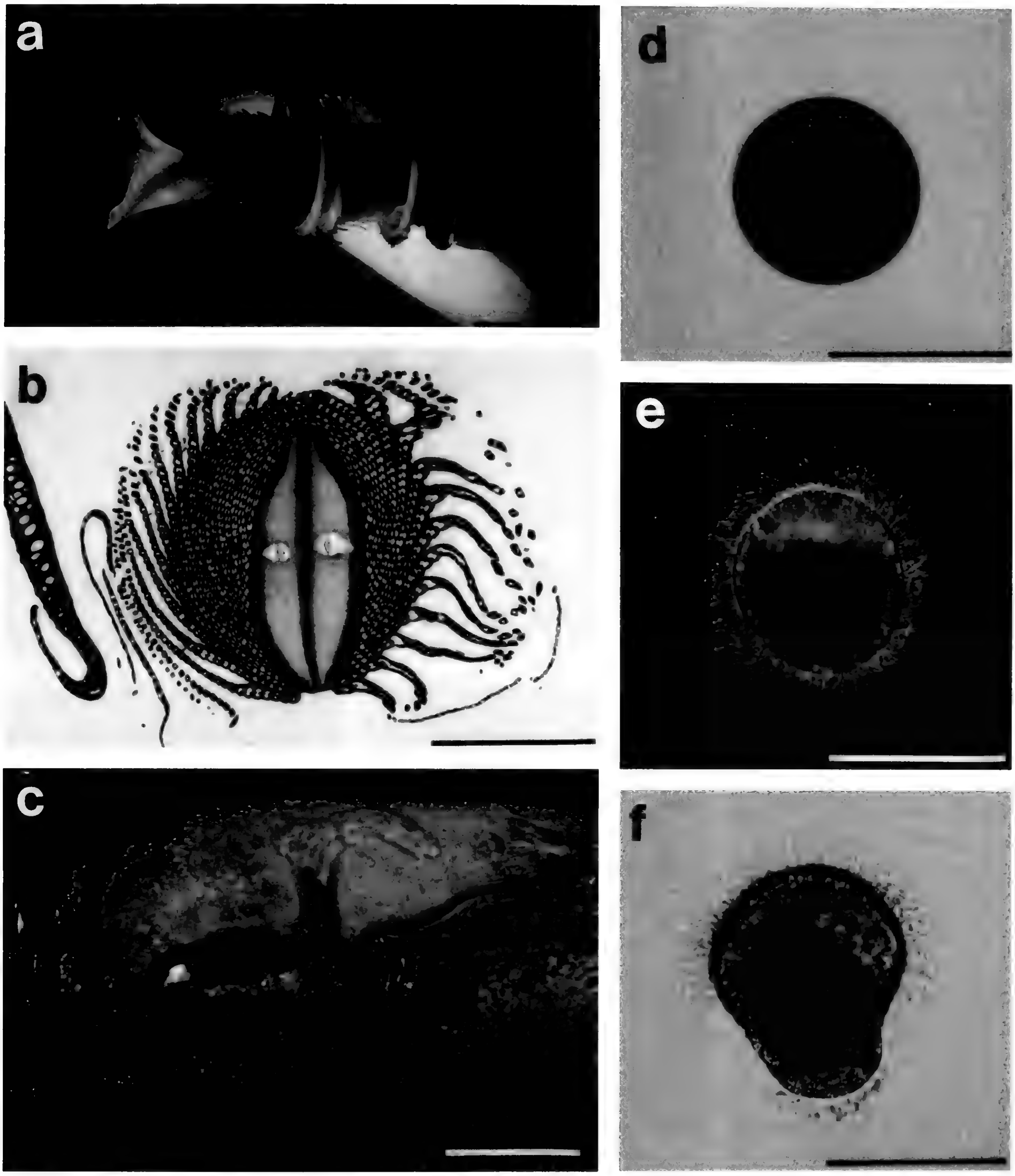

Fig. 2. Lab-reared specimens and embryos of *Lamellibrachia satsuma.*—a, Anterior end with the obturaculum, branchiae and the lamellar sheaths extending from the tube, scale = 3 mm; b, Transverse section near base of obturaculum, scale = 1 mm; c, Regenerated posterior ends of tubes attached to the glass bottle surface, scale = 10 mm; d, Released egg, scale = 0.1 mm; e, Trochophore-like larva about two-weeks old, in anterior view (upper hemisphere), scale = 0.1 mm; f, Same, in latero-posterior view (lower hemisphere with telotroch-like ciliated area), scale = 0.1 mm.

luymesi van der Land & Nørrevang, 1975, seven pairs in *L. victori* Mañe-Garzón & Montero, 1985, and 8–16 pairs in *L. columna* Southward, 1991. In *L. satsuma,* more than half of examined specimens has three to four pairs of lamellar sheaths, but only one or two pairs are large enough to cover the branchial region in most case. One very small specimens considered as a juvenile of *L. satsuma* has no lamellar

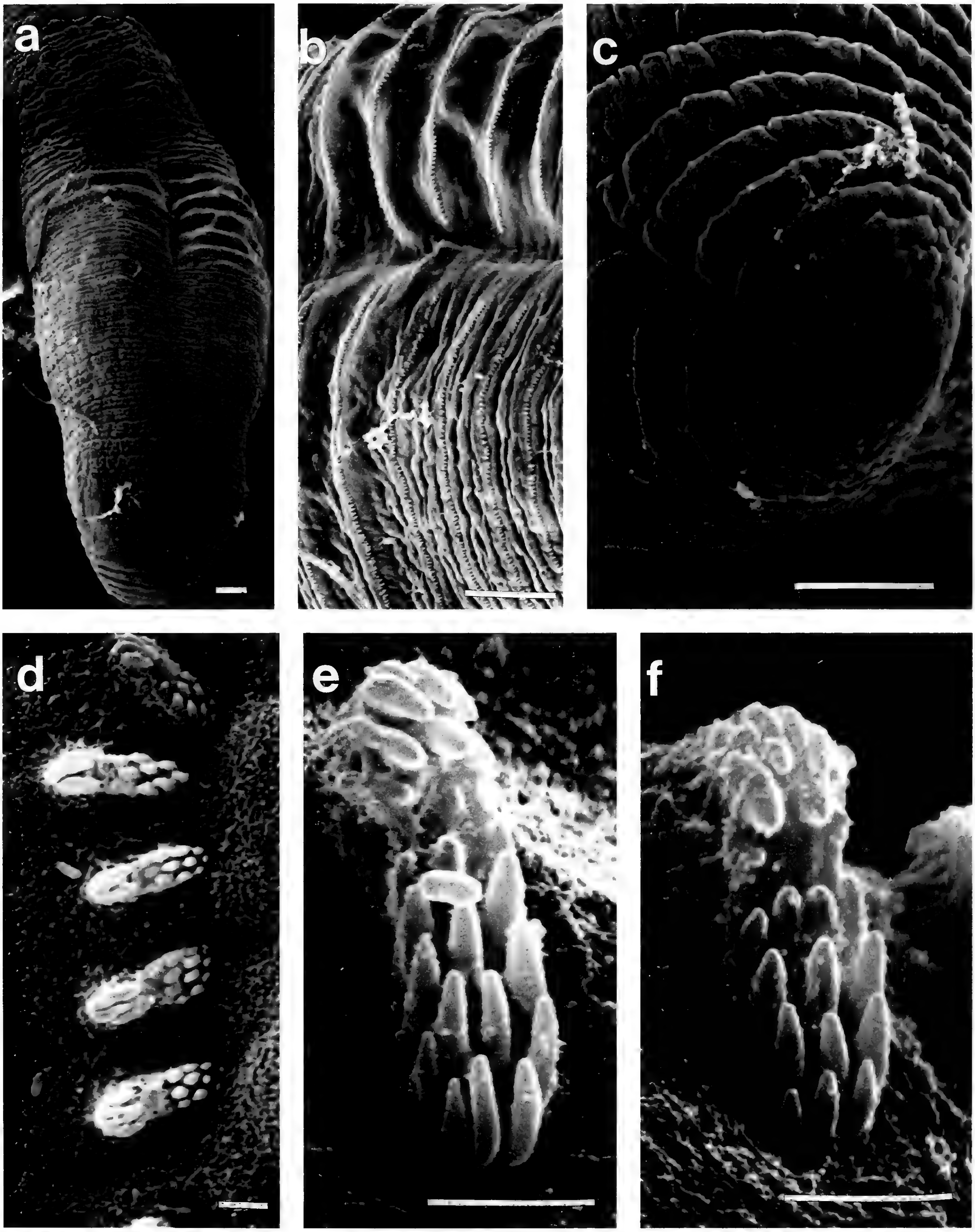

Fig. 3. *Lamellibrachia satsuma,* new species.—a, Regenerated opisthosome from a lab-reared specimen; b, Anterior portion of the same enlarged; c, Posterior portion of the same enlarged; d, Portion of opisthosome with a single row of setae; e, and f, Setae. Scale bars = 0.1 mm for a–c and 0.002 mm for d–f.

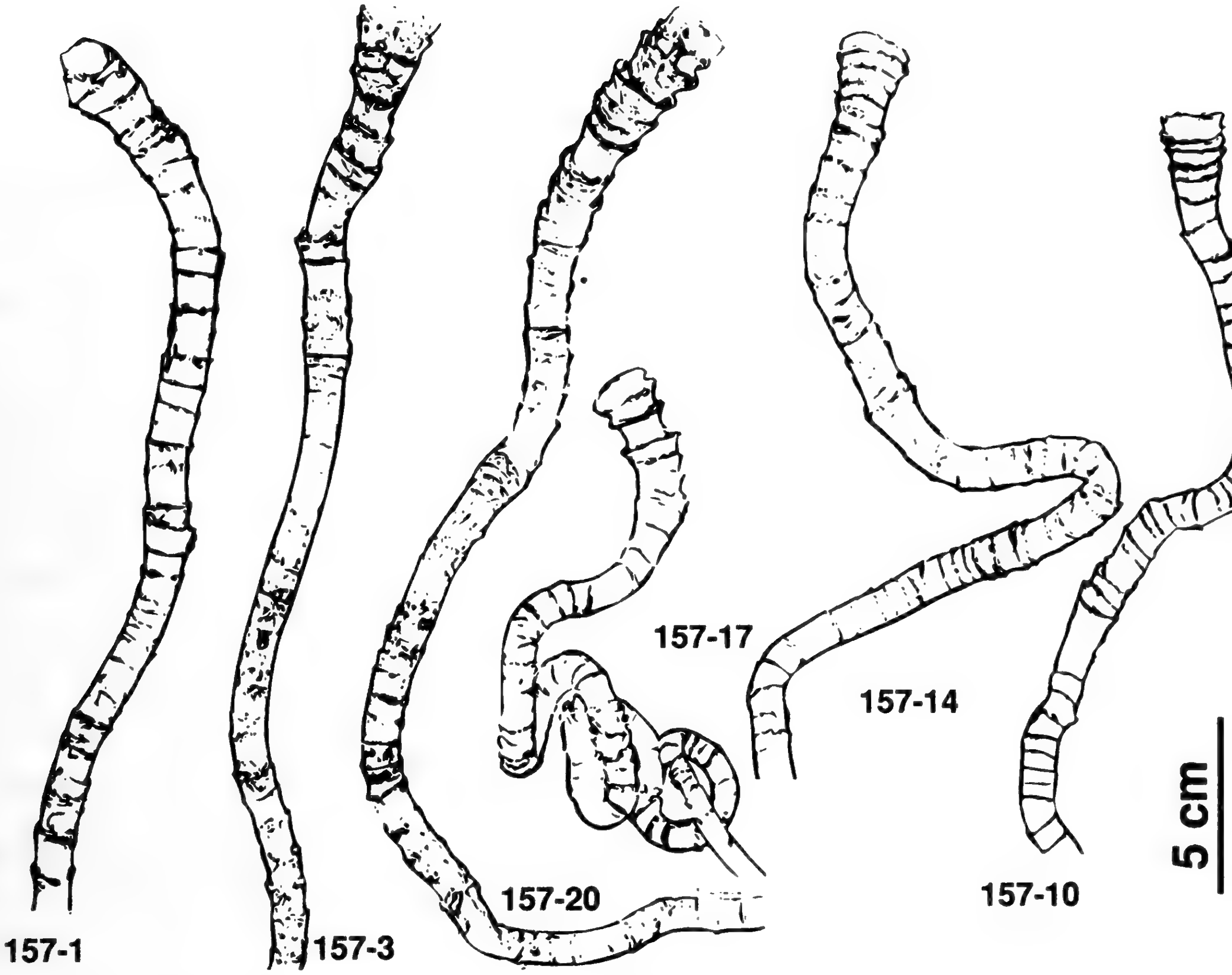

Fig. 4. *Lamellibrachia satsuma,* new species.—Anterior portion of tubes of selected paratypes.

sheaths. *Lamellibrachia satsuma* has up to 19 pairs of branchial lamellae; this number is smaller than in *L. barhami* which has as many as 25 pairs of branchial lamellae (Webb 1969; Jones 1985). The ratio of obturacular length to width ovewrlaps in these two species, but more variable in *L. barhami* (Fig. 5). *Lamellibrachia satsuma* is slightly smaller in size and has a shorter vestimentum and obturaculum (Fig. 5).

The diameter of cuticular plaques on the vestimentum and the trophosome are measured for *L. columna* (vestimental plaques 65–90 μm, trunk plaques 70–120 μm) and for *L. barhami* (60–115 μm, 115–160 μm, respectively) by Southward (1991, also her personal communication). These plaques are smaller in *L. satsuma* (35–63 μm, 51–82 μm, respectively) than the above two species.

The tube form is slightly different in *L. barhami* and *L. satsuma.* The tubes are twisted throughout the length in *L. barhami,* whereas the anterior parts of tubes are relatively straight in *L. satsuma. Lamellibrachia satsuma* forms very crowded clumps on the sediment and the tubes appear to be apart from one another in growing straightly (Fig. 2 in Hashimoto et al. 1993). These two species differ from each other also in their vertical and ecological distribution, i.e. *L. satsuma* lives in volcanic vents at depths of 98–110 m and perhaps also in cold seep sites of about 300 m depth, whereas *L. barhami* is presently known only in cold seep sites at depths of 1100–2000 m.

Observation of living worms in laboratory.—The worms extended the anterior part of their body from the tube, exposing the obturaculum and the lamellar sheaths (Fig. 2a). The anterior end was extended whether light was on or off, even when the strobe light was flashed. However, the

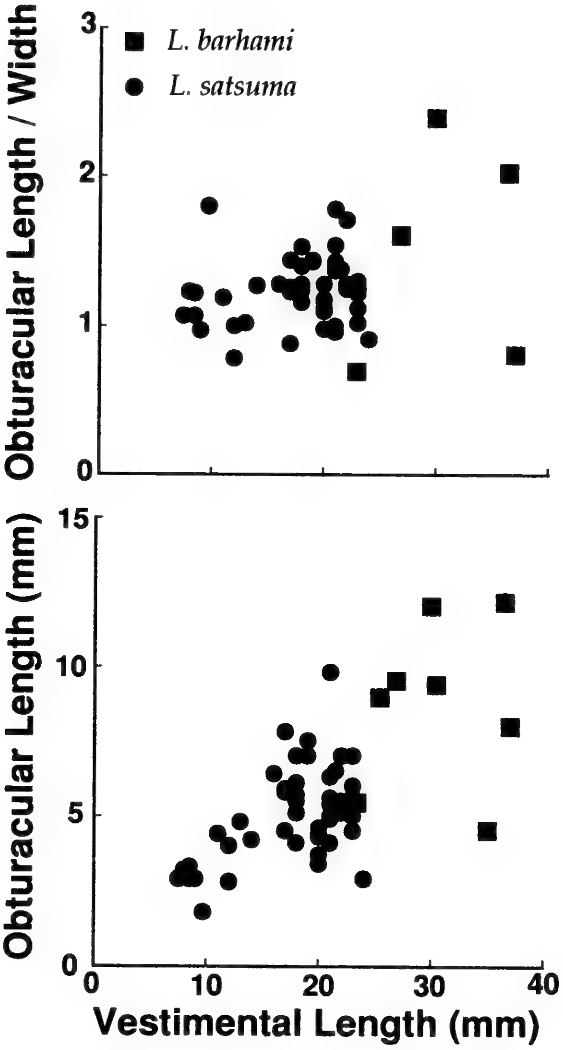

Fig. 5. Relationship between obturacular length and vestimental length (lower) and between obturacular length/width ratio and vestimental length (upper) in *Lamellibrachia satsuma* (closed circle, present study) and *L. barhami* (closed square, data from Jones 1985).

worms were very sensitive to vibration and withdraw into the tube when the tank was shaken. Retraction was very quick.

Among 43 living specimens maintained in the laboratory tank, six died in the first 75 days. Some of the remaining specimens were occasionally removed and dissected to check their condition. About 20 specimens were maintained alive for more than 400 days.

During the maintenance experiment in the laboratory, the worms regenerated their damaged posterior ends. Regenerated opisthosomes were observed at least two months after capture. The posterior ends of tubes were repaired and elongated to attach to a glass bottle which was used as a sinker for a bundle of worm tubes (Fig. 2c). Elongation of the anterior ends of tubes was not observed.

Spawning.—Some bottles of specimens were kept in the refrigerator of the research vessel at about 5°C for less than 6 days after their capture before transfer to the rearing tank. In a bottle containing about ten specimens, one released eggs from its tube opening when it was transferred to a tank filled with seawater at about 15°C (room temperature). The newly released eggs were photographed (Fig. 2d) and recorded on videotape. The eggs ranged in diameter from 0.10–0.11 mm ($\bar{X}$ 0.102, $n = 11$). The eggs were neutrally buoyant in seawater and formed a cloud-like mass drifting in the water, but most eggs transferred to a shallow petri dish floated at the surface. Cleavage of these eggs did not occur in the next five days. Observation was then abandoned.

Larvae.—In another bottle kept in the refrigerator, developing embryos were found five days after collection. Most of them were in a swimming, blastula-like stage. These embryos were kept in a small dish at room temperature ranging from 14.0 to 15.5 °C. Most of the embryos developed into trochophore-like larvae (Fig. 2e, f) 0.10 mm in diameter and 0.12–0.13 mm in length ($n = 7$). The larva had a well-ciliated anterior hemisphere with a prototroch-like ciliated band (Fig. 2e). A telotroch-like ciliated area was also well developed (Fig. 2f). A dark mass observed inside the larva (Fig. 2f) was thought to be comparable with the primitive gut of the early polychaete trochophore, but no blastopore or proctodaeum were observed. The gut-like structure of the larva was completely closed. No larvae had settled after two weeks of observation, when most larvae became inactive.

Discussion

Kojima et al. (1995) recognized three genetic types of *Lamellibrachia* in the waters around Japan by differences in the amino acid sequences of the mitochondrial cytochrome c oxidase I. Some *Lamellibrachia* specimens collected from Kagoshima Bay (82–110 m) and those from the Kanasunose Bank of the Nankai Trough (300 m) cluster into one of their types, living shallower than 300 m, which is the species described here as *L. satsuma.* This is thought to be distributed widely on the Southwest coast of Japan in less than 300 m deep. Judging by our preliminary examination of a single specimen from Sagami Bay, another types of *Lamellibrachia* from deeper sites (Kojima et al. 1995) is probably distinguishable from *L. satsuma* in morphological characters such as the body size, tube form, and the number of lamellar sheaths.

As shown in our maintenance experiment, it is not difficult to keep the mouthless worms alive if a suitable chemical energy source such as hydrogen sulfide is supplied. The expanded, blood-red branchiae forming flower-like fans at the top of the tubes may also serve to take up oxygen and carbon dioxide from the water. On the other hand, the source of nitrogen required for their growth or maturation is not yet identified. Since no growth except for some regeneration of posterior parts was observed in reared specimens, a suitable source of nitrogen such as nitrate or dissolved amino acid might have been scarce in the laboratory conditions.

Young et al. (1996) reported observations on the development of two vestimentiferans *Lamellibrachia* sp. and *Escarpia* sp. in the Gulf of Mexico. *Lamellibrachia satsuma* has eggs as large as those of the former but some differences can be seen. The larva of *L. satsuma* has a teminal telotroch-like ciliated area and an internal gut-like dark mass of cells, which were not found in the two species reported by Young et al. (1996). It is not yet clear if these differences are species-specific or not. Our study on the early development of *L. satsuma* is not yet completed and more details will be published elsewhere. The length of the planktonic larval life of *L. satsuma* suggested by the slightly buoyant eggs and a trochophore-like larva able to swim for more than two weeks is enough to explain their distribution in several sites along the Southwest coast of Japan washed by the strong Kuroshio Current. The Kagoshima Bay population of *L. satsuma* might have been formed originally by pioneer larvae released from a neighboring population outside the bay. The larvae might have settled at the active volcanic vents which are thought to have been more numerous and active in the bay during its formative period than at present. The northern part of the bay has been almost closed by the formation of Mt. Sakurajima during 13,000 years (Aramaki & Ui 1966), since the postulated colonization by the pioneer worms.

Acknowledgments

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Literature Cited

Aramaki, S., & T. Ui. 1966. The Aira and Ata pyroclastic flows and related calderas and depressions in southern Kyushu, Japan.—Bulletin of Volcanology 29:29–47.

Danndo, P. R., A. J. Southward, E. C. Southward, D. R. Dixon, A. Crawford, & M. Crawford. 1992. Shipwrecked tube worms.—Nature 356:667.

Hashimoto, J., S. Ohta, K. Fujikura, & T. Miura. 1995. Microdistribution pattern and biogeography of the hydrothermal vent communities of the Minami-Ensei Knoll in the Mid-Okinawa Trough, Western Pacific.—Deep-Sea Research, Part I, Oceanographic Research Papers 42:577–598.

———, ———, T. Tanaka, H. Hotta, S. Matsuzawa, & H. Sakai. 1989. Deep-sea communities dominated by the giant clam, *Calyptogena soyoae,* along the slope foot of Hatsushima Island, Sagami Bay, Central Japan.—Palaeogeography, Palaeoclimatology, and Palaeoecology 71:179–192.

———, T. Miura, K. Fujikura, & J. Ossaka. 1993. Discovery of vestimentiferan tube-worms in the euphotic zone.—Zoological Science 10:1063–1067.

Jones, M. L. 1985. On the Vestimentifera, new phylum: Six new species, and other taxa, from hydrothermal vents and elsewhere.—Bulletin of the Biological Society of Washington 6:117–158.

Kojima, S., J. Hashimoto, & S. Ohta. 1995. The distribution and the phylogenies of the species of genus *Calyptogena* and those of vestimentiferans around Japan.—JAMSTEC Journal of Deep Sea Research 11:243–248. (In Japanese with English abstract).

———, ———, M. Hasegawa, S. Murata, S. Ohta, H. Seki, & N. Okada. 1993. Close phylogenetic relationship between Vestimentifera (tube worms) and Annelida revealed by the amino acid sequence of elongation factor-1α.—Journal of Molecular Evolution 37:66–70.

Mañé-Garzón, F., & R. Montero. 1985. Sobre una nueva forma de verme tubícola—*Lamellibrachia victori* n. sp. (Vestimentifera)—Proposición de un nuevo phylum: Mesoneurophora.—Revista de Biologia del Uruguay 8:1–28.

Oki, S., & S. Hayasaka. 1978. Geological study on Kagoshima Bay, South Kyushu, Japan. Part IV—A note on the peculiar mode of occurrence of foraminifers in the bottom sediments of the bay-head area.—Report of Faculty of Science, Kagoshima University, in Earth Science and Biology 11:1–11.

Rouse, G. W., & K. Fauchald, 1995. The articulation of annelids.—Zoologica Scripta 24:269–301.

Southward, E. C. 1991. Three new species of Pogonophora, including two vestimentiferans, from hydrothermal sites in the Lau Back-arc Basin (Southwest Pacific Ocean).—Journal of Natural History 25:859–881.

———, & S. V. Galkin, 1997. A new vestimentiferan (Pogonophora: Obturata) from hydrothermal vent fields in the Manus Back-arc (Bismarck Sea), Papua New Guinea, Southwest Pacific Ocean.—Journal of Natural History 31:43–55.

———, V. Tunnicliffe, & M. Black. 1995. Revision of the species of *Ridgeia* from northeast Pacific hydrothermal vents, with a redescription of *Ridgeia piscesae* Jones (Pogonophora: Obturata = Vestimentifera).—Canadian Journal of Zoology 73:282–295.

Suzuki, T., T. Takagi, K. Okuda, T. Furukohri, & S. Ohta. 1989. The deep-sea tube worm hemoglobin: Subunit structure and phylogenetic relationship with annelid hemoglobin.—Zoological Science 6:915–926.

van der Land, J., & A. Nørrevang. 1975. The systematic position of *Lamellibrachia* (Annelida, Vestimentifera).—Zeitschrift für zoologische Systematik und Evolutionsforschung, Sonderheft 1975:86–101.

Webb, M. 1969. *Lamellibrachia barhami,* gen. nov., sp. nov. (Pogonophora), from the northeast Pacific.—Bulletin of Marine Science 19:18–47.

Williams, N. A., D. R. Dixon, E. C. Southward, & P. W. H. Holland. 1993. Molecular evolution and diversification of the vestimentiferan tube worms.—Journal of the Marine Biological Association of the United Kingdom 73:437–452.

Young, C. M., E. Vázquez, A. Metaxas, & P. A. Tyler. 1996. Embryology of vestimentiferan tube worms from deep-sea methane/sulphide seeps.—Nature 381:514–516.

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110(3):457–470. 1997.

The polychaetous annelids from oil platforms areas in the southeastern Gulf of Mexico: Phyllodocidae, Glyceridae, Goniadidae, Hesionidae, and Pilargidae, with description of *Ophioglycera lyra,* a new species, and comments on *Goniada distorta* Moore and *Scoloplos texana* Maciolek & Holland

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Abstract.—The distribution and composition of the polychaete families Phyllodocidae, Glyceridae, Goniadidae, Hesionidae and Pilargidae of the oil platforms area of Campeche Sound, southeastern Gulf of Mexico are analyzed. They involve the identification of 14 species and the revision of some of the material reported by authors in Uebelacker & Johnson (1984) for these families. *Ophioglycera lyra,* a new goniadid species is described, diagnosis of genus *Ophioglycera* is emended. *Goniada distorta* Moore, 1903 is removed from *Ophioglycera* and maintained in the genus *Goniada. Ancistrosyllis* sp. B of Wolf, 1984 is reported as *A. commensalis* Gardiner, 1976, and *Naineris* sp. A of Taylor, 1984 is reported as *Scoloplos texana* Macioleck & Holland, 1978.

Despite the fact that the Campeche Sound, in the southeastern Gulf of Mexico, is the most important area of oil extraction activity coupled with the most important shrimp fishery zone in Mexico, its fauna is poorly known. A few years ago, regional surveys were undertaken under our direction to study the benthic fauna of the area surrounding the offshore oil platforms. Part of the results of the extensive polychaete collections made during these studies are presented here. Previous taxonomic reports on other polychaetes collected during these studies include Granados-Barba (1994), Granados-Barba & Solís-Weiss (1994), Solís-Weiss et al. (1994, 1995) and Granados-Barba & Solís-Weiss (1997).

When doubts arose over the taxonomic position of several species, comparisons were made with material collected in the northern and eastern continental shelves of the Gulf of Mexico by different authors who collaborated in the Taxonomic Guide of the Polychaetes of the Northern Gulf of Mexico by Uebelacker & Johnson (1984) and deposited in the Smithsonian Institution (USNM) collection, since affinities with the study area environment were obvious. The appropriate remarks are herein reported where relevant.

Study area.—The study area is located in Campeche Sound, between 18°46′–20°03′N and 91°33′–92°34′W, covering the offshore oil platforms area and part of the continental shelf down to about 200 m depth (Fig. 1). The sediment in the oil platforms area is mainly mud, although there are some isolated patches of sandy mud (Granados-Barba 1994).

Materials and methods.—Sampling was done on board the R/V *Justo Sierra,* as part of the interdisciplinary projects IMCA-DINAMO during expeditions IMCA—1 (I-1, March 1988), IMCA—2 (I-2, September 1988), IMCA—3 (I-3, March 1989), DINAMO—1 (D-1, March 1990) and DINAMO—2 (D-2 November 1990). Sixteen stations are herein considered (Fig. 1). The

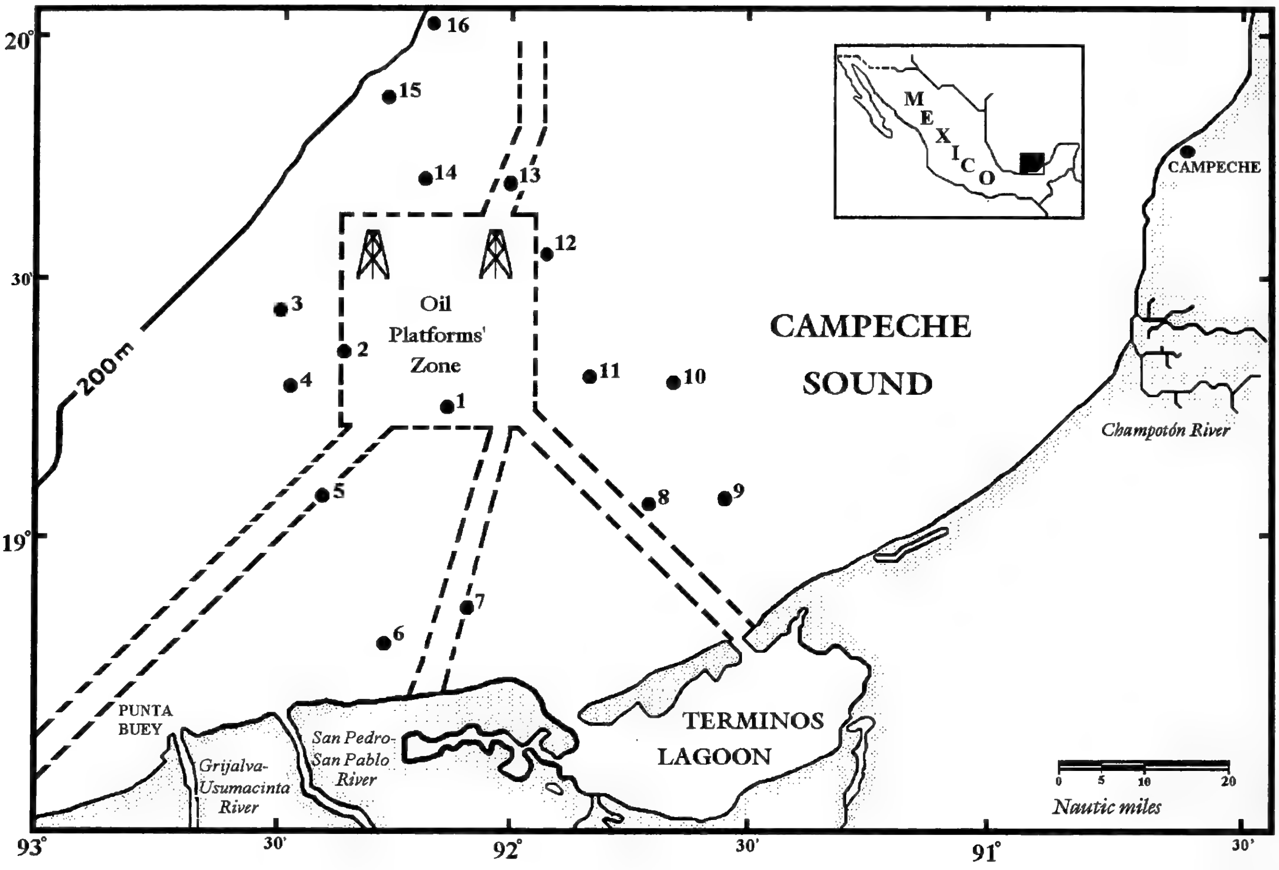

Fig. 1. Study area. 1 Sampling stations.

coordinates and depths of each station are presented in Table 1. The polychaetes were collected with a 0.1 m² Smith-McIntyre grab. At each station, about 40 liters of sediment were screened through a 0.5-mm sieve, and specimens fixed in 10% formalin. In the laboratory, specimens were washed, sorted, and transferred to 70% ethanol. Depth, salinity, and temperature were recorded at each station with a Niels-Brown C.T.D.

Table 1.—Positions (Latitude and Longitude) and depths (m) of the sampling stations.

Station	Latitude (N)	Longitude (W)	Depth
1	19°15′	92°08′	31.2
2	19°23′	92°21′	75.6
3	19°18′	92°28′	102.6
4	19°15′	92°28′	71.8
5	19°05′	92°23′	32.6
6	18°49′	92°16′	16
7	18°50′	92°06′	16
8	19°04′	91°42′	16.2
9	19°04′	91°33′	16.6
10	19°20′	91°39′	31.2
11	19°20′	91°49′	32.4
12	19°33′	91°54′	56
13	19°42′	92°00′	70.2
14	19°43′	92°10′	98.2
15	19°52′	92°16′	148.4
16	20°03′	92°09′	127.2

For each species, selected synonyms, habitat and reported worldwide distribution are included. Environmental factors measured in this and previous studies that are included when available are cited with the following abbreviations: D = depth (m); T = temperature (°C); S = salinity (%); OM = organic matter in the sediment (% of organic carbon) and OD = dissolved oxygen (ml/1). The specimens are deposited in the Polychaetological Collection of the Instituto de Ciencias del Mar y Limnologia (CPICML), UNAM, Mexico, City. The type material for *Ophioglycera lyra* is deposited in the following museums: National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; Los Angeles County Museum of Natural History (LACMNH-AHF), California, USA.

Family Phyllodocidae Örsted, 1843

The family Phyllodocidae is represented by about 31 genera and 306 species. In this study, 11 specimens belonging to two genera and four species were collected. Pleijel (1991:232) clarified the authorship of the family. See also Blake (1994a).

Genus *Paranaitis* Southern, 1914
Paranaitis gardineri Perkins, 1984

Paranaitis gardineri Perkins, 1984:563, figs. 4a–i.—Granados-Barba, 1994:112.

Paranaitis polynoides.—Gardiner, 1976: 110.—Gathof, 1984:19.21, fig. 19.18 [not *Anaitis polynoides* Moore, 1909].

Material examined.—5 specimens: Mar 1989, sta. 5(1), 9(1), 11(1); Mar 1990, sta. 16(1); Oct–Nov 1990, sta. 16(1).

Remarks.—Perkins (1984) erected the species *P. gardineri* to include specimens reported by Gardiner (1976) as *P. polynoides* separating Atlantic Ocean specimens from *P. polynoides* Moore, 1909, based on the fact that *P. gardineri* has dorsal cirri narrower and shorter than the acicula that are not covering the dorsum in the posterior region, in addition to the shape of the anal cirri, which are long and filiform rather than short, thick and cylindrical. The specimens examined in this study agree with the description of *P. gardineri.* Perkins further remarked that the North Carolina specimens were twice as large as the ones from Florida. In this study, the specimens are about half the size of the Florida specimens.

Previously reported habitat.—Intertidal to 125 m, in mud, muddy sand, coarse to fine sand, sand with gravel and shells, T = 20–26; S = 36.48–37.43; OM = 0.19–1.17.

Occurrence.—In mud, D = 16–127; T = 20; S = 36.48; OM = 1.17.

Distribution in Mexico.—Southern Gulf of Mexico.

Distribution.—North Carolina; Florida; northern Gulf of Mexico.

Genus *Phyllodoce* Lamarck, 1818
Phyllodoce (*Phyllodoce*) *arenae* Webster, 1879

Phyllodoce (*Anaitides*) *arenae*.—Pettibone, 1963:82, fig. 18a.—Day, 1973:23.—Gardiner, 1976:117, figs 8d.

Phyllodoce arenae.—Gathof, 1984:19.21, figs. 19.18a–e.—Granados-Barba, 1994: 112, pl. 15b.

Phyllodoce (*Anaitides*) *panamensis*.—Day, 1973:24, fig. 3n–p.—Gardiner, 1976:117. *Phyllodoce panamensis*.—Granados-Barba, 1994:114. (not *Phyllodoce panamensis* Treadwell, 1917.)

Material examined.—4 specimens: Sep 1988, sta. 13(1); Mar 1989, sta. 9(3).

Material of other species examined.—*Phyllodoce panamensis* USNM 16831, Holotype from Port Chame, Panama, Sta. 362, 30°11′48″N, 88°43′40″W. USNM 51028, 2 specimens from Beaufort, North Carolina, USA 34°24′N, 75°57′W, 80 m.

Remarks.—Day (1973) separated North Carolina specimens he reported as *P. panamensis* from *P. arenae* based on the difference in color patterns of both species. Whereas in the former there is a middorsal continuous band, the latter is characterized by the presence of fusiform dark dorsal spots in the intersegmental furrows. In one of the specimens examined for this study, a middorsal continuous band is present, so that it was formerly identified as *P. panamensis* by one of us (Granados-Barba 1994). However, a recent comparison between Day's specimens, the holotype of *P. panamensis* and our specimens showed that *P. panamensis* Treadwell is considerably larger than the specimens from the Gulf of Mexico and North Carolina and that it does not have the middorsal band. We could conclude that both our specimens and Day's North Carolina specimens are *P. arenae.*

Previously reported habitat.—Intertidal to 200 m, in mud, sandy mud, muddy sand and coarse sand with shells, T = 27.5; S = 36.21–36.76; OM = 0.64–1.01; DO = 3.45.

Occurrence.—In mud, D = 16–70.

Distribution in Mexico.—Tamiahua Lagoon, Veracruz; southern Gulf of Mexico.

Distribution.—New England; North Carolina; northern Gulf of Mexico.

Phyllodoce (*Anaitides*) *madeirensis* Langerhans, 1880

Phyllodoce (*Anaitides*) *madeirensis.*—Day, 1973:23.—Gardiner, 1976:115, figs. 7q, 8a–c.

Anaitides madeirensis.—Gathof, 1984: 19.39, figs. 34a–e.

Phyllodoce madeirensis.—Mountford, 1991:161, figs. 2–3a–c.—Pleijel, 1991: 257; 1993a:33.—Granados-Barba, 1994: 113.

Material examined.—1 specimen: Mar 1990, sta. 13(1).

Remarks.—The specimen examined agrees with the redescription of Mountford (1991) of this species; the revision by this author of some phyllodocids from Puerto Rico led to the synonymy of *P. oculata* and *P. madeirensis,* and the separation of *P. erythrophylla* and *P. madeirensis,* based on color patterns. See also the list in Pleijel (1991).

Previously reported habitat.—Intertidal to 200 m, on rocks and corals, in silt, clay, mud, sandy mud, muddy sand, sand and fine sand, T = 14–31; S = 34.44–37.4; OM = 0.18–5.5; DO = 1.03–5.4.

Occurrence.—In mud, D = 70; OM = 1.47.

Distribution in Mexico.—Southern Baja California; Gulf of California; Jalisco; Colima; Guerrero; Gulf of Tehuantepec; Isla de Enmedio Veracruz; central and southern regions of the Gulf of Mexico.

Distribution.—Cosmopolitan in intertidal areas and continental shelves of tropical seas; South Africa; pacific coast of Panama; North Carolina; northern Gulf of Mexico; Puerto Rico.

Phyllodoce (*Anaitides*) *mucosa* Örsted, 1843

Phyllodoce (*Anaitides*) *mucosa.*—Pettibone, 1963:81, fig. 18f.—Gardiner, 1976: 113, fig. 7.

Anaitides mucosa.—Gathof, 1984:19.33, fig. 19.28.

Phyllodoce mucosa.—Pleijel, 1991:259; 1993:51, figs. 33–34.—Granados-Barba, 1994:114.

Material examined.—1 specimen: Sep 1988, sta. 15(1).

Remarks.—The examined specimen agrees with description of Gathof (1984).

Previously reported habitat.—Intertidal to 425 m, in mud, sand, muddy sand, sand and shells, and gravel, T = 13–15; S = 35–35.46; OM = 3–6.9; DO = 0.8–3.09.

Occurrence.—In mud, D = 148; T = 21; S = 36.42; OM = 1.15.

Distribution in Mexico.—Baja California; west of Baja California Sur; Gulf of California; Guerrero; southern Gulf of Mexico.

Distribution.—Northern Europe; Azores Islands; western North America from Alaska to Mexico; western Africa; New England; North Carolina; northern Gulf of Mexico; Cuba.

Family Glyceridae Grube, 1850

The family Glyceridae is represented by three genera and about 80 species. For this study, we collected 15 specimens belonging to one genus and three species.

Genus *Glycera* Savigny *in* Lamarck, 1818

Glycera americana Leidy, 1855

Glycera americana.—Pettibone, 1963:213, figs. 54a–e.—Gardiner, 1976:161, figs. 17l–n.—Gilbert, 1984a:32.15, fig. 32.12.—Granados-Barba, 1994:152.—Hilbig, 1994a:200, fig. 6.1.

Material examined.—7 specimens: Mar 1988, sta. 7(1); Sep 1988, sta. 9(1), 14(1); Mar 1989, sta. 6(2), 7(1), 9(1).

Remarks.—Everted branchiae were observed from setiger 14, but we consider that they could be retracted in anterior setigers. In very small specimens, the branchiae could not be seen; however, all the other characters agree with description of *G. americana.*

Previously reported habitat.—Intertidal, continental shelf and slope, in mud, sandy mud, muddy sand and fine to medium sand, D = 22–106; T = 13–28; S = 35.06–37.19; OM = 0.47–3.9; OD = 1.04–5.4.

Occurrence.—In mud and muddy sand, D = 16–98; T = 22–28; S = 35.51–37.19; OM = 0.39–1.05.

Distribution in Mexico.—Baja California; west of Baja California Sur; Gulf of California; Veracruz; Tamiahua Lagoon, Veracruz; central and southern regions of the Gulf of Mexico.

Distribution.—Magellan Strait, New Zealand; Australia; Eastern Pacific Ocean, from southern Canada to Peru; Western Atlantic Ocean from New England to Argentina; northern Gulf of Mexico; Bermuda.

Glycera robusta Ehlers, 1868

Glycera robusta.—Hartman, 1950:69, pl. 10, figs. 7–8.—Pettibone, 1963:218, figs. 54f–g.—Gardiner, 1976:162, fig. 17o.—Gilbert, 1984a:32.22, figs. 32.20a–i.—Granados-Barba, 1994:153.

Material examined.—2 specimens: Mar 1990, sta. 2(1), 9(1).

Remarks.—In one of the specimens, six to seven long structures resembling branchiae or cirri were observed on the first 10 setigers (very similar in shape to those found among the cirratulids); they do not follow a determined pattern, since some can be seen emerging above or below the dorsal cirrus, while others emerge from below the ventral cirrus. Hilbig (pers. comm.) suggests that these structures could be algae or fungi, or some other parasite/commensal.

Previously reported habitat.—Intertidal to 380 m, in mud, sandy mud, sand, sand with gravel and shells, T = 27.5–28; S = 36.5–36.7; OM = 0.59–1.6; DO = 3.9.

Occurrence.—In mud, D = 16–75; OM = 0.59–1.66.

Distribution in Mexico.—Gulf of California; southern Gulf of Mexico.

Distribution.—Central California to Mexico; New England; North Carolina; northern Gulf of Mexico.

Glycera tesselata Grube, 1863

Glycera tesselata.—Hartman, 1950:77, pl. 10, fig. 11.—Granados-Barba, 1994:154, pl. 23a.—Hilbig, 1994a:208, fig. 6.5.

Material examined.—6 specimens: Sep 1988, sta. 2(2), 3(1), 15(1); Mar 1989, sta. 14(1); Oct–Nov 1990, sta. 16(1).

Remarks.—*Glycera tesselata* resembles closely *G. capitata, G. abranchiata,* and *Glycera* sp. F of Gilbert (1984a), but differs from the first by the presence of bilobed, rather than entire postsetal lobes, from the second by the presence of smooth instead of striated proboscidial papillae, and from the last by the presence of only one, rather than two types of proboscideal papillae. These species were compared to material of both named species collected elsewhere.

Previously reported habitat.—Continental shelf down to 97 m, in mud with gravel, coarse to fine sand, T = 13–25.8; S = 34.92–37.4; OM = 0.52–6.9; DO = 0.63–5.4.

Occurrence.—In mud, D = 75–148; T = 19–24.5; S = 36.42–36.48; OM = 1.12–1.33.

Distribution in Mexico.—Baja California Peninsula; Revillagigedo Islands; Sinaloa; Gulf of Tehuantepec, Oaxaca; Tamiahua Lagoon, Veracruz; southern Gulf of Mexico; Quintana Roo.

Distribution.—Mediterranean Sea; Red Sea; from England to Morocco; India; Japan; Canada; California; Atlantic coast of Panama; North Carolina.

Family Goniadidae Kinberg, 1866

The family Goniadidae is represented by nine genera (Hilbig, 1994) and about 75 species. In this study 14 specimens, in two genera and two species, were collected.

Genus *Goniada*
Audouin & Milne Edwards, 1833
Goniada cf. *maculata* Örsted, 1843

Goniada maculata.—Hartman, 1950:20, pl. 1, figs. 7–8.—Pettibone, 1963:225, fig. 58.—Day 1973:51.—Gardiner, 1976:167, figs. 19c–f.—Gilbert, 1984b:33.11, fig. 33.8.—Granados-Barba, 1994:157.—Hilbig, 1994b:226, fig. 7.5.

Material examined.—2 specimens: Mar 1989 sta. 15(1); Mar 1990 sta. 15(1).

Remarks.—The specimens examined agree with description of Gilbert (1984b) for this species. However Hartman (1950: 20) recorded 39–41 setigers with uniramous parapodia (rather then 25). For this reason the identity of the species must be considered doubtful. We think that specimens from the Gulf of Mexico could be a new species, but we need to examine type specimens in order to confirm it. In some of the specimens, most of the body was dark brown, but we think this could be the result of fixation. One specimen had pairs of ventrolateral black spots located in the intersegmental furrows from setigers 24–25 to the end of the fragment.

Previously reported habitat.—Intertidal to 3020 m, in silt, silty sand, clay, mud, sandy mud, muddy sand, sand with shells, medium to fine sands and sands, T = 16–28; S = 35.3–37.6; OM = 0.18–0.96; DO = 1.14–3.

Occurrence.—In mud, D = 148; OM = 1.18.

Distribution.—Northern Japan; western Europe; Alaska; South Africa; California, New England; North Carolina; northern Gulf of Mexico.

Distribution in Mexico.—West of Baja California Sur; Gulf of Tehuantepec; Laguna de Tampamachoco, Veracruz; central and southern regions of the Gulf of Mexico.

Genus *Ophioglycera* Verrill, 1885, emended

Type species: *Ophioglycera gigantea* Verrill, 1885.

Diagnosis.—Body long, cylindrical; prostomium with 9 or 10 annulations and four antennae of equal length; no eyes. No chevrons on pharynx. Notosetae acicular; neurosetae compound spinigers and lyrate setae can be present.

Remarks.—This diagnosis includes the presence of lyrate setae first observed in *Ophioglycera lyra*; such setae had not previously been reported in this genus.

Ophioglycera lyra, new species
Figs. 2–3

Ophioglycera sp. A.—Gilbert, 1984b: 33.19, figs. 33.16a–j; Granados-Barba, 1994:158.

Material examined.—12 specimens: Mar 1988 sta. 1(1), 7(1), 12(3); Sep 1988 sta. 1(1); Mar 1990 sta. 1(1), 7(1), 11(1); Mar 1990 sta. 1(1), 7(1), 10(1).

Type locality.—Sta. 10, holotype, USNM 175433, Gulf of Mexico, 10, 19°20.9′N, 91°39.6′W, 13 Mar 1990. Paratypes: Sta. 1, 19°15.2′N, 92°08.3′W, 9 Mar 1988, (1) USNM 175434. Sta. 7, 18°50.1′N, 92°06.2′W, 8 Mar 1988, (1) USNM 175435. Sta. 1, 19°15.2′N, 92°08.3′W, 25 Sep 1988, (1) USNM 175436. Sta. 1, 19°15.2′N, 92°08.3′W, 12 Mar 1989, (1) LACM-AHF POLY 1886. Sta. 7, 18°50.1′N, 92°06.2′W, 11 Mar 1989, (1) LACM-AHF POLY 1887. Sta. 11, 19°20′N, 91°49.8′W, 3 Mar 1989, (1) CPICMLPOP-42-002. Sta. 6, 18°49.2′N, 92°16.2′W, 9 Mar 1990, (1) CPICMLPOP-42-001. Sta. 12, 19°33.3′N, 91°54.7′W, 11 Mar 1988, (3) CPICMLPOP-42-003.

Gulf of Mexico specimens identified as *Ophioglycera* sp. A by Gilbert 1984b: USNM 089828, southern Louisiana, Gulf of Mexico, Sta. 03P, 28°40′02″N, 90°14′43″W. USNM 089829, Texas, Gulf of Mexico, Sta. S-52, 26°10′N, 97°01′W.

Material of other species examined.—*Goniada distorta* Moore 1903, USNM 15720 Honshu Island, Japan, sta. 3739 (moved to *Ophioglycera* by Hartman, 1950: 36). *Ophioglycera gigantea* Verrill 1873, USNM 13417 syntype, Newport Harbor, sta. 901, surface, 1980.

Description.—The description is based on the holotype unless specified otherwise. Holotype a large specimen, 69 mm long and 1.8 mm wide without parapodia, almost complete, with 175 setigers. Paratypes and additional material incomplete with 45–117 setigers, 9–29 mm long × 0.2–0.8 mm wide. Body long, cylindrical, tapering towards posterior end, last 10 to 12 setigers very small, crowded. Parapodia and part of dorsum pigmented giving appearance of ophiuroid arm (Fig. 2h). Prostomium semiconical with ten annulations (Fig. 2a) (8–10 in paratypes and additional material) four semiglobular antennae, distal pair distinctly shorter. Basal ring of prostomium laterally expanded as small lappets, no eyes. Pharynx without chevrons (Fig. 2a), very long (6.5 mm long, almost 2 mm wide on holotype and somewhat damaged) covered with papillae. Proboscidial papillae of two forms: triangular with large base and beak slightly recurved (Fig. 2b–d); and very small and rounded. Macrognaths (not visible in holotype) with 3–5 teeth, micrognaths 20–27 in dorsal arc, 7–8 in ventral arc (Fig. 2e). First 65 setigers uniramous (49–52 in paratypes, this character somewhat size related) with three transitional setigers (0–3 in paratypes), then biramous. From setiger 65 two midventrally located black dots present close to intersegmental furrows (Fig. 2f), in longitudinal midventral groove; dots and groove absent from last 27–30 segments.

Middle anterior region with two dorsolateral pale bands (darker than the body color) subdivided maximally into 10 thin longitudinal bands (Fig. 2g); bands decreasing in number but increasing in width down to three in middle region; thereafter two and finally one much broader, diffuse band present towards the end of body. Dorsal and ventral cirri with dark pigmentation and entire notopodium pigmented on biramous setigers. Pigmentation in paratypes similar but less conspicuous, with smaller pigmented areas and dorsolateral pigmentation not in form of longitudinal bands.

First parapodia with pair of dorsolateral cirri and single presetal lobe. Single presetal lobe present either in first or in first and second parapodia in paratypes, apparently related to size; first two setigers of specimens from northern Gulf of Mexico having that single presetal lobe (Gilbert 1984b). Thereafter, two digitiform slender presetal lobes present, dorsal one longer, at first distinctly so, then subequal. Postsetal lobes shorter than presetal lobes, slender, digitiform, broader at base, similar on all parapodia. Dorsal cirrus broad basally, pointed distally, more rounded (bulbous) in uniramous parapodia (Fig. 3a–b), more flattened in biramous parapodia (Fig. 3c–d). Ventral cirri elongate, pointed distally, longer than neuropodial lobes (Figs. 3a–b), becoming broader in transitional setigers, thereafter tapering and pointed distally (Fig. 3c–d). Two acicular notosetae and one acicula of same width in notopodia (Fig. 3c). Neuropodia with two acicula and compound spinigers (Fig. 3e–h) throughout the body; biramous parapodia with additional one to four lyrate setae in upper position (Fig. 3i).

Remarks.—*Ophioglycera lyra,* n. sp. differs from related species by having biramous parapodia starting on setigers 49–65, two long acicular notosetae, and one to four superior lyrate neurosetae. This species is similar to *O. gigantea* from which it differs in being smaller, having a much larger number of uniramous setigers, and having a different setal composition, particularly the lyrate setae not previously reported for the genus.

Gilbert (1984b) stated that *Ophioglycera* sp. A and *G. distorta* Moore, 1903 were "most similar" because they had a similar

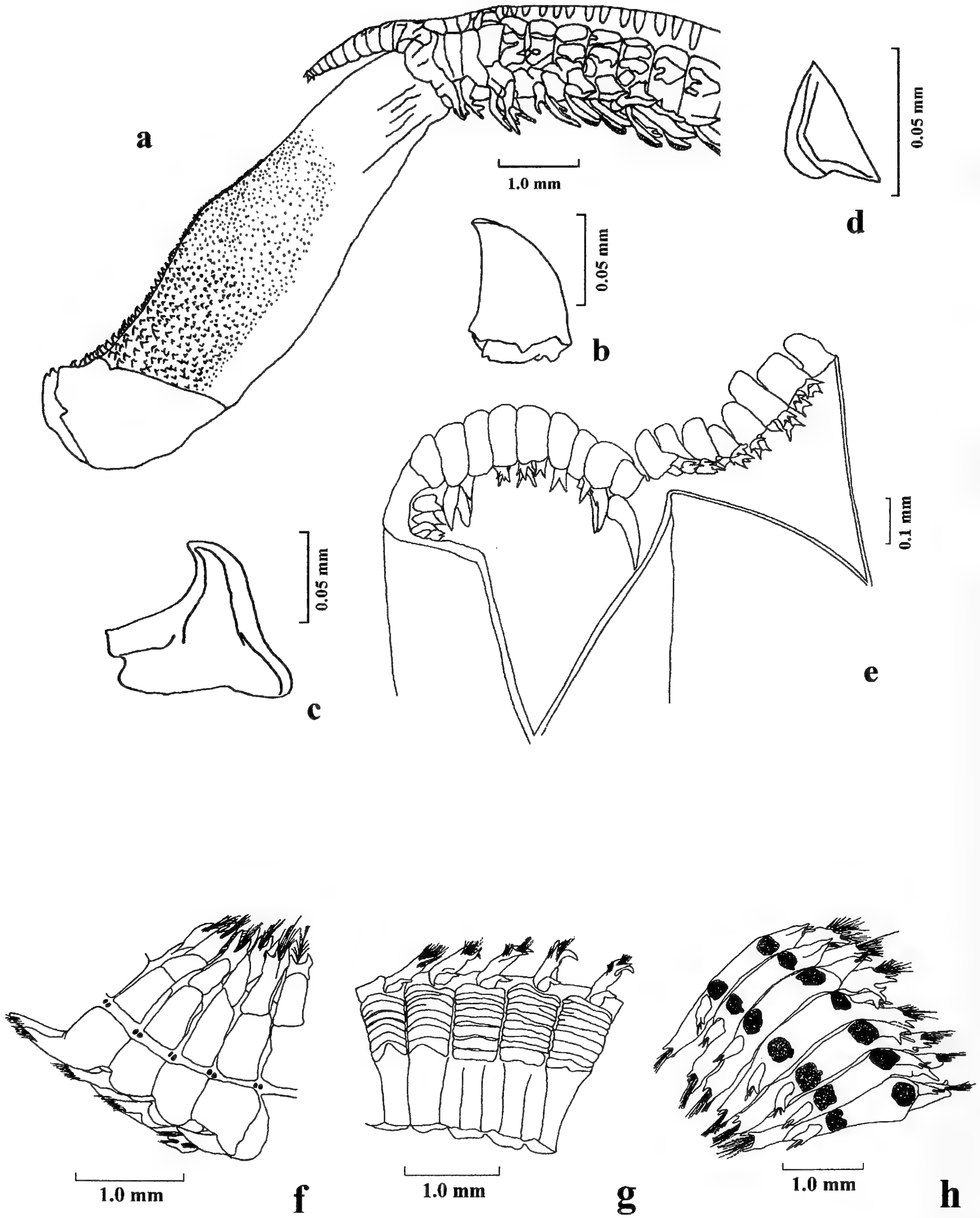

Fig. 2. *Ophioglycera lyra* n. sp. a) Anterior end with everted proboscis; b–d) Proboscidial papillae; e) Distal portion of the proboscis, dissected; f) Middle body (biramous parapodia) showing coloration patterns, ventral view; g) Anterior setigers showing ventrolateral bands; h) Anterior setigers showing dorsal coloration patterns.

number of uniramous parapodia. However, upon examination of the holotype of *G. distorta* (which is in good condition and anteriorly dissected) we found that this species has chevrons, and thus cannot be even maintained in the genus *Ophioglycera,* which lacks them by definition. Those two species are therefore not comparable or

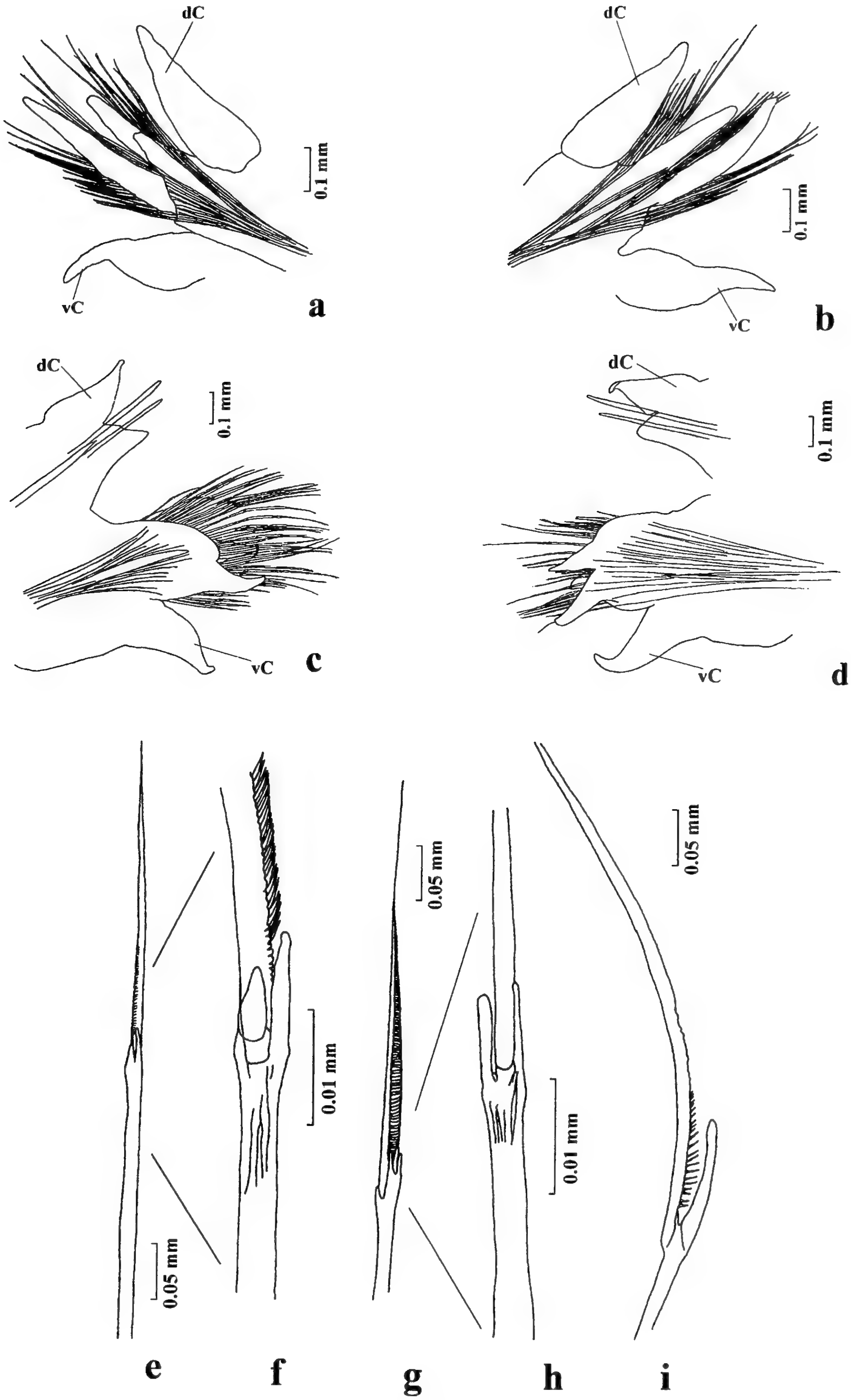

Fig. 3. *Ophioglycera lyra* n. sp. a) Uniramous parapodium from setiger 17, posterior view; b) Uniramous parapodium from setiger 18, anterior view; c) Biramous parapodium from setiger 74, posterior view; d) Biramous parapodium from setiger 75, anterior view; e–h) Compound spinigers from setiger 18; i) Lyrate neuroseta from setiger 74.

close. Hartman (1950:36) did not examine type material of *Goniada distorta* when placing it in the genus *Ophioglycera,* probably believing that if Moore 1903 did not report chevrons for the species, they did not exist. After examination of the holotype, where the chevrons are clearly seen, we maintain *Goniada distorta* in the genus *Goniada* as originally described by Moore.

Etymology.—The specific name refers to the lyrate setae of the new species, the first to be reported in the genus.

Previously reported habitat.—15–98 m, in silt, mud, sand, and silty sand.

Occurrence.—In mud, D = 16–56; T = 24–27; S = 35.94–37.19; OM = 0.68–1.65.

Distribution in Mexico.—Southern Gulf of Mexico.

Distribution.—Northern Gulf of Mexico.

Family Hesionidae Grube, 1850

The family Hesionidae is represented by 30 genera and about 150 species (Hilbig 1994c). In this study six specimens in one genus and one species were collected.

Genus *Podarkeopsis* Laubier, 1961

Podarkeopsis levifuscina Perkins, 1984

Podarkeopsis levifuscina Perkins, 1984: 575, fig. 10.

Gyptis vittata.—Taylor, 1971:155.—Day, 1973:25 [not Webster & Benedict, 1887].

Gyptis brevipalpa.—Gardiner, 1976:119, figs. 8q–t, 9a.—Uebelacker, 1984:28.27, figs. 28.26a–e.—Granados-Barba, 1994: 134, pl. 19a–h [not *Oxydromus brevipalpa* Hartmann-Schröder, 1959].

Material examined.—6 specimens: Mar 1989, sta. 11(1); Mar 1990 sta. 9(2); Oct–Nov 1990 sta. 1(1), 9(2).

Remarks.—The genera of hesionids are currently being reviewed by Pleijel (Fauchald, pers. comm.) and the position of most species thus remains doubtful.

Previously reported habitat.—10–189 m, clay, mud, sandy mud and sand, T = 14.5–28; S = 35.45–37.22; OM = 0.44–6.9; DO = 3.09–3.17.

Occurrence.—In mud and sandy mud, D = 16–32; T = 28; S = 36.94; OM = 0.59.

Distribution in Mexico.—Gulf of California; Tamiahua Lagoon, Veracruz and Terminos Lagoon, Campeche; southern Gulf of Mexico.

Distribution.—North Carolina; Florida; northern Gulf of Mexico.

Family Pilargidae Saint-Joseph, 1899

The family Pilargidae is represented by 10 to 13 genera (Blake 1994b) and about 56 species. In this study 25 specimens in three genera and four species were collected.

Genus *Ancistrosyllis* McIntosh, 1879

Ancistrosyllis commensalis Gardiner, 1976

Ancistrosyllis commensalis Gardiner, 1976: 123, figs. g–k.

Ancistrosyllis sp. B.—Wolf, 1984:29.17, fig. 29.12.—Granados-Barba, 1994:137, pl. 20b.

Material examined.—1 specimen: Mar 1989 sta. 8(1).

Additional material examined.—*Ancistrosyllis commensalis* USNM 052902, holotype, Banks Channel, Wrightsville Beach, North Carolina, USA, sta. 11. USNM 052903, paratypes, 3 specimens from Banks Channel Wrightsville Beach, North Carolina, USA, sta. 10, in burrows of *Notomastus lobatus.* USNM 86930, 1 specimen from Texas, USA, sta. S49-6, as *Ancistrosyllis* sp. B Wolf, 1984.

Remarks.—The examination of the holotype of *A. commensalis* and Wolf's voucher material of *Ancistrosyllis* sp. A from Texas and its comparison to our material shows that all are indeed the same species, the only difference being their size. Specimens from North Carolina are larger than those from the southern Gulf of Mexico, which in turn are larger than those from the northern Gulf of Mexico.

Previously reported habitat.—Intertidal to 30 m, commensal with *Notomastus lob-*

atus, in muddy clay, muddy silt and mud, T = 27; S = 37.04; OM = 0.9.

Occurrence.—In mud, D = 16.

Distribution in Mexico.—Southern Gulf of Mexico.

Distribution.—North Carolina; northern Gulf of Mexico.

Genus *Cabira* Webster, 1879

Cabira incerta Webster, 1879

Cabira incerta.—Pettibone, 1966:178, figs. 11a–c, 12a–e.—Wolf, 1984:29.5, figs. 29.2a–f.—Salazar-Vallejo & Orensanz, 1991:272, figs. 2e–f.—Granados-Barba, 1994:138.

Material examined.—2 specimens: Mar 1989 sta. 7(1); Mar 1990 sta. 2(1).

Remarks.—A large number of broken setae were present in the specimens collected during this study, especially on anterior segments, making proper identification difficult.

Previously reported habitat.—1–75 m, in mud, muddy sand, silty sand and very fine to medium sand.

Occurrence.—In mud, D = 16–70; OM = 1.66.

Distribution in Mexico.—Gulf of Tehuantepec, Oaxaca; southern Gulf of Mexico.

Distribution.—Chesapeake Bay; northern Gulf of Mexico.

Genus *Sigambra* O. F. Müller, 1858

Sigambra tentaculata (Treadwell, 1941)

Ancistrosyllis tentaculata Treadwell, 1941: 1, figs. 1–3.

Sigambra tentaculata.—Pettibone, 1966: 182, figs. 14a–f, 15a–e.—Gardiner, 1976: 121, fig. 9c.—Wolf, 1984:29.8, figs. 29.6a–h.—Granados-Barba, 1994:138, pl. 20a.—Blake, 1994b:285, fig. 10.6.

Material examined.—19 specimens: Mar 1988, sta. 6(1), 14(1); Sep 1988, sta. 4(1), 9(1); Mar 1989, sta. 6(1), 7(1), 9(1), 10(1), 11(1); March 1990, sta. 2(2), 5(3), 9(1), 12(3), 16(1).

Remarks.—On all specimens examined in this study, the notopodial hooks start on setiger 4, except for two specimens in which they start on setiger 5.

Previously reported habitat.—Intertidal to 5121 m, in sandy silt, mud, sandy mud, muddy sand, sand, and sand with gravel and shells, T = 13–31; S = 34.44–37.72; OM = 0.18–3.72; DO = 0.54–4.32.

Occurrence.—In mud and sandy mud, D = 16–127; T = 21–28; S = 35.51–36.99; OM = 0.39–1.58.

Distribution in Mexico.—Baja California Peninsula, Gulf of California, Sinaloa, Colima, Jalisco, Gulf of Tehuantepec, Tamiahua Lagoon, Veracruz, and central and southern regions of the Gulf of Mexico.

Distribution.—Black Sea, Red Sea, California, northwestern USA, New England to North Carolina, northern Gulf of Mexico, northeastern South America, and South Africa.

Sigambra wassi Pettibone, 1966

Sigambra wassi Pettibone, 1966:186, figs. 17a–f, 18a–e.—Wolf, 1984:29.8, figs. 29.4a–j.—Granados-Barba, 1994:139.

Material examined.—1 specimen: Sep 1988, sta. 6(1).

Previously reported habitat.—11–37 m, in sandy mud and silty sand.

Occurrence.—In mud, D = 16; T = 21–28; S = 35.59–36.52; OM = 1.1–1.32.

Distribution in Mexico.—Southern Gulf of Mexico.

Distribution.—Chesapeake Bay, northern Gulf of Mexico, and Cuba.

Family Orbiniidae Hartman, 1942

Some time after the galley proofs for the paper "The polychaetous annelids of the oil platforms area from the southeastern Gulf of Mexico: Orbiniidae and Cossuridae" by Granados-Barba & Solís-Weiss (1997) were sent to the press, we had the opportunity to examine material reported as *Naineris* sp. A by Taylor (1984) deposited in the Smithsonian Institution and the paratypes of *Scoloplos texana.* The results of our examination of this material are presented below.

Scoloplos (*Scoloplos*) *texana* Maciolek & Holland, 1978

Scoloplos texana Maciolek & Holland, 1978:161, figs. 1–4.—Taylor, 1984:1.31, fig. 1.32a.

Naineris sp. A.—Taylor, 1984:1.5, figs. 1.2a–f.—Granados-Barba, 1994:29, pl. 3d.—Granados-Barba & Solís-Weiss, 1997.

Material examined.—8 specimens: Sep 1988, sta. 6(1); Mar 1989, sta. 7(1), 9(1), 11(1); Oct–Nov 1990, sta. 6(1), 7(1), 9(1), 10(1).

Additional material examined.—*Scoloplos texana* USNM 52733, paratype, Corpus Christi Bay, Texas, Gulf of Mexico, USA, sta. 147-1, 22°49′N, 92°08′22″W. USNM 52732, paratypes, 2 specimens from Corpus Christi Bay, Texas, Gulf of Mexico, USA, sta. 122-6, 27°48′38″N, 97°20′17″W. BLM 2423C, Jul 1976, B-23-1, 2 specimens as *Naineris* sp. A., USNM 090117, 1 specimen from southern Louisiana, Gulf of Mexico, USA, sta. 04P, 28°34′09″N, 90°24′32″W, as *Naineris* sp. A.

Material of other species examined.—*Scoloplos treadwelli* Eisig, 1914 USNM 16067, as *Aricia cirrata* Treadwell, 1901, Mayaguez Harbor, Blackbuoy, Puerto Rico, sta. (133)6061. USNM 16066, as *A. cirrata* Treadwell, 1901, Mayaguez Harbor, E of P. Algarrobo, Puerto Rico, sta. (136)6066.

Remarks.—Taylor's (1984) *Naineris* sp. A, are in fact *Scoloplos texana* also cited in Taylor (1984). The confusion probably stems from the definition of the prostomium shape for the genus *Naineris* (rounded or square). The prostomium of *S. texana* is not clearly pointed nor triangular as happens with most other species of *Scoloplos* neither it is rounded or square as is typical of *Naineris*; however, the presence of branchiae in abdominal setigers and the characteristic shape of the abdominal neuropodia (especially the setal insertion), so reminiscent of *S. texana,* left no doubt as to the proper identity of the former *Naineris* sp. A.

Specimens of *S. treadwelli* and *S. texana* are similar; they basically differ in that in the first, the neuropodial acicular spines present in anterior setigers are arranged in two rows, whereas in the second there is only a single row.

Maciolek & Holland (1978), stated that, characteristically, in *S. texana,* the branchiae are never present in the thorax whereas in *S. treadwelli* they can start anywhere from last two thoracic to the first two abdominal segments. The latter arrangement was not observed in any of the specimens of this study.

Previously reported habitat.—15–45 m, in clay, mud, sandy mud and fine sand, T = 28; S = 35.59–36.94; OM = 0.59–1.65.

Occurrence.—In mud and sandy mud, D = 15–33; T = 28; S = 35.59–36.94; OM = 0.59–1.65.

Distribution in Mexico.—Gulf of California, southern Gulf of Mexico.

Distribution.—Northern Gulf of Mexico.

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Literature Cited

Blake, J. A. 1994a. Phyllodocidae. Pp 115–186 *in* J. Blake & B. Hilbig, eds. Taxonomic Atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 4. The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History Publications, 377 pp.

———. 1994b. Pilargiidae. Pp. 271–294 *in* J. Blake & B. Hilbig, eds. Taxonomic Atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 4. The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History Publications, 377 pp.

Day, J. H. 1973. New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. NOAA Technical Reports NMFS Circ. 375, 139 pp.

Gardiner, S. L. 1976. Errant Polychaete Annelids from North Carolina.—Journal of Elisha Mitchell Science Society 91:77–270.

Gathof, J. M. 1984. Phyllodocidae. Pp. 19.1–19.42 *in* J. M. Uebelacker & P. G. Johnson, eds., Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Final report to the Minerals Management Service, contract 14-12-001-29091, Barry A. Vittor & Assoc., Inc., Mobile, Alabama.

Gilbert, K. M. 1984a. Glyceridae. Pp. 32.1–32.26 *in* J. M. Uebelacker & P. G. Johnson, eds., Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Final report to the Minerals Management Service, contract 14-12-001-29091, Barry A. Vittor & Assoc., Inc., Mobile, Alabama.

———. 1984b. Goniadidae. Pp. 33.1–33.19 *in* J. M. Uebelacker & P. G. Johnson, eds., Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Final report to the Minerals Management Service, contract 14-12-001-29091, Barry A. Vittor & Assoc., Inc., Mobile, Alabama.

Granados-Barba, A. 1994. Estudio sistemático de los anélidos poliquetos de la región de plataformas petroleras del Sur del Golfo de México.—Tesis Maestría, Facultad de Ciencias, Universidad Nacional Autónoma de México, 287 pp.

———, & V. Solís-Weiss. 1994. New records of polychaetous annelids (Order: Eunicida) from the southeastern Gulf of Mexico.—Bulletin of Marine Science 54(2):420–427.

———, & ———. 1997. The polychaetous annelids of the oil platforms area from the southeastern Gulf of Mexico: Orbiniidae and Cossuridae.—Bulletin of Marine Science. 60(2), March 1997.

Hartman, O. 1950. Goniadidae, Glyceridae and Nephtyidae.—Allan Hancock Foundation Pacific Expeditions 15(1):1–181.

Hilbig, B. 1994a. Glyceridae. Pp. 197–214 *in* J. Blake & B. Hilbig, eds., Taxonomic atlas of the Benthic Fauna of the Santa Maria Basin and western Santa Barbara Channel. Vol. 4. The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History Publications, 377 pp.

———. 1994b. Goniadidae. Pp. 215–230 *in* J. Blake & B. Hilbig, eds., Taxonomic atlas of the Benthic Fauna of the Santa Maria Basin and western Santa Barbara Channel. Vol. 4. The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History Publications, 377 pp.

———. 1994c. Hesionidae. Pp. 243–269 *in* J. Blake & B. Hisbig, eds., Taxonomic atlas of the Benthic fauna of the Santa Mariabasin and western Santa Barbara Channel. Vol. 4. The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History Publications, 377 pp.

Maciolek, N. J., & J. S. Holland. 1978. *Scoloplos texana:* a new orbiniid polychaete from South Texas, with notes on the related species *Scoloplos treadwelli* Eisig.—Contribution to Marine Science 21:161–169.

Moore, J. P. 1903. Polychaeta from the coastal slope of Japan and from Kamchatka and Bering Sea.—Proceedings of the Academy of Natural Sciences of Philadelphia 55:401–490, pls. 23–27.

———. 1909. The polychaetous annelids dredged by the USS "Albatross" off the coast of southern California in 1904. I. Syllidae, Sphaerodoridae Hesionidae and Phyllodocidae.—Proceedings of the Academy of Natural Sciences of Philadelphia 61:321–351.

Mountford, K. N. 1991. Redescription of *Phyllodoce erythrophylla* (Schmarda, 1861) and *P. madeirensis* Langerhans, 1880 (Polychaeta: Phyllodocidae), with comments on some related taxa.—Ophelia Supplement 5:157–168.

Perkins, T. H. 1984. New species of Phyllodocidae and Hesionidae (Polychaeta), principally from Florida.—Proceedings of the Biological Society of Washington 97:555–582.

Pettibone, M. H. 1963. Marine polychaete worms of the New England region.—United States National Museum Bulletin 227(1):1–356.

———. 1966. Revision of the Pilargidae (Annelida: Polychaeta) including descriptions of new species, and redescription of the pelagic *Podarmus ploa* Chamberlin (Polynoidae).—United States National Museum Bulletin 118(3525):155–207.

Pleijel, F. 1991. Phylogeny and classification of the Phyllodocidae (Polychaeta).—Zoologica Scripta 20:225–261.

———. 1993. Polychaeta Phyllodocidae Marine Invertebrates of Scandinavia number 8. Scandinavian University Press, Norway, 159 pp.

Salazar-Vallejo, S. I., & J. M. Orensanz. 1991. Pilárgidos (Annelida: Polychaeta) de Uruguay y Argentina.—Cahiers de Biologie Marine 32:267–279.

Solís-Weiss, V., V. Rodríguez-Villanueva, A. Granados-Barba, V. Ochoa-Rivera, L. Miranda-Vázquez, & P. Hernández-Alcántara. 1994. Annelid polychaete populations of the Order Eunicida from the southern Gulf of Mexico.—Mémoires du Muséum. National d Histoire Naturelle 162:559–566.

———, A. Granados-Barba, V. Rodriguez-Villanueva, L. Miranda-Vázquez, V. Ochoa-Rivera, & P. Hernández-Alcántara. 1995. The Lumbrineridae of the continental shelf in the Mexican portion of the Gulf of Mexico.—Mitteilungen des Hamburgischen Zoologischen Museum Institut Band 92, Ergbd S, pp. 61–75.

Taylor, J. L. 1984. Orbiniidae. Pp. 1.1–1.38 *in* J. M. Uebelacker & P. G. Johnson, eds., Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Final report to the Minerals Management Service, contract 14-12-001-29091, Barry A. Vittor & Associates. Inc., Mobile, Alabama.

Treadwell, A. L. 1917. Polychaetous annelids from Florida, Puerto Rico, Bermuda, and the Bahamas.—Carnegie Institute of Washington, Department of Marine Biology Papers 11:255–268.

———. 1941. Polychaetous annelids from the New England Region, Porto Rico and Brazil.—American Museum Novitates New York (1138): 4 pp.

Uebelacker, J. M. 1984. Hesionidae. Pp. 28.1–28.39 *in* J. M. Uebelacker & P. G. Johnson, eds., Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Final report to the Minerals Management Service, contract 14-12-001-29091, Barry A. Vittor & Assoc., Inc., Mobile, Alabama.

———, & P. G. Johnson (eds.). 1984. Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Final report to the Minerals Management Service, contract 14-12-001-29091, Barry A. Vittor & Assoc., Inc., Mobile, Alabama.

Webster, H. E., & J. E. Benedict. 1887. The Annelida Chaetopoda from Eastport, Maine.—U.S. Commision Fishery of Washington Reports 1885: 707–755.

Wolf, P. S. 1984. Pilargidae. Pp. 29.1–29.41 *in* J. M. Uebelacker & P. G. Johnson, eds., Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico. Final report to the Minerals Management Service, contract 14-12-001-29091, Barry A. Vittor & Assoc., Mobile, Alabama.

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Stratiodrilus (Annelida: Polychaeta: Histriobdellidae) associated with a freshwater decapod, with the description of a new species

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Abstract—A new species of Histriobdellidae (Annelida; Polychaeta) from Brazil, belonging to the genus *Stratiodrilus* (commensal polychaete) is described. *Stratiodrilus arreliai* is distinguished by the characteristics of the body appendages, and mandible apparatus as well as by its biogeographical distribution. A brief discussion is made on the association between the genus *Stratiodrilus* and the anomuran genus *Aegla.*

Freshwater decapod crustaceans are known to show a wide range of ectosymbiont invertebrates. These include protozoans, platyhelminths, nematodes, rotifers, annelids and small crustaceans. The occurrence and distribution of these associations as well as nutritional aspects of the physiology of some of these symbionts have been investigated (Cannon & Jennings 1987).

There are records of species of *Stratiodrilus* as symbionts of the following decapod genera: *Parastacus, Cherax, Trichodactylus, Astacoides* and, more frequently, *Astacopsis* and *Aegla* (Haswell 1900, Cordero 1927, Harrison 1928, Mouchet 1932, Vila & Bahamonde 1985, Nonato 1985, Cannon & Jennings 1987). In Brazil, the genus *Stratiodrilus* has been noted as commensal on the brachiuran *Trichodactylus petropolitanus* by Nonato (1985) and, in the present work, on the anomuran genus *Aegla.*

Among the several epibionts that are commonly associated with the Aeglidae, are the polychaetes that coexist with temnocephalid platyhelminths (Moyano et al. 1993). Several families of the Class Polychaeta have commensal species that live in the tubes or cavities of other polychaetes and crustaceans, in corals, and in echinoderms. Among these, the family Histriobdellidae includes some species with odd characteristics in morphology and life history. These are divided in only two genera, *Histriobdella* and *Stratiodrilus,* epizootic polychaetes respectively of marine and freshwater invertebrates. The small polychaete *Stratiodrilus* occurs frequently among the branchial lamellae of crabs and feeds on the microflora that grows in the branchial cavity of the host (Cannon & Jennings 1987).

In this paper we record the association between *Aegla* and *Stratiodrilus* and describe the new species *S. arreliai* from Southeast Brazil. We also discuss briefly the main interspecific characters of the genus.

The Genus *Stratiodrilus*

Stratiodrilus presents no distinction into prostomium and peristomium; head with seven appendages, five of these being tentacles (one medium and two lateral pairs). The second pair is bisegmented having sensorial (tactile) function (Haswell 1900). The other two appendages (anterior limbs) may aid in locomotion, according to Haswell (1900).

The mandible apparatus is black and extremely complex. It is composed of different pieces arranged in two sets: the upper and lower jaws. The upper jaws consist of a median piece, "the fulcrum", and two sets of lateral pieces composing the rami. The lower jaws are paired throughout.

The body is constricted at regular intervals, and may be described as imperfectly divided into six segments (Haswell 1900). The first segment ("neck") is short and has no cirri. The second, third and fifth segments have each a mammiform elevation that bears the lateral cirri of the body (C1, C2, C3). The caudal region bears the posterior limbs which are not retractile and have one or two pairs of posterior cirri (C4, C5), which may be single or double. These characters are of great taxonomic significance to the species level. The tentacles and the cirri alike are tipped with fine sensory cilia.

The sexes are separate and dimorphic. The male has a pair of retractile ventral claspers in the fourth segment of the body very conspicuous, which are totally absent in the female. In the female the eggs are also easily distinguished as rounded volumes of different sizes.

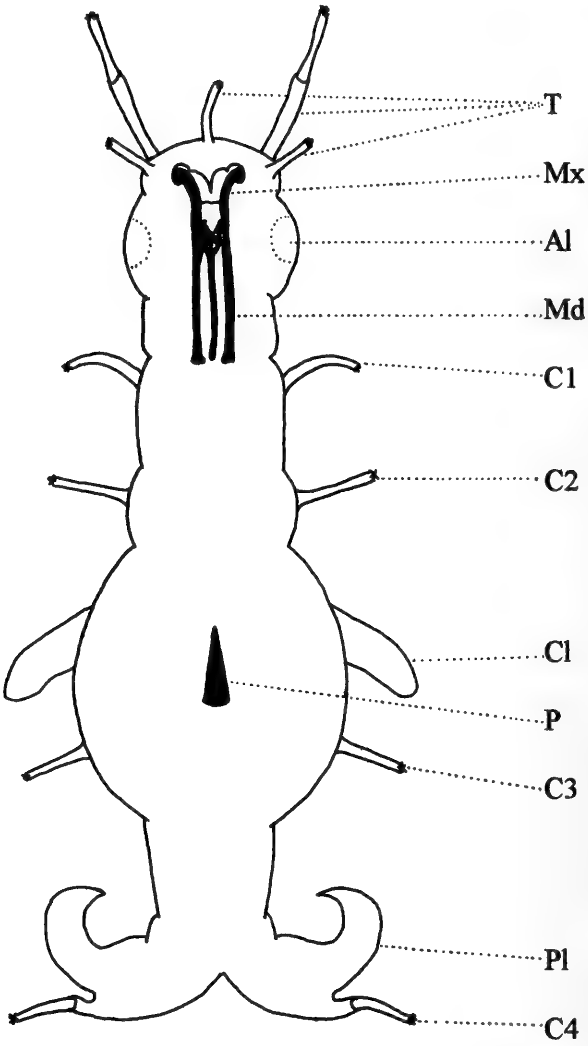


Fig. 1. *Stratiodrilus arreliai* new species (ventral view); anterior limbs (A1); 1st to 5th pair body cirri (C1–5); clasper (CL); mandible (Md); maxilla (Mx); penis (P); posterior limbs (P1); tentacles (T).

Stratiodrilus arreliai, new species
Fig. 1

The record of individuals of *Stratiodrilus* completely confined to the branchial chambers of anomurans comes from specimens of *Aegla perobae* collected at Gruta da Peroba in the municipality of São Pedro, São Paulo state (22°55′S; 47°87′W). This anomuran species was described in 1977 and, to date, has not been recorded for other localities (Bond-Buckup & Buckup 1994).

The study of the above mentioned *Stratiodrilus* specimens led us to the conclusion that they belong to a new species, which we called *Stratiodrilus arreliai.* The new species show some similarities with the ones already described, but is distinguished mainly by the characteristics of the body appendages, the disposition of the mandible apparatus and by its geographical distribution.

Material examined.—A total of 18 specimens and 5 eggs of *Stratiodrilus* were found in only one individual of *Aegla perobae* (ten and eight individuals in either side of the branchial chamber). Five of these (three males and two females) were stained and slide mounted for microscopical study. The holotype is deposited in the "Museu de História Natural da Universidade Estadual de Campinas" (MHN-BPO-54).

Individuals of the new species are very small, like individuals of the other species of the genus. The total length of males and females, was in average 0.681 mm (n = 3) and 0.745 mm (n = 2), respectively. Measures for mandible apparatus averaged 0.145 (n = 3) and 0.144 mm (n = 2), respectively for males and females. One em-

Table 1.—Species of *Aegla* recorded in the state of São Paulo and their sites of occurrence.

Species	Site
A. marginata Bond-Buckup & Buckup 1994	Iporanga (cave)
A. castro Schmitt 1942	Itatinga and Ourinhos (river)
A. franca Schmitt 1942	Perus and Franca
A. strinatii Türkay 1972	Registro (river), Iporanga (cave) and Eldorado Paulista (river and cave)
A. paulensis (Schmitt 1942)	Perus and Paranapiacaba
A. leptochela Bond-Buckup & Buckup 1994	São Pedro (cave)
A. perobae Hebling & Rodrigues 1977	Iporanga (cave)
A. cavernicola Türkay 1972	Iporanga (cave)
A. microphthalma Bond-Buckup & Buckup 1994	Iporanga (cave)

bryo and one immature were also measured (total length 0.137 and 0.370 mm, and mandible apparatus 0.081 and 0.099 mm, respectively).

The tentacles of the head are elongated, those of the first anterior pair (T2) being as long as the median one. The second pair (T3) is three times as long as the first, with one distinct division (Fig. 1). The three pairs of lateral cirri (C1, C2, C3) are long and unsegmented. On the posterior border of each limb there is a long cylindrical tentacle (cirrus C4). The posterior cirri (C4) emerge from a support that is an extension of the body. The mandible apparatus is very long, reaching the first segment. In the embryo, the mandible apparatus is fully developed, being almost the size of the whole egg.

Etymology.—The name of the new species was given in honor of Arrelia (Waldemar Seyssel), a famous Brazilian clown. This is in accordance with the meaning of the family name Histriobdellidae, which stands for animal similar to a stage-player (clown-like, in a free translation).

The Host Anomuran *Aegla*

The genus *Aegla* has its distribution restricted to the temperate and subtropical regions of South America. It is characterized as being the only anomuran genus inhabiting exclusively freshwater. It occurs in lagoons, streams, swift flowing rivers and cave rivers (Bond-Buckup & Buckup 1994). In the neotropical region its limits of distribution are, to the North, the municipality of Franca (São Paulo state, Brazil), and, to the South, the province of Ultima Esperanza, in Chile.

Of the 34 species at present recorded from Brazilian freshwaters, 29 may be considered endemic. As noted by Bond-Buckup & Buckup (1994) this fact supports the hypothesis that most species of *Aegla* have small areas of occurrence. There are records of nine species for the state of São Paulo (Table 1).

Detailed information on the genus *Aegla* may be found in Bond-Buckup & Buckup (1994) which present a review of the family Aeglidae as well as the description of twenty new species.

Discussion

To this moment, seven species of *Stratiodrilus* have been described (including one described here), plus one in Chile that was mentioned by Moyano et al. (1993) as new, but remains undescribed (Table 2).

The main differences between these species, regarding the structure and number of the cirri (C1–C5) are presented in Fig. 2. *Stratiodrilus arreliai* seems to be most closely related to *S. aeglaphilus*, mainly for being a small sized species and for having long appendages. About the terminology used to characterize the cirri C4 and C5, the term "forked" does not seem adequate, since all the references about the described

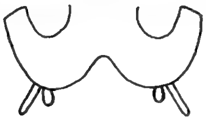
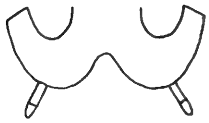
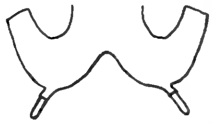
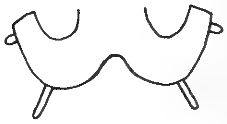
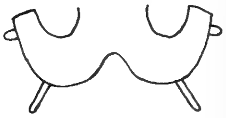
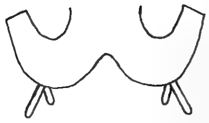
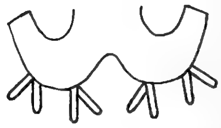
Species	**Lateral Cirri (C1, C2, C3)**	**Features of the Posterior Limbs Posterior Cirri (C4, C5)**	
S. tasmanicus Haswell	**Bisegmented**	**C4 double** non-segmented **C5 absent**	
S. novaehollandiae Haswell	**Bisegmented**	**C4 single** bisegmented **C5 absent** (dorsal lobe)	
S. arreliai n. sp.	**Non-segmented**	**C4 single** non-segmented basal support **C5 absent**	
S. haswelli Harrison	**Non-segmented** Distal, forked	**C4 single** bisegmented **C5 absent** **small tubercle**	
S. Aeglaphilus Vila & Bahamondi	**Non-segmented**	**C4 single** non-segmented **C5 absent** **small tubercle**	
S. platensis Cordeiro	**Non-segmented**	**C4 double** non-segmented **C5 absent**	
S. pugnaxi Vila & Bahamondi	**Non-segmented**	**C4 double** **C5 double** non-segmented	
Stratiodrilus sp. (in Moyano *et al.* 1993)	**Non-segmented**	**C4 double** **C5 single** non-segmented	

Fig. 2. Main differences among species, concerning the cirri (C1–C5).

species (including Moyano et al. 1993) indicate that they are double. Therefore, the term "forked" was replaced by "double" in this work, as it was mentioned in the discussion by Moyano et al. (1993). After consulting Haswell (1900) and Lang (1949), we concluded that the correct number of segments is six instead of five as mentioned by Vila & Bahamonde (1985). Besides the structural differences as compared to fig. 3 of Moyano et al. (1993), these species may also be distinguished by their host species and geographical distribution. The genus *Stratiodrilus* (Haswell 1900) includes epizootic species exclusive to freshwater, with a high degree of specialization and peculiar geographical distributions. This supports the alleged geologi-

Table 2.—Species of *Stratiodrilus* and their hosts, with their geographical distribution.

Species	Host	Geographic distribution
S. tasmanicus Haswell 1900	*Astacopsis franklinii* (Gray)	Tasmania
S. tasmanicus Haswell 1900	*A. franklinii tasmanicus* Erickson	Tasmania
S. novaehollandiae Haswell 1913	*Astacopsis serratus* Shaw	Australia
S. platensis Cordero 1927	*Aegla laevis* (Latreille)	Uruguay, Argentina
S. haswelli Harrison 1928	*Astacoides madagascariensis* Milne Edwards	Madagascar
S. aeglaphilus Vila & Bahamonde 1985	*Aegla laevis* (Latreille)	Chile
S. pugnaxi Vila & Bahamonde 1985	*Parastacus pugnax* (Poeppig)	Chile
S. arreliai new species	*Aegla perobae* Hebling & Rodrigues	Brazil

cal relationship between Australia, Madagascar and South America, as mentioned by Harrison (1928) and Vila & Bahamonde (1985).

The geographical distribution of *Stratiodrilus,* with such similar representatives in such distant continents and the coexistence on the same host with *Temnocephala* both in South America and in Australia, is no coincidence, as was mentioned by Cordero as early as 1927. The study of these distribution patterns may bring valuable insights to the comprehension of the vicariance model of biogeography of these groups, as well as to the understanding of the origin of the environments in which they are found.

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Literature Cited

Bond-Buckup, G., & L. Buckup. 1994. A familia Aeglidae (Crustacea, Decapoda, Anomura).—Arquivos de Zoologia, Museu de Zoologia da Universidade de São Paulo, São Paulo 32(4): 159–346.

Cannon, L. R. G., & J. B. Jennings. 1987. Occurrence and nutritional relationships of four ectosymbiotes of the freshwater crayfishes *Cherax dispar* Riek and *Cherax punctatus* Clark (Crustacea: Decapoda) in Queensland.—Australian Journal of Marine and Freshwater Research 38: 419–427.

Cordero, E. H. 1927. Un nuevo Arquianélido, *Stratiodrilus platensis* n.sp., que habita sobre *Aegla laevis* (Latr.). Nota preliminar.—Physis, 7:574–578.

Harrison, L. 1928. On the genus *Stratiodrilus* (Archiannelida: Histriobdellidae), with a description of a new species from Madagascar.—Records Australian Museum 16:116–121.

Haswell, W. A. 1900. On a new Histriobdellidae.—Quarterly Journal of Microscopical Science N.S. 43:299–335.

———. 1913. Notes on Histriobdellidae.—Quarterly Journal of Microscopical Science N.S., 59:91–99.

Lang, K. 1949. Morphology of *Stratiodrilus platensis* Cordero (Histriobdellidae).—Arkiv för Zoologi 42A(23):1–30.

Mouchet, S. 1932. Notes sur la biologie du Galathéide *Aeglea laevis* (Latr.). Bulletin de la Societé Zoologique de France 57:316–340.

Moyano, H. I., C. Franklin, & S. Gautéia. 1993. Sobre las espécies chilenas de *Stratiodrilus* Haswell 1900 (Polychaeta, Histriobdellidae).—Boletin de la Sociedad de Bioliologia de Concepcion Chile, 64:147–157.

Nonato, E. F. 1985. Biologia de *Stratiodrilus platensis* Cordero 1927 (Annelida, Polychaeta). Pp. 42 *in* Resumos XII Congresso Brasileiro de Zoologia. Campinas, Brasil, 12.

Vila, P. I., & N. Bahamonde. 1985. Two new species of *Stratiodrilus, S. aeglaphilus* and *S. pugnai* (Annelida, Histriobdellidae) from Chile.—Proceedings of the Biological Society of Washington, 98:347–350.

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A new polyclad flatworm, *Tytthosoceros inca* (Plathyhelminthes: Polycladida: Cotylea: Pseudocerotidae), from Chilean coastal waters.

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Abstract.—A new polyclad species, *Tytthosoceros inca* is described from Chilean coastal waters. It resembles *Pseudoceros luteus* (Plehn, 1898) Hyman 1953 incerta sedis but differs in having ear-like pseudotentacles, a brown marginal band, and dark brown spots on the dorsal surface of the body. *Tytthosoceros inca* is associated with the colonial ascidians *Ciona intestinalis* and *Pyura chilensis,* living on or near them. This is the first record of the genus from Chilean coastal waters and the second report of the family from cold temperate waters, although this time from the southern hemisphere.

Pseudocerotidae is one of the most populous families of polyclad flatworms (Hyman 1954, Newman & Cannon 1994). Marcus (1950) cited an extensive list of over 70 species, mainly *Pseudoceros* sensu lato, described from around the world. Hyman (1959a) extended the list to approximately 120, adding many species overlooked by Marcus (1950) and others described by her. Another 60 new species described by Hyman (1959b), Faubel (1984), Prudhoe (1981, 1989), and Newman & Cannon (1994, 1995, 1996a, 1996b) must now be added to the list of species described worldwide, increasing the total number of known species to at least 200.

Most species of the family occur in tropical and subtropical waters of the Indo-Pacific region (Hyman 1954). They have been reported less frecuently from warmer temperate waters around the world, and only one species, *Pseudoceros canadensis* Hyman, 1953 from cold temperate waters around British Columbia, Canada (Hyman 1953). However, this species is considered incerta sedis due to its incomplete description (Faubel, 1984; Newman & Cannon, 1984).

At present, the following 14 pseudocerotid genera are recognized; *Thyzanozoon* Grube, 1840, *Acanthozoon* Collingwood, 1876, *Pseudoceros* Lang, 1884, *Yungia* Lang, 1884, *Nymphozoon* Hyman, 1959, *Cryptoceros* Faubel, 1984, *Cryptobiceros* Faubel, 1984, *Monobiceros* Faubel, 1984, *Pseudobiceros* Faubel, 1984, *Parapseudoceros* Prudhoe, 1989, *Bulaceros* Newman & Cannon 1996, *Tytthosoceros* Newman & Cannon 1996, *Maiazoon* Newman & Cannon 1996, and *Phrikoceros* Newman & Cannon 1996. They can be easily distiguished by details of the male and female reproductive systems (presence or absence of prostate and seminal vesicle, and the number of gonopores and complexes), the alimentary system (presence or absence of anal pores), and by external characters, such as the shape of the body, pseudotentacles, pharynx and pharyngeal lobes, and the arrangement of the cerebral and pseudotentacular eyes (Newman & Cannon 1994, 1995, 1996a, 1996b).

Nevertheless, species recognition and differentiation within each genus presents problems in this group, like in many others that lack solid structures. Marcus (1950), Hyman (1954, 1959a), Faubel (1984), Prudhoe (1989), and Newman & Cannon (1994) have commented extensively on the subject. Authors based species identification primarily on body colour pattern (Hyman 1954, 1959a, Prudhoe 1989, Newman & Cannon 1994). Aspects of the male copulatory apparatus, such as the relationship between size of the seminal and prostatic vesicles, cannot be used, due to the extreme similarity of the complex within each genus and considering that some features can change during development or can be deformed by histological procedures (see Prudhoe 1989, Newman & Cannon 1994).

In Chile, the only study on polyclad flatworms is that of Marcus (1954), based on specimens collected by the Lund's University Chile Expedition. No other research has been conducted and Pseudocerotidae species have not been reported from the country to date.

During exploratory diving in northern Chile we observed a pseudocerotid polyclad which belongs to the recently described genus, *Tytthosoceros* Newman & Cannon, 1996. This is the first record of the genus from Chilean coastal waters (Marcus 1951) and the second report of the family that we have noticed from cold temperate waters, in this case in the southern hemisphere.

Materials and Methods

Tytthosoceros inca specimens were collected from lantern nets with *Argopecten purpuratus* (Lamarck, 1819) (Pectinidae) located along a dock at the Universidad Católica del Norte, in Bahía La Herradura, Coquimbo (29°58′S, 71°22′W), Chile. Flatworms were observed on the fouling of the lanterns, typically in association with the ascidian *Ciona intestinalis* (Linnaeus, 1767).

Four specimens were mounted *in toto* after fixation in Bouin-Hollande, stained with Delafield's hematoxylin, and cleared with xylol.

For histology, specimens were fixed in Bouin-Hollande, embedded in paraffin, serial sectioned at seven micrometers, and stained with Harris hematoxylin and eosin. Photographs were taken using a Nikon Biophot microscope and drawings of the male and female copulatory apparatus were made.

The specimens selected as type material were fixed in Bouin-Hollande, preserved in 70% ethanol, and deposited in the Museo Nacional de Historia Natural, Santiago, Chile (MNHNC) and in the Sala de Sistemática, Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago (SSUC).

Results and Discussion

Tytthosoceros inca, new species
Figs. 1–3

Material examined.—North Chile: Bahía La Herradura, Coquimbo, 2 m, D. Véliz & L. M. Pardo coll., from scallop lantern nets associated with the ascidian *Ciona intestinalis,* 26 Feb 1996, holotype (MNHNC-PL. 11143), 2 paratypes (MNHNC-PL. 11144 and 11145), and 1 specimen (SSUC 6765); Bahía La Herradura, from lantern nets, 1 m, J. A. Baeza coll., Oct 1994, 7 specimens (4 cleared and 3 sectioned); Bahía La Herradura, associated with *Pyura chilensis* Molina, 1782 (Tunicata), 0.5 m, R. Acuña, P. Romero and J. C. Villarroel coll., Apr 1993, 7 specimens.

Description.—External morphology: Mature living specimens are extremely soft and thin, reaching a maximum length and width of 11 cm and 6 cm, respectively. The body is ovoid in small animals, becoming elongated-ovoid in worms over 5 cm long. The body margins are broadly folded, caudal and anterior margins are rounded. The dorsal surface is smooth. A pronounced middorsal ridge extends along the animal, ending blindly some distance before the posterior margin (Figs. 1, 2A). Marginal pseudotentacles are weakly developed and ear-like, formed as is usual by the upfolding

Fig. 1. *Tytthosoceros inca,* new species. Photograph of living organism, dorsal view. Scale bar in centimeters.

of the anterior margin (Figs. 2B, C). Each pseudotentacle has a pronounced auricular groove ventrally (Fig. 2C).

On living animals, the mouth opens in the mid-ventral line, in middle of the pharynx. The pharynx begins on the second ninth of the animal, occupying about one fourth or one fifth of body length. The male gonopore opens beneath the posterior end of the pharynx over a promontory. The female pore is located close behind it, about one half the distance between the mouth and the male apperture. The ventral sucker is conspicuous and circular, lying anterior to the middle of the body. The distance between the sucker and female apperture is about three or four times the distance between the male and female pores (Fig. 2A).

Color: The ground color of the dorsal surface on living animals is brownish-yellow with a narrow marginal white stripe and a broader border-band of pale brown around the body, except on the pseudotentacles (Fig. 1). The dorsal surface also shows many dark brown dots with no special arrangement, decreasing in size to the margins but increasing in number. A narrow black stripe extends along the center of middorsal ridge. This stripe begins at the proximal end of the pharynx, immediately behind cerebral eyespot, ending somewhat before the ridge (Figs. 1, 2B). Only the tip presents the white marginal stripe on the pseudotentacles. Along the inner border of each pseudotentacle, a dark brown stripe exists, narrowing towards the tips and widening at the pseudotentacular bases. Both stripes are not connected with the middorsal one. Another pair of dark brown stripes extends marginally between pseudotentacular bases (Fig. 2B). Ventrally, the color is brownish-yellow with a marginal white stripe and pale brown border-band around the body.

Eyes: Ocelli of chalice type. Cerebral eyespot present as a single oval cluster in small animals or horseshoe shaped in worms over 6 cm length (Fig. 2B). In all animals over 6 cm length, a pair of precerebral eyes lies deep in the parenchyma some distance before the cerebral cluster. Few pseudotentacular eyes extend along the dorsal surface of pseudotentacles. There are also eyes scattered dorsally, between pseudotentacular bases (Fig. 2B). Ventrally, pseudotentacular eyes are more numerous, extending as two irregular clusters along the margins of pseudotentacles, ending as a pair of inverted triangles between the pseudotentacular bases (Fig. 2C).

Digestive system: Ruffled pharynx deeply folded and contained inside the pharyngeal chamber formed by the anterior portion of the central ridge. Behind the pharynx chamber, the ridge contains the main intestinal branch that extends to the posterior end of the body, giving rise along its course to numerous branches that divide to

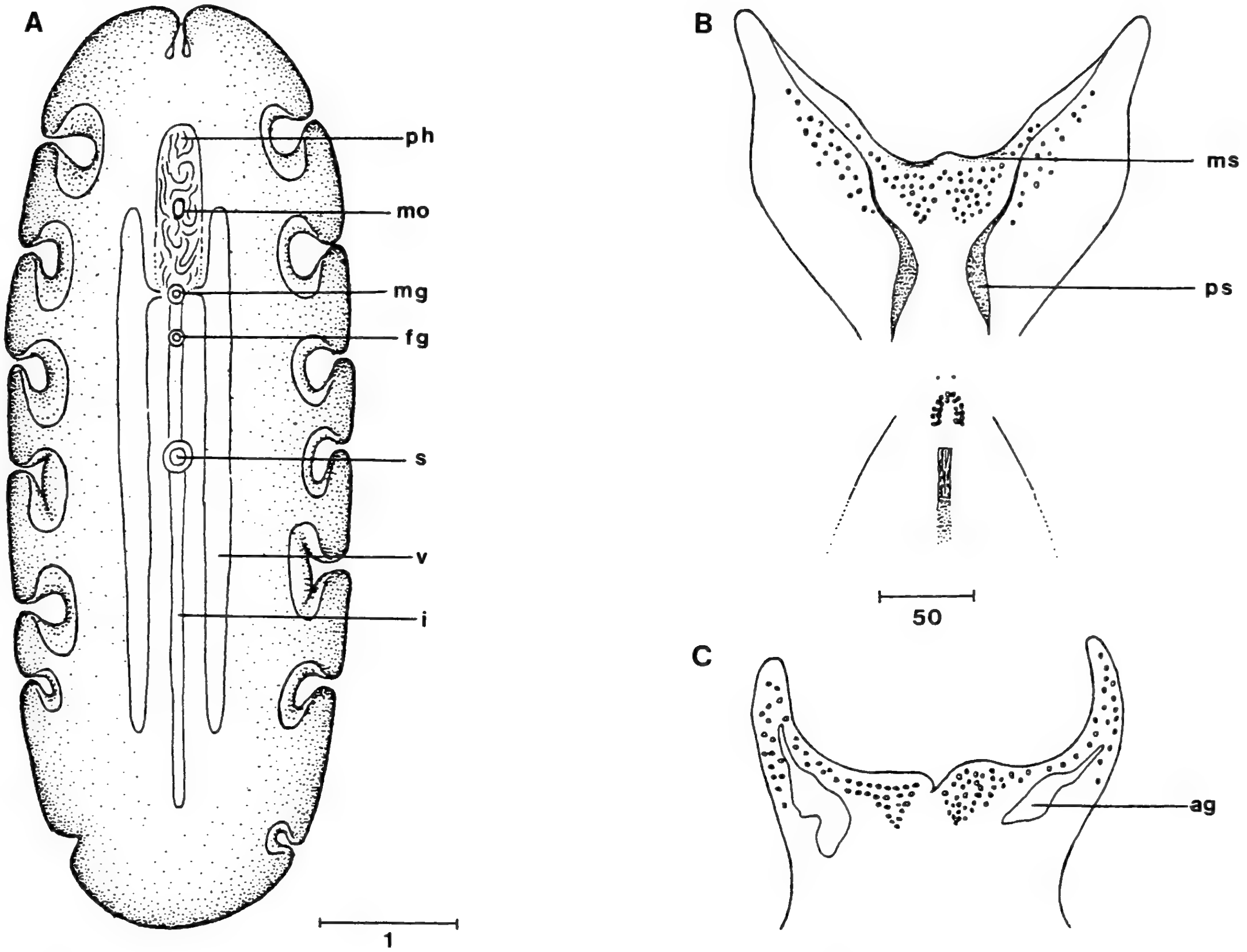

Fig. 2. *Tytthosoceros inca,* new species. A, ventral view of body; B, anterior portion of body in dorsal view, showing pseudotentacle morphology, eye arrangement and color pattern; C, pseudotentacles, ventral view (MNHNC-PL. 11143). Scale bars in centimeters (A) and micrometers (B and C). Abbreviations: ag = auricular groove, fg = female gonopore, i = main intestine, mg = male gonopore, ms = marginal inter-pseudotentacular stripe, mo = mouth, ph = pharynx, ps = dorsal pseudotentacular stripe, s = sucker, v = vas deferens.

form a dense anastomosed network. It seems that the main intestine does not extend further over the pharynx, but some diverticules can be found.

Copulatory apparatus: The vas deferens form a prominent network extending forward and backward, running along each side of the main intestine. A single male copulatory complex exists (Fig. 3). Two sperm ducts connect spermiductal vesicles with the posterolateral extremes of an oval-elongated seminal vesicle. At its proximal end it narrows to form a sinuous ejaculatory duct that joins the base of a conical penis papilla. At the same location on papilla the ovoid prostate or prostatic vesicle is connected by a short prostatic duct. The seminal vesicle is about three times the size of the prostate. The penis papilla is armed with a short and wide cuticular stylet both surrounded by a penis sheath. The length: width ratio of the stylet is 1:3.5. The male antrum is narrow and deep.

The female gonopore leads into a deep female antrum that opens into a laterally expanded cement pounch. On all sectioned specimens, the vagina was never observed connected with any cement gland. From the cement pounch the vagina ascends, surrounded by the cement gland. The vagina then curves and receives the uteri (Fig. 3).

Geographical distribution.—Known from Bahía La Herradura (29°58′S,

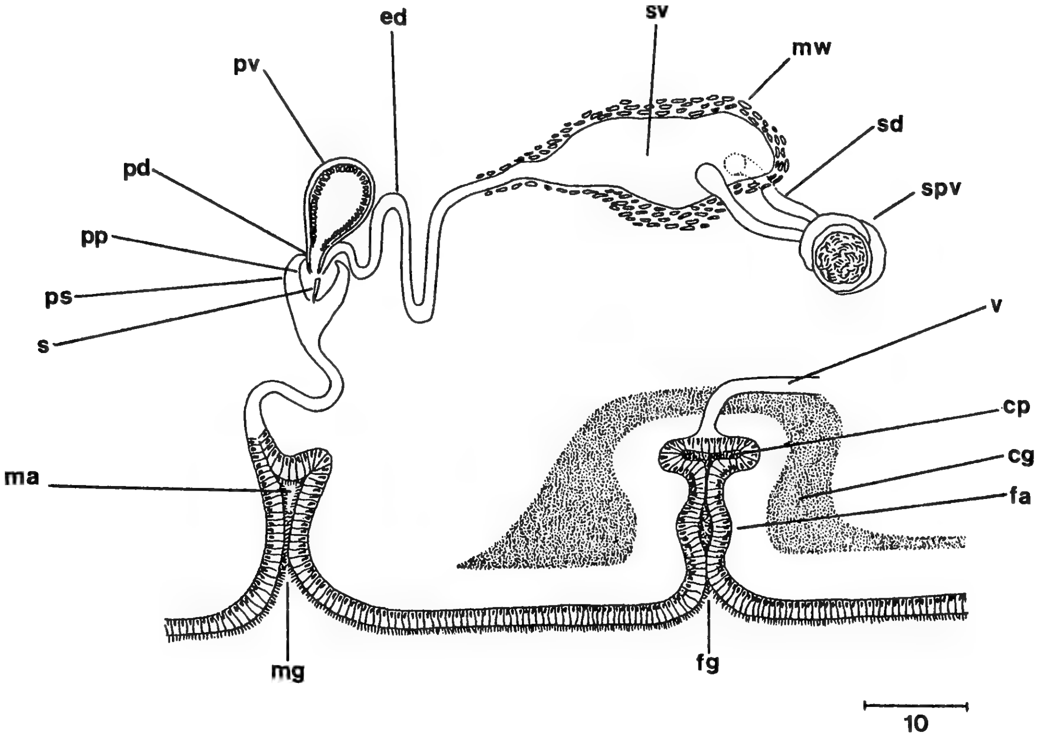

Fig. 3. *Tytthosoceros inca,* new species. Male and female copulatory apparatus, sagital view. Scale bar in micrometers. Abbreviations: cg = cement gland, cp = cement pounch, ed = ejaculatory duct, fa = female antrum, fg = female gonopore, ma = male antrum, mg = male gonopore, mw = muscular wall, pd = prostatic duct, pp = penis papilla, ps = penis sheath, pv = prostatic vesicle, s = stylet, sd = sperm ducts, spv = spermiductal vesicles, sv = seminal vesicle, v = vagina.

71°22′W), Guanaqueros Bay (30°04′S, 71°23′W), and Tongoy Bay (30°14′S, 71°28′W), north Chile.

Taxonomical remarks.—The presence of small ear-like pseudotentacles, the arrangement of dorsal eyes, and the short and wide penial stylet allow us to classify the studied type specimens as *Tytthosoceros,* a genus recently erected by Newman & Cannon (1996a). This genus has a single reproductive system, but on its overall morphology it resembles *Pseudobiceros* Faubel, 1984 wich possesses paired male systems (Newman & Cannon 1994). Studied specimens can be distinguished from *Bulaceros* Newman & Cannon 1996, which has two cerebral eye clusters (not a horseshoe shaped cerebral eyespot), a flat body shape (without a pronounced ridge) and a weakly sclerotised, small, and narrow penial stylet. Moreover, the pronounced central ridge of the body, the ear-like tentacles, and the dorsal eye arrangement of type specimens distinguish *T. inca* from *Pseudoceros,* which has a flat body shape, simple pseudotentacles, and dorsal eyes disposed in two to three scattered lines across the anterior pseudotentacular rim (Newman & Cannon 1994).

With regard to the overall body shape and the colour pattern (ground colour of the body and medial black stripe), *Tytthosoceros inca* resembles only one species, *Pseudoceros luteus* (Plehn, 1898) previously reported from Monterrey Bay and Corona del Mar, California coast (Hyman 1953). The latter is considered as incerta sedis, since Newman & Cannon (1994) did not considered it as a member of *Pseudoceros* sensu stricto when they reviewed the taxonomy of the group.

Both species can be distinguished by details of pseudotentacular morphology and colour pattern. While in *P. luteus* the tentacles are broad and flap-like (Marcus 1953), in *T. inca* they are weakly developed and ear-like, with respect to body marks, *P. luteus* lacks the pale brown border-band and the dark brown spots on the dorsal surface observed on the body of *T. inca.* Also, the middorsal stripe in *P. luteus* forks before the cerebral eyes and continues along the anterior margin of the body to connect with a pair of large oval spots (Plehn 1898, Hyman 1953), while in *T. inca* this stripe ends immediately behind the cerebral eyes and is not associated with any other markings.

All features mentioned above have been considered as important diagnostic characters by Marcus (1950), Hyman (1954), Prudhoe (1984), and Newman & Cannon (1994, 1995, 1996a, b), allowing us to differentiate *Tytthosoceros inca* from *Pseudoceros luteus* and to describe the former as a new species.

Hyman (1953) also reports a mottled gray color variant of *Pseudoceros luteus.* In our opinion, it is probably another species due to colour pattern differences with *P. luteus.* It is also appropriate to compare the new species with this color variant. *P. luteus* and the color variant of *P. luteus* present the same morphological differences with respect to *T. inca.* Concerning body marks, the color variant can be distinguished from *T. inca* because it lacks the middorsal black stripe and the pale brown border-band found in the new species.

The main diagnostic characters that differ between this new species and other *Tytthosoceros* are; the pronounced male antrum, the extremely short prostatic duct and the long ejaculatory duct, the long and narrow stylet (largest in *T. inca,* length:width ratio 1:1.35, compared to 1:2 for *T. lizardensis* Newman & Cannon 1996 and *T. nocturnus* Newman & Cannon 1996), and the presence of a pair of pre-cerebral eyes lying deep in the parenchyma in all animals over 6 cm length (not present in others congeners). Due to these differences, it is possible that the present specimens warrant a new genus (Newman, pers. comm.). However, due to the lack of complete morphological and anatomical information on previously described pseudocerotids, we considered our specimens as members of *Tytthosoceros.* We believe that more information is needed on several species in order to erect a new genus.

Etymology.—The name *inca* refers to the Incan civilization that occupied the northern and north-central area of Chile during the Pre-Hispanic age.

Ecological remarks.—This species has also been observed in Bahía La Herradura and Tongoy in shallow waters, living close to or on the colonial ascidian *Pyura chilensis.* It probably feeds directly on the ascidians or may prey on the bivalves when inhabiting lantern nets. The former feeding habit has been previously described for other species of the family (Hyman 1951, Newman & Cannon 1994). *Tytthosoceros inca* also can be observed in dense aggregations on the bottom or swimming towards the surface with undulating movements.

This is the first record of the genus *Tytthosoceros* from coastal Chilean waters. Since until now only one species of Pseudocerotidae has been cited for cold temperate waters, this appears to be the second record for the family, although this time from the southern hemisphere.

Acknowledgment

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Literature Cited

Faubel, A. 1984. The Polycladida, Turbellaria. Proposal and establishment of a new system. Part II. The Cotylea.—Mitteilungen aus dem hamburgischen Zoologischen Museum und Institut, Hamburg 81:189–259.

Hyman, L. H. 1951. The Invertebrates II. Platyhelminthes and Rhynchocoela. McGraw-Hill Book Company, New York, 550 pp.

———. 1953. The polyclad flatworms of the Pacific coast of North America.—Bulletin of the American Museum of Natural History, New York 100:265–392.

———. 1954. The Polyclad genus *Pseudoceros,* with special reference to the Indo-Pacific region.—Pacific Science 8:219–225.

———. 1959a. A further study of micronesian polyclad flatworms.—Proceedings of the United States National Museum 108:543–597.

———. 1959b. Some Australian polyclads (Turbellaria).—Records of The Australian Museum, Sydney 25:1–17.

Marcus, E. 1950. Turbellaria Brasileiros (8).—Boletin da Faculdade de Filosofia Ciencias e Letras Universidada de Sao Paulo, Zoologia 15:5–192.

———. 1954. Reports of the Lund University Chile Expedition 1948–1949. 11.—Acta Universitatits Lundensis 49(13):1–115.

Newman, L. J., & L. R. G. Cannon. 1994. *Pseudoceros* and *Pseudobiceros* (Platyhelminthes, Polycladida, Pseudocerotydae) from eastern Australia and Papua New Guinea.—Memoirs of the Queensland Museum 37(1):205–266.

———. 1995. Colour pattern variation in the tropical flatworm, *Pseudoceros* (Platyhelminthes, Polycladida), with descriptions of three new species.—The Raffles Bulletin of Zoology 43(2): 435–446.

———. 1996a. *Bulaceros,* new genus, and *Tytthosoceros,* new genus, (Platyhelminthes: Polycladida) from the great barrier reef, Australia and Papua New Guinea.—The Raffles Bulletin of Zoology 44(2):479–492.

———. 1996b. New genera of pseudocerotid flatworms (Platyhelminthes, Polycladida) from Australian And Papua New Guinean coral reefs.—Journal of Natural History 30:1425–1441.

Plehn, M. 1898. Drei neuen Polycladiden.—Jenaische Zeitschrift für Naturwissenschaft, Jena 31:90–99.

Prudhoe, S. 1981. Polyclad turbellarians from the southern coasts of Australia.—Records of the South Australian Museum 18:361–384.

———. 1989. Polyclad turbellarians recorded from African waters.—Bulletin of the British Museum (Natural History), Zoology 55:47–96.

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2906 *Anomalina* d'Orbigny, 1826 (Foraminiferida): proposed designation of *A. ariminensis* d'Orbigny in Fornasini, 1902 as the type species.

2940 *Riisea* and *riisei* Duchassaing & Michelotti, 1860 (Cnidaria, Anthozoa): proposed conservation as the correct original spellings of generic and specific names based on the surname Riise.

2999 *Umbellula* Cuvier, [1797] (Cnidaria, Anthozoa): proposed conservation as the correct original spelling, and corrections to the entries relating to *Umbellularia* Lamarck, 1801 on the Official Lists and Indexes of Names in Zoology.

2939 *Galba* Schrank, 1803 (Mollusca, Gastropoda): proposed designation of *Buccinum truncatulum* Müller, 1774 as the type species.

2963 *Roeslerstammia* Zeller, 1839 and *Acrolepiopsis* Gaedike, 1970 (Insecta, Lepidoptera): proposed conservation by the designation of *Alucita erxlebella* Fabricius, 1787 as the type species of *Roeslerstammia*; and *A. erxlebella* and *Tinea imella* Hübner, [1813] (currently *Roeslerstamnia erxlebella* and *Monopis imella*): proposed conservation of the specific names by the designation of a neotype for *A. erxlebella.*

2988 *Euchroeus* Latreille, 1809 and *Chrysis purpurata* Fabricius, 1787 (currently *E. purpuratus*) (Insecta, Hymenoptera): proposed conservation of usage; and *Chrysis gloriosa* Fabricius, 1793: proposed suppression of the specific name.

2920 *Diemenia atra* Macleay, 1884 (currently *Demansia atra*; Reptilia, Serpentes): proposed conservation of the specific name.

2921 *Trigonocephalus pulcher* Peters, 1863 (currently *Bothrops pulcher*) and *Bothrops albocarinatus* Shreve, 1934 (currently *Bothriechis oligolepis albocarinatus*) (Reptilia, Serpentes): proposed conservation of the specific and subspecific names by the designation of a neotype for *T. pulcher.*

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Case No.

2943 *Aporcelaimus* Thorne & Swanger, 1936 (Nematoda): proposed designation of *Dorylaimus superbus* de Man, 1880 as the type species.

2996 *Pila* Röding, 1798 and *Pomacea* Perry, 1810 (Mollusca, Gastropoda): proposed placement on the Official List, and AMPULLARIIDAE Gray, 1824: proposed confirmation as the nomenclaturally valid synonym of PILIDAE Preston, 1915.

2990 *Disparalona* Fryer, 1968 (Crustacea, Branchiopoda): proposed conservation.

2986 *Dasineura* Rondani, 1840 (Insecta, Diptera): proposed designation of *Tipula sisymbrii* Schrank, 1803 as the type species.

3043 *Varanus teriae* Sprackland, 1991 (Reptilia, Squamata): proposed conservation of the specific name.

3042 *Hydrosaurus gouldii* Gray, 1838 (currently *Varanus gouldii*) and *Varanus panoptes* Storr, 1980 (Reptilia, Squamata): proposed conservation of the specific names by the designation of a neotype for *H. gouldii.*

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1860. *Acanthoteuthis* Wagner *in* Münster, 1839 and *Muensterella* Schevill, 1950 (Mollusca, Cephalopoda): placed on the Official List.
1861. *Octopus vulgaris* Cuvier, [1797] and *Loligo vulgaris* Lamarck, 1798 (Mollusca, Cephalopoda): specific names conserved.
1862. *Aspidiphorus* Ziegler *in* Dejean, 1821 (Insecta, Coleoptera): conserved as the correct original spelling, and SPHINDIDAE Jacquelin du Val, [1861]: given precedence over ASPIDIPHORIDAE Kiesenwetter, 1877 (1859).
1863. *Sphaerocera* Latreille, 1804 and *Borophaga* Enderlein, 1924 (Insecta, Diptera): conserved: *Musca subsultans* Linnaeus, 1767: specific name placed on the Official List.
1864. *Chaetodacus latifrons* Hendel, 1915 (currently *Bactrocera latifrons*; Insecta, Diptera): given precedence over *Dacus parvulus* Hendel, 1912.
1865. *Eudistoma* Caullery, 1909 (Tunicata): given precedence over *Paessleria* Michaelsen, 1907.
1866. *Hydromantes* Gistel, 1848 (Amphibia, Caudata): *Spelerpes platycephalus* Camp, 1916 designated as the type species.
1867. *Phyllophis carinata* Günther, 1864 (currently *Elaphe carinata*; Reptilia, Serpentes): specific name conserved.

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1868. *Patella longicosta* Lamarck, 1819 (Mollusca, Gastropoda): specific name conserved.
1869. *Monstrilla* Dana, 1849 and *Thaumaleus* Krøyer, 1849 (Crustacea, Copepoda): conserved.
1870. *Sicus* Scopoli, 1763 and *Myopa* Fabricius, 1775 (Insecta, Diptera): conserved by the designation of *Conops ferrugineus* Linnaeus, 1761 and *C. buccatus* Linnaeus, 1758 as the respective type species; and *Coenomyia* Latreille, 1796 placed on the Official List.
1871. *Iodotropheus sprengerae* Oliver & Loiselle, 1972 (Osteichthyes, Perciformes): holotype replaced by a neotype.
1872. *Siboma atraria* Girard, 1856 (currently *Gila atraria*; Osteichthyes, Cypriniformes): specific name conserved.
1873. HEMIDACTYLIINI Hallowell, 1856 (Amphibia, Caudata): conserved.
1874. *Aptornis* Owen, 1848 (Aves): conserved as the correct original spelling.

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Pachyrotula, a new genus of freshwater sponges from New Caledonia (Porifera: Spongillidae)

Cecilia Volkmer-Ribeiro and Klaus Rützler

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(KR) Department of Invertebrate Zoology, National Museum of Natural History Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Abstract.—Characteristics found during a review of the type material of *Spongilla (Stratospongilla) raceki* Rützler from New Caledonia point to a new, monotypic genus, *Pachyrotula.* This new genus is closely related to *Heterorotula* Penney & Racek and to *Houssayella* Bonetto & Ezcurra De Drago. *Heterorotula* also occurs in New Caledonia and is represented by the species *H. caledonensis* new species and *H. multidentata* (Weltner). These species, along with *Oncosclera diahoti* (Rützler), new combination, are indicators of a rare and particular freshwater sponge fauna of this island.

For the past three decades, the freshwater sponges of New Caledonia have been known only from the specimens described by Rützler (1968). It recently became clear that this material needed to be reexamined, especially in the light of Penney & Racek's (1968) comprehensive study of all gemmule-producing genera of freshwater sponges and Racek's (1969) extensive work on Australia's freshwater sponges, which provided new insight into the generic and specific relationships of these faunas and revealed their heretofore unsuspected richness. That work and several subsequent studies on the freshwater sponges of South America indicated the need for a taxonomic and systematical updating of the New Caledonia description. As a result of this updating, a new genus is being proposed, with *Spongilla (Stratospongilla) raceki* Rützler as the type species; also, *Ephydatia multidentata* (Weltner) forma *caledonensis* Rützler is elevated to a full species in the genus *Heterorotula* Penney & Racek, and *Spongilla (Stratospongilla) diahoti* Rützler is transferred to the genus *Oncosclera* Volkmer-Ribeiro.

Material and Methods

The material examined consisted of types and paratypes of *Spongilla (Stratospongilla) diahoti, S. (Stratospongilla) raceki,* and *Ephydatia multidentata* f. *caledonensis* (Rützler 1968), all deposited at the National Museum of Natural History, Washington D.C. (USNM); slides of *Houssayella iguazuensis* Bonetto & Ezcurra de Drago, 1966, provided by I. Ezcurra de Drago; and slides of species of the genus *Heterorotula* provided by A. A. Racek; the latter deposited at Museu de Ciencias Naturais (MCN) of Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil.

A minute fragment of *Spongilla (S.) raceki* with gemmules was dissociated after boiling in nitric acid and washed several times in distilled water. When completely dry, the suspended clean spicules were dropped on a stub and coated with gold in preparation for scanning electron microscopic (SEM) observations. Some dry gemmules were hand-sectioned under a stereomicroscope and their halves glued to a stub and also gold-coated for SEM examination. Photomicrographs were obtained with an

MCN JEOL-5200 microscope equipped with a Pentax SF7 35 mm camera.

Systematics

Pachyrotula, new genus

Type species.—*Spongilla (Stratospongilla) raceki* Rützler, 1968. Genus monotypic.

Diagnosis.—Spongillidae with stout, heavily spined birotulate gemmoscleres with knobby rotules progressively reduced from the inside to the outside of the gemmular coat.

Description.—Sponges forming slender, greyish, small, irregular, soft crusts with gemmules loosely distributed near the basal spongin plate. Oscula and pores inconspicuous. The skeleton consists of a dense polygonal network of spicules bound together by scanty spongin. No main fibers are discernible.

Three classes of megascleres. The most abundant are the alpha megascleres, which are finely spined oxea, abruptly and acutely pointed, and with a denser spine arrangement at the extremities. The beta megascleres measure half to two-thirds the length of the alpha megascleres, are curved or even bent oxea or styles, are strongly spined with abruptly and sharply pointed extremities that are enhanced by a distal swelling and a concentration of minute spines turned toward the point. These megascleres are tangentially packed around the gemmules under a loose and haphazard arrangement of the alpha megascleres. The third class consists of very rare, smooth, thin, long oxea with differing mucronated extremities.

Microscleres absent.

Gemmoscleres are dumb-bell-shaped birotules, with knobby rotules ranging from irregularly sculptured, tuberculate, or spiny bulbs to merely knobbed expansions of the shaft (Figs. 1, 2). As the rotules become smaller, the shafts become longer. Sharpened, lanceolated extremities of the shaft may protrude from one or both of the rotules or terminal knobs, thus morphologically grading into beta megascleres. Shafts are spined, some are displaying a few tubercules capped by rosettes of spines.

Gemmules abundant, located at the basal part of the sponge. Inner layer thick; pneumatic layer thin, with small, irregular air spaces and only a few short gemmoscleres radially embedded in it. The longer gemmoscleres form a loose radial arrangement and, together with the derived acanthoxea (beta megascleres), turn more tangential toward the gemmule periphery. The outer rotules and the largest part of the shafts of most gemmoscleres protrude at the gemmular surface. One single foramen in each gemmule.

Pachyrotula raceki (Rützler), new combination
Figs. 1–5, 9

Spongilla (Stratospongilla) raceki.—Rützler, 1968:60, figs. 5–9.

Holotype.—USNM 23882, New Caledonia; Ferdinand Starmühler leg. 18 Sep 1965.

Paratype.—USNM 23883, same location as for holotype.

Type locality.—River Le Diahot, New Caledonia (Fig. 9).

Description.—Soft, grayish, tiny patches 1 mm thick on the lower surface or in concavities of stones. Sponge surface smooth, porous. Oscula inconspicuous. Skeleton a confused arrangement of megascleres with scanty spongin at the crossing points. A tangential packing of the megascleres around the gemmules produces a thickening of the skeleton at the basal portion of the sponge.

Alpha megascleres are microspined, straight to more often slightly curved oxea with abruptly pointed, spined extremities. Oxea vary noticeably in length. Spines at tips turned outward. These megascleres form the skeleton mesh and also occur in a loose and confused manner around each gemmule.

Beta megascleres are short, slightly to

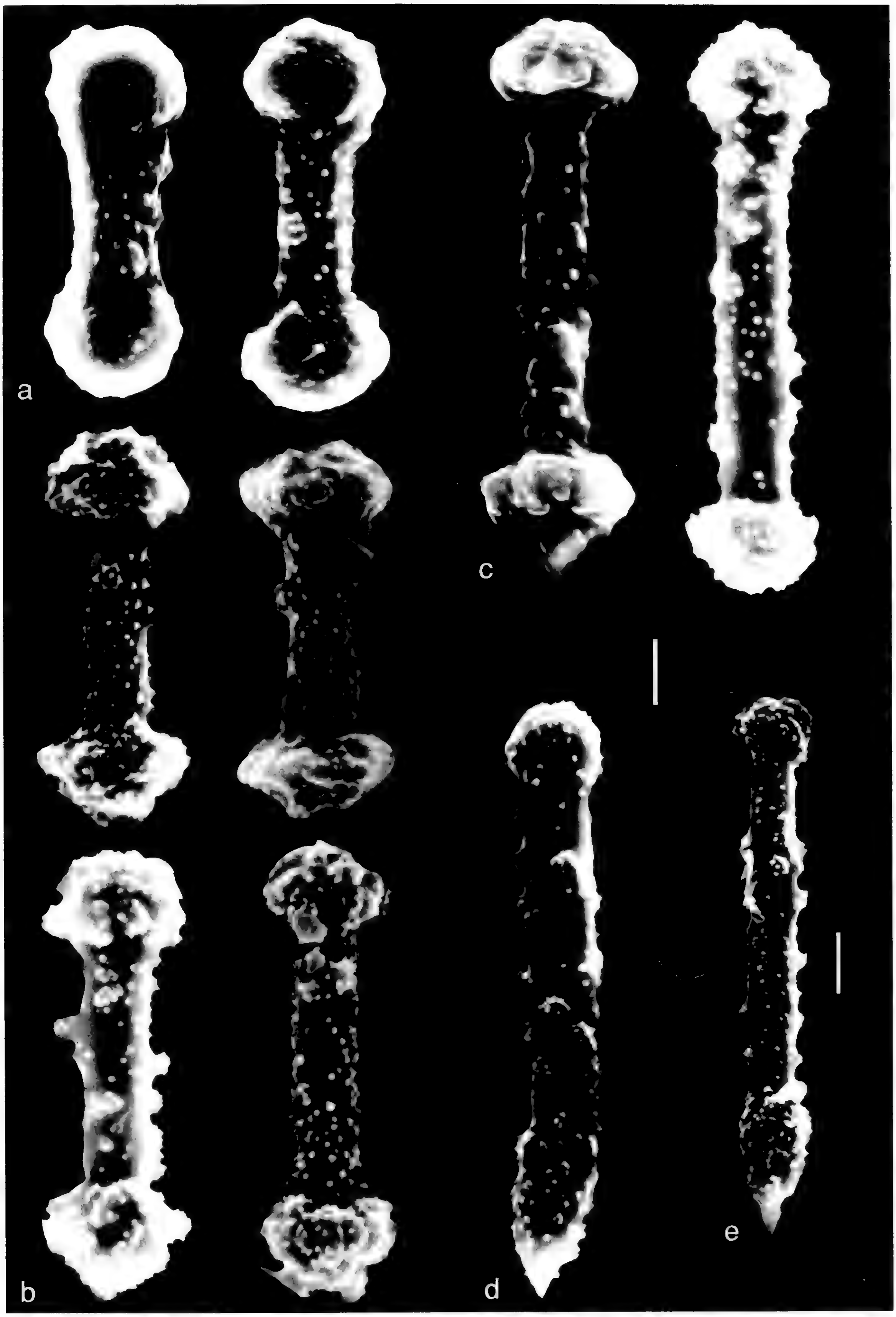

Fig. 1. Gemmoscleres of *Pachyrotula raceki* (Rützler) (SEM). a, Immature or poorly developed spicules; b, Average development; c, Largest class of gemmoscleres exhibiting differentiated rotular reduction; d, Further differentiation; e, Same as d, reduced scale. Scales = 10 μm.

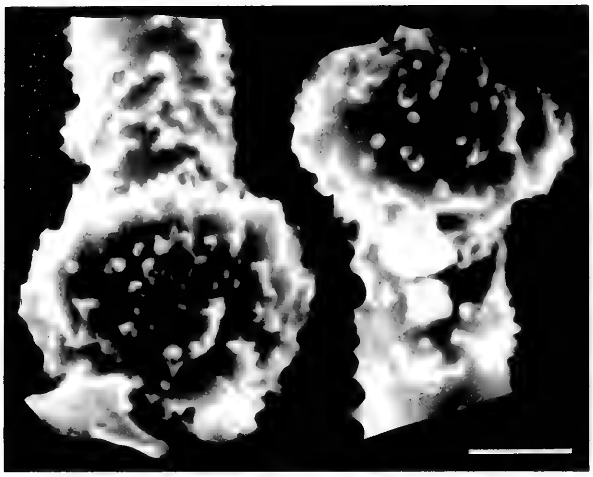

Fig. 2. Enlarged rotules of *Pachyrotula raceki* (Rützler) gemmosclere in Fig. 1b (lower right); note different size of the rotules (SEM). Scale = 5 μm.

strongly curved or even bent, strongly spined oxea or styles with very abruptly pointed extremities. Usually marked by a subterminal swelling or bulb with a heavier covering of spines turned to the spicule extremities. Some beta megascleres are embedded in the gemmular wall together with the gemmoscleres, but for the most part are tangentially packed around the gemmules.

Long, smooth thin megascleres are very rare but certainly belong to the sponge, as became evident once the series grading from very thin and short ones was perceived in the original preparations. These spicules may be up to four times longer and thinner than the alpha megascleres. However, they are too scarce to determine their locale in the skeleton.

Gemmoscleres stout, strongly spined birotulates of conspicuously large range of lengths. With thick shafts and, terminally, with spool- to knob-like rotules irregularly ornamented by spined lobes, rosettes, or tubercules. The shorter gemmoscleres display larger, more conspicuous rotules, the outer one usually smaller than the inner one. The bulbous endings of the longer gemmoscleres gradually taper, thus changing the spicules into straight or gradually curved oxeas with piercing points enhanced by a slight subterminal swelling of the shaft. Such spicules grade into what are here classed as beta megascleres because they are not embedded in the gemmular wall but are packed around the gemmules (Figs. 1, 2, 3b; and Rützler 1968, figs. 6–8).

Gemmules abundant. They occur from the base to the middle portion of the thin crusts. Because the sponge was in the process of producing gemmules, it is possible to describe the manner in which the gemmular wall is formed. Wherever gemmules are about to be formed, and even prior to the congregation of the thesocytes, a gathering of cells secreting the alpha megascleres takes place, joined shortly thereafter by spicule-forming beta megasclerocytes and gemmosclerocytes. By the time the inner gemmular wall is formed, a large number of the short and longer gemmoscleres are already present and beginning to become inserted at the base of the inner gemmular wall. During the formation of the thin pneumatic coat around the gemmosclere layer, more and more gemmoscleres contribute to this coat. At the same time, the beta and alpha megascleres congregate tightly around the forming gemmule, until only a round mass of alpha megascleres can be perceived. The presence of some gemmoscleres (particularly shorter ones) radially embedded in the pneumatic coat (Fig. 3) indicates that a radial orientation was abandoned for a tangential one. The outer gemmular wall is thin; the foraminal tube is short and does not reach beyond the longer birotulates.

For spicule and gemmule measurements, refer to the original descriptions (Rützler 1968).

Habitat.—The sponge encrusts the lower surface of stones in running and standing waters with extreme low conductivity (28–56) and slightly acidic to neutral pH (6.6–7.1).

Remarks.—Penney & Racek (1968) elevated Annandale's subgenus *Stratospongilla* to a genus, defining its gemmoscleres (p. 40) as "more or less strongly bent amphistrongyles . . . or slightly curved spined amphioxea, or a combination of both" and its

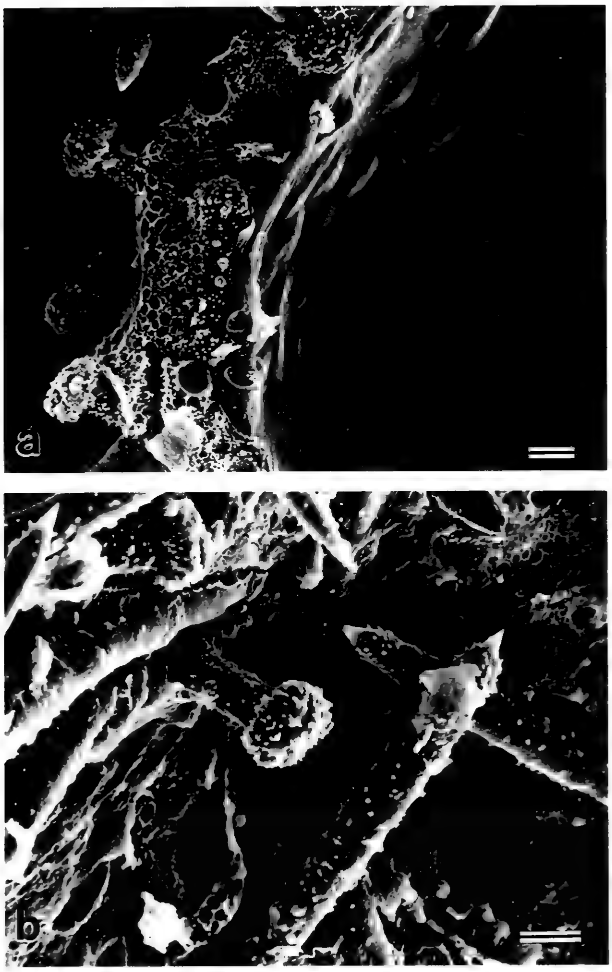

Fig. 3. Gemmular wall in *Pachyrotula raceki* (Rützler) (SEM). a, A cross-section exposes the irregularly smooth surface of the inner coat and the irregular air spaces of the pneumatic coat, with some short birotulates radially embedded and some longer ones tangentially embedded, both kinds projecting beyond the thin outer gemmular coat; b, Gemmular surface, with rotule of one short gemmosclere projecting and several beta megascleres tangentially embedded in the growing pneumatic coat. Scales = 10 μm.

microscleres as "shorter and slender amphioxea." They suggested, however, that *Stratospongilla* species lacking microscleres might be grouped under a new genus. Volkmer-Ribeiro (1970) followed up on this suggestion by defining the genus *Oncosclera*, with *Oncosclera jewelli* (Volkmer 1963) as the type species. *Oncosclera* species not only lack microscleres but differ markedly from *Stratospongilla* in their gemmular structure. At the time the genus *Oncosclera* was defined, it was assigned several South American species previously described as *Stratospongilla* by Bonetto & Ezcurra de Drago (1966). Also included in the genus were the Oriental and Ethiopian *Stratospongilla* species reported to be lacking microscleres (Penney & Racek 1968).

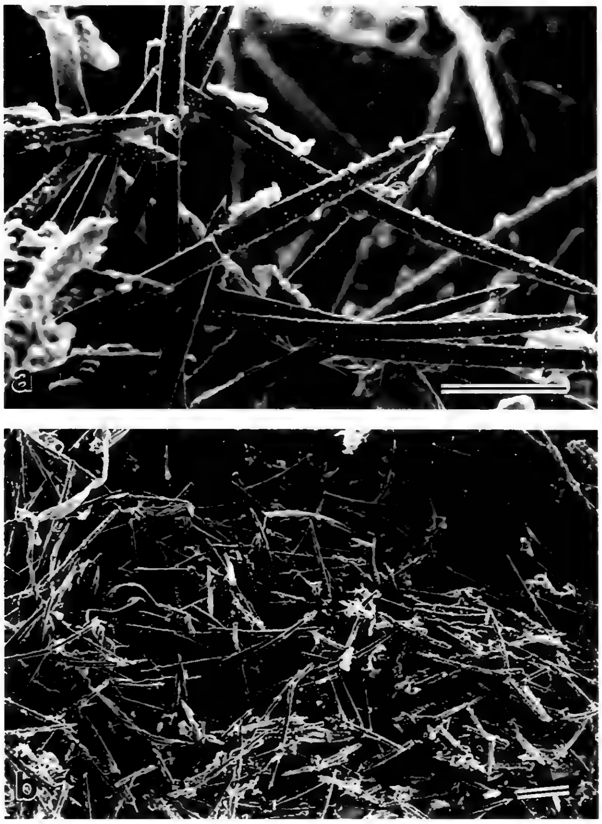

Fig. 4. Skeletal arrangement in *Pachyrotula raceki* (Rützler) (SEM). a, Detail of the loose arrangement of the alpha megascleres cemented by scanty spongin; b, Cross section of the sponge crust showing the loose skeletal arrangement of the megascleres. Scales = 50 μm (a); 100 μm (b).

A reexamination of the spicular set and gemmular coat of *Spongilla (Stratospongilla) raceki* shows its gemmoscleres to be birotulates, modified by a graded reduction in the size of their rotules that depends on their position relative to the inside or outside of the gemmular coat; this morphological series ends in highly variable acanthoxeote or acanthostylote forms. Just as such gemmoscleres cannot be considered strongyles, the gemmular structure of *Pachyrotula* has no parallel in the large mammilate gemmules that are cemented to the substrate in both *Stratospongilla* and *Oncosclera*. Neither of these genera show any trace of radially arranged gemmoscleres that are evident in *Pachyrotula* new genus. Nor are the size, the shape, or the localization of the

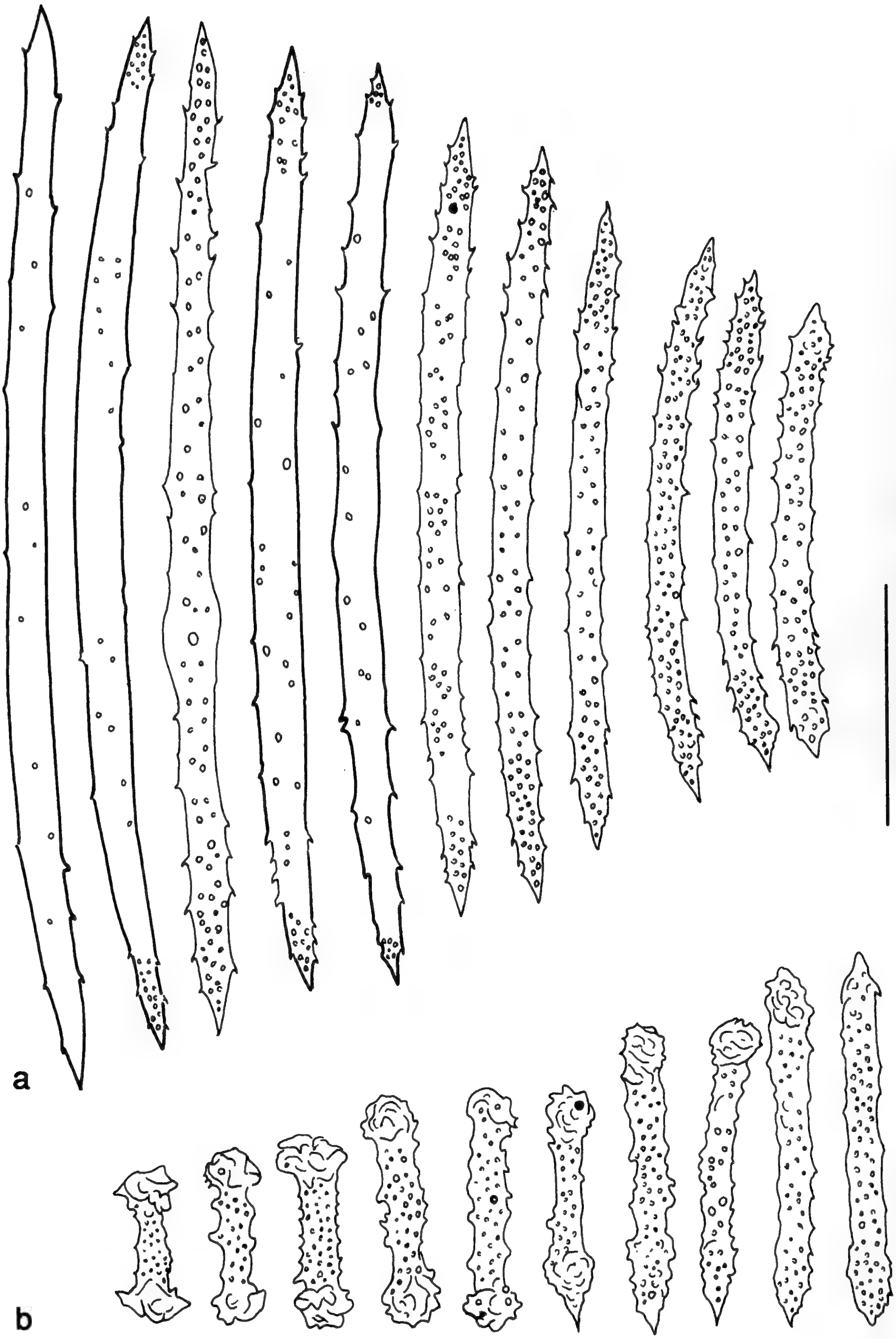

Fig. 5. Camera lucida drawings of spicules of *Pachyrotula raceki* (Rützler). a, Alpha megascleres grading to beta megascleres; b, Gemmoscleres. Scale = 50 μm.

acanthoxea or acanthostyles around the gemmules characteristic of microscleres. Rather, they point to a second category of megascleres. The selective process responsible for the production of such megascleres also caused the birotulate spicules in the gemmular wall to depart from a radial pattern. The new genus is closer to genus *Het-*

erorotula Penney & Racek, 1968, which at the time of its discovery was known only from Australia and New Zealand. Only a recent study of some spongillite (ore) deposits from Brazil (Volkmer-Ribeiro & Motta 1995) has brought to light the first neotropical species of the genus. The new genus clearly stands apart from *Heterorotula,* whose diagnostic characteristic consists of gemmoscleres with "slender, usually granulated shafts and terminally with comparatively wide and flat rotules of moderately to greatly varying diameter, the inner invariably larger than the outer" (Penney & Racek 1968:96). Furthermore, the very distribution of *Pachyrotula raceki,* which appears to be the most widely occurring species on New Caledonia (Fig. 9) and is also known for its broad range of habitats, indicates that it cannot be a mere ecomorph of a *Heterorotula* species.

Heterorotula caledonensis, new species
Figs. 6, 9

Ephydatia multidentata (Weltner) f. *caledonensis* Rützler, 1968:63, figs. 13–19.

Holotype.—USNM 23884 (the gemmule slide preparation figured in Rützler, 1968, fig. 15), sta. FNK 36 (in Rützler 1968:58), New Caledonia; Ferdinand Starmühlner leg. 25 Jul 1965.

Paratypes.—USNM 39463 (5 slides), sta. FNK 36 (in Rützler 1968:58) New Caledonia, Ferdinand Starmühlner leg. 25 Jul 1965.

Remarks on the syntypic series.—The description of the new species is based on several fragments from three specimens. The fragments in alcohol and five slides (two of them with entire gemmules) representing the three specimens are deposited in the USNM.

Type locality.—Sta FNK 36 (in Rützler 1968:58), near La Foa, southwest New Caledonia (Fig. 9).

Diagnosis.—Heterorotula species with stout megascleres and stout, highly variable spined to granulated gemmoscleres that make up a series, running from quite long acanthoxea with bulbous, strongly spined extremities to more typical birotules, to quite short, irregularly shaped "aster-like" spicules. The series of regular, birotulate *Heterorotula* gemmoscleres tends to form freak rotules and displays granulated to almost smooth shafts.

Description.—Rützler's (1968:65) detailed description of *Ephydatia multidentata* f. *caledonensis* holds for *Heterorotula caledonensis* new species. In addition, a series of very short "aster-like" gemmoscleres not referred to originally may be seen in Rützler's, 1968, fig. 16 alongside the gemmoscleres in the pneumatic coat. Such birotulate-derived gemmoscleres are abundant in the original slides examined.

Remarks.—Ephydatia multidentata Weltner 1895 was one of the species that Penney & Racek (1968) transferred to their new genus *Heterorotula.* Racek (1969) found it to be one of the most common freshwater sponge species in eastern Australia and reported considerable variation in its spicular components. On New Caledonia, *H. multidentata* (Weltner 1895) occurs almost sympatrically with *H. caledonensis* new species (sta. FNK 36 and 44, both described in Rützler, 1968) and in quite similar water-quality and substrate conditions. The great variations in the gemmoscleres of *H. caledonensis* new species could not be found in specimens of *H. multidentata* from either eastern Australia or New Caledonia and are now considered to be of such magnitude that they denote a new species.

Oncosclera diahoti (Rützler), new combination
Fig. 9

Spongilla (Stratospongilla) diahoti Rützler, 1968:59, figs. 2–4.

Holotype.—USNM 23881 (5 fragments), New Caledonia, Ferdinand Starmühlner leg. 16 Sept 1965.

Type locality.—River Le Diahot near Quénia, sta. FNK 105, North New Caledonia (Fig. 9).

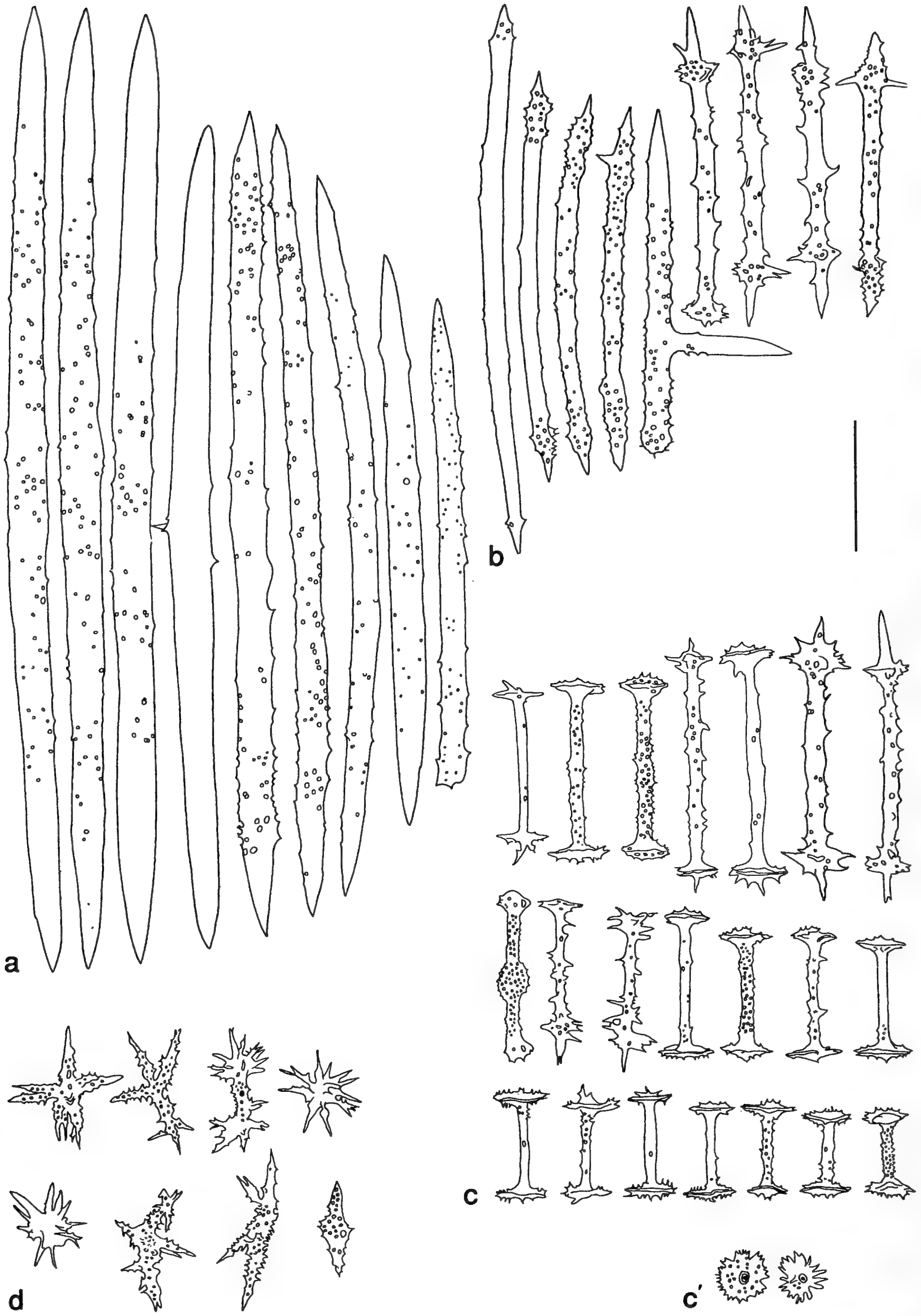

Fig. 6. Camera lucida drawings of spicules of *Heterorotula caledonensis*, new species. a, Megascleres; b, acanthoxeote gemmoscleres; c, birotulate gemmoscleres (c', head-on view of rotules); d, "aster-like" gemmoscleres. Scale = 50 μm.

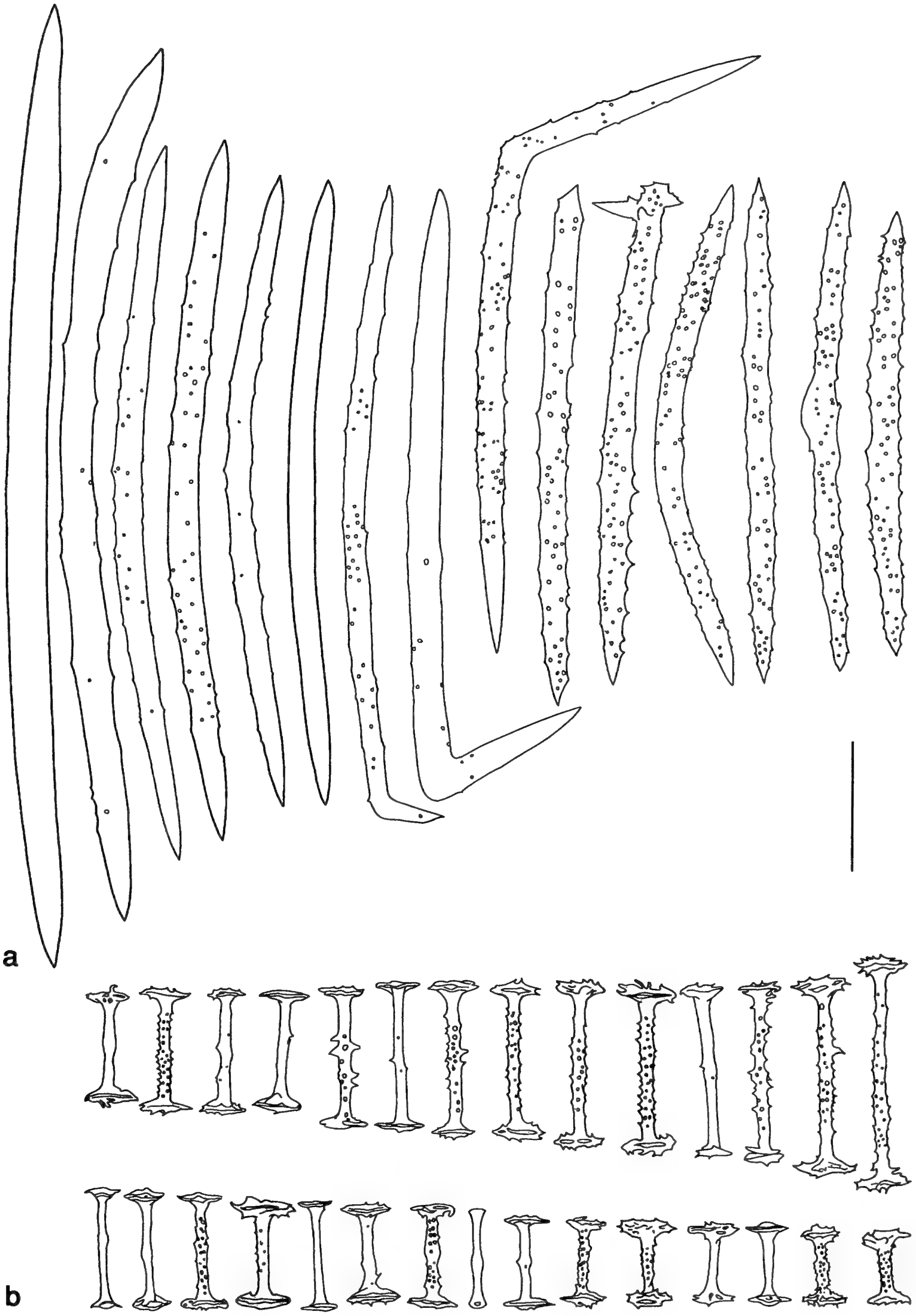

Fig. 7. Camera lucida drawings of the spicules from several specimens of *Heterorotula multidentata* (Weltner) from Australia. a, Megascleres, b, Gemmoscleres. Scale = 50 μm.

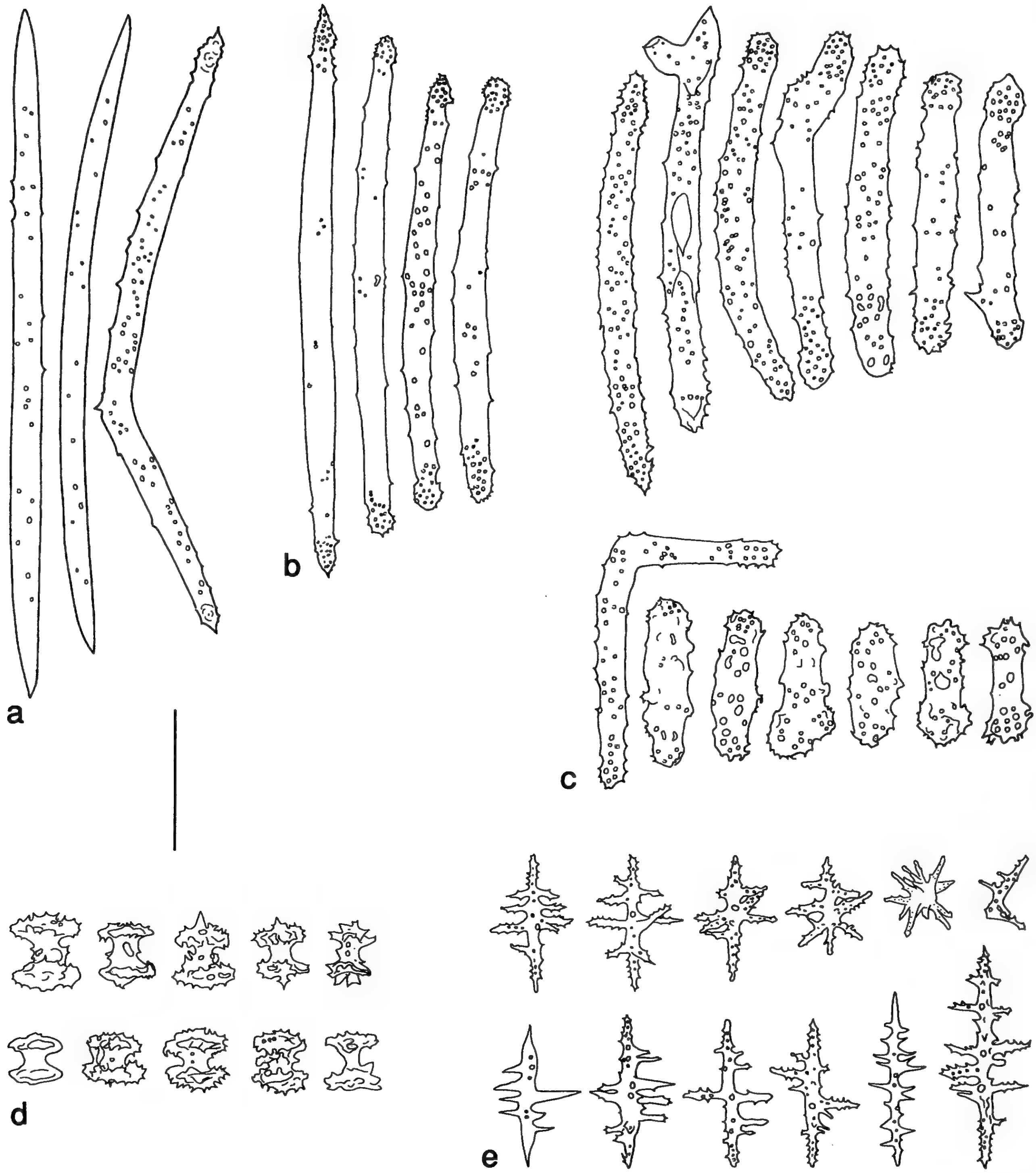

Fig. 8. Camera lucida drawings of the spicules in *Houssayella iguazuensis* Bonetto & Ezcurra de Drago. a, Tornote megascleres; b, Strongylote megascleres. c, Beta megascleres; d, gemmoscleres; e, "Aster-like" microscleres. Scale = 50 μm.

Remarks.—From Rützler's (1968) detailed description and illustrations of *Spongilla (S.) diahoti,* particularly of the gemmular structures, it appears the species belongs to the genus *Oncosclera* Volkmer-Ribeiro, 1970, which by definition contains *Stratospongilla*-like species that lack microscleres and have their gemmoscleres loosely and tangentially arranged in the outer gemmular coat. *Oncosclera diahoti* stands very close to *O. navicella* from South America, which also has small oxea with a middle thickening as gemmoscleres. However, the gemmoscleres of *O. navicella* all have a strong middle curvature that makes them look like small boomerangs.

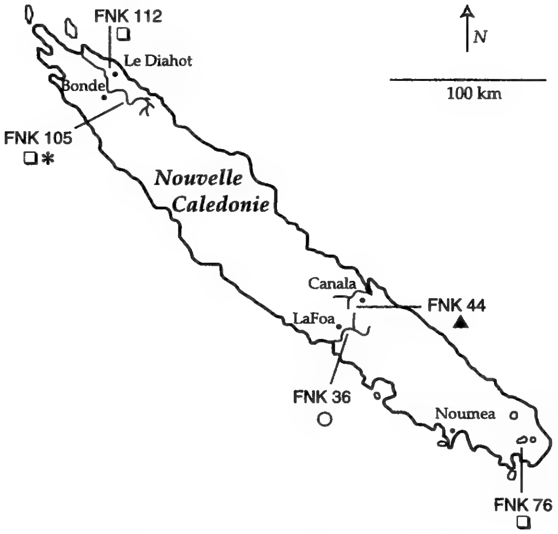

Fig. 9. Map of New Caledonia showing the collecting stations and the distribution of the freshwater sponge fauna. Square = *Pachyrotula raceki* (Rützler); asterisk = *Oncosclera diahoti* (Rützler); open circle = *Heterorotula caledonensis* n. sp.; triangle = *Heterorotula multidentata* (Weltner 1895). Adapted from Rützler (1968).

Discussion

In updating the only known survey of New Caledonian freshwater sponges, we found three genera: *Pachyrotula* new genus, *Heterorotula* Penney & Racek, 1968, and *Oncosclera* Volkmer-Ribeiro, 1970. We also found four species: *P. raceki* (Rützler 1968), *H. multidentata* (Weltner 1895), *H. caledonensis* new species, and *O. diahoti* (Rützler 1968) new combination. The new genus occurs in the northern and southern extremities of New Caledonia (Fig. 9), in both lotic and lentic environments, whereas the genus *Heterorotula* is found near the southern third of the island and the genus *Oncosclera* occurs only on the northern part of the island.

Most of the freshwater sponge fauna of New Caledonia seem to have evolved around the genus *Heterorotula* (with two species) and the new monotypic genus *Pachyrotula,* which stands closer to *Heterorotula* than to any other known genus of freshwater sponge on account of its thick, dissimilar-sized rotules of gemmoscleres with scalloped profiles, its lack of microscleres, and the fact that the outer part of the pneumatic layer is reinforced with a second category of megascleres of evident birotulate origin.

Five species of *Heterorotula* have also been recorded in Australia (Penney & Racek 1968, Racek 1969), one species in New Zealand (Penney & Racek 1968), and one species in South America (Volkmer-Ribeiro & Motta 1995). The highest species diversity occurs in Australia, where one species is restricted to the arid central part and thus to standing saline waters, another occurs only in the swampy area east of the Dividing Range, and the other three have a marked east-west distribution (Racek 1969). Australia's species show a number of variations, such as the occurrence in some *H. multidentata* specimens of a spicule that does not seem to fit the category of a microsclere and the reinforcement in some species of the outer pneumatic layer with normal megascleres or with a second category of megascleres (Racek 1969, Fig. 7).

Heterorotula's presence in South America was first reported by Volkmer-Ribeiro & Motta (1995), in their description of *H. fistula* from southwestern Brazil. *Heterorotula* spicules have recently been found in pond sediments in the northeastern and southern coastal areas of the country (Volkmer-Ribeiro, unpublished). This suggests that the genus may also be present in the eastern part of South America.

The distribution pattern of the genus *Heterorotula* thus resembles an arch extending from eastern South America to New Caledonia. The area richest in species is Australia. Zinmeister (1979, 1982) has suggested that such a faunistic distribution may have existed in the past, in the Low Tertiary Weddelian Province, as indicated by a fossil molluscan fauna. At that time, the Antarctic-Australian bloc occupied a central position in a splitting land arch that had isolated the South Circum-Pacific for a considerable period of geological time.

It may be that the genus *Pachyrotula* stands for the eastern branch of an old parental stock with *Heterorotula* relationship. This suggestion is supported by the similarity in characteristics, the central position of the Antarctic and Australian in the Weddelian Province, and the fact that the highest *Heterorotula* species diversity occurs in Australia. Could a western branch of that group also have evolved in South America? This question brings to mind the monotypic genus *Houssayella* with *H. iguazuensis* Bonetto & Ezcurra de Drago, 1966, described from the lower Parana River rocky bottom in Argentina and later from the lower Uruguay River in southern Brazil (Volkmer-Ribeiro 1971, Fig. 8). In *H. iguazuensis,* the short birotulates with thick shafts are arranged radially in the gemmules. This species is also known for its irregularly sculptured granulated rotules of dissimilar size, and for a series of beta megascleres that form a palissade packing around the gemmules; this series of beta megascleres ends in short, almost birotulate spicules quite similar to the ones found in *P. raceki.* The megascleres in *H. iguazuensis* vary from tylote to strongylote and are spined, with a concentration of spines near both ends. A third category of highly variable strongylote spicules with bulbed ends approaches the shape of beta megascleres of *Heterorotula caledonensis* new species. At the same time, *H. iguazuensis* has aster-like microscleres that closely resemble the aster-like gemmoscleres found in *H. caledonensis* new species.

No fossil or extant freshwater sponges have yet been reported from Antarctica. However, the freshwater sponge genera considered in this discussion may well have evolved from an ancient Weddelian *Heterorotula*-like stock.

Conclusions

The geographical distribution and the characteristics shared by the freshwater sponge genera *Heterorotula* (Penney & Racek 1968), *Pachyrotula* new genus, and *Houssayella* Bonetto & Ezcurra de Drago, 1966, indicate that these genera may be the recent branches of an ancient fauna that thrived during the early Tertiary in the southern Circum-Pacific continents, which by then had already begun to drift. This region, also known as the Weddelian Province (Zinmeister 1979, 1982), included southern South America, Antarctica, Australia, New Zealand, and New Caledonia.

Heterorotula caledonensis new species may have the largest number of characteristics indicative of the ancient group, such as long megascleres; long birotulate gemmoscleres that include transitions to beta megascleres; short gemmoscleres, some of which grade into an "aster-like" spicule situated in the gemmule or outside it; and the regular, spiny to granulated birotulates with thick, unequal and ragged rotules.

Acknowledgments

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This paper is dedicated to the memory of A. A. Racek, eminent freshwater-sponge systematist who died in early 1997.

Literature Cited

Bonetto, A. A., & Ezcurra de Drago. 1966. Nuevos aportes al conocimiento de las Esponjas Argentinas.—Physis 26(71):129–140.

Penney, J. T., & A. A. Racek. 1968. Comprehensive revision of a worldwide collection of freshwater sponges (Porifera: Spongillidae).—United States National Museum Bulletin 272:1–184.

Racek, A. A. 1969. The freshwater Sponges of Australia (Porifera: Spongillidae).—Australian Journal of Marine and Freshwater Research 20: 267–310.

Rützler, K. 1968. III. Freshwater sponges from New Caledonia.—Cahiers ORSTOM, Sér. Hydrobiologie 2:57–66.

Volkmer-Ribeiro, C. 1970. *Oncosclera,* a new genus of freshwater sponges with redescription of two species.—Amazoniana 2:435–442.

———. 1971. *Houssayella iguazuensis* Bonetto & Ezcurra de Drago, 1966 (Porifera—Spongillidae) in Itú River, Rio Grande do Sul, Brazil.—Iheringia, Série Zoológica 40:53–60.

———, & J. F. M. Motta. 1995. Esponjas formadoras de espongilitos em lagoas no Triângulo Mineiro e adjacências, com indicação de preservação de habitat.—Biociencias 3(2):183–205.

Zinsmeister, W. J. 1979. Biogeographic significance of the Late Mesozoic and Early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. Pp. 349–355 *in* J. Gray & A. Boucot, eds., Biogeography, Plate Tectonics and the Changing Environment. Proceedings, 37th Annual Biology Colloquium and Selected Papers. Oregon State University Press, Corvallis.

———. 1982. Late Cretaceous—early Tertiary molluscan biogeography of the southern Circum Pacific.—Journal of Paleontology 56:84–102.

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The genus *Julavis* de Laubenfels (Porifera: Halichondrida)

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Abstract.—*Julavis jamaicensis* new species is reported from Northern Jamaica. This represents the second record of the genus and the first from the Atlantic basin. *Julavis* de Laubenfels 1936 was erected to accomodate *Tedania levis* Kirkpatrick 1900 from the Funafuti Atoll, Central Pacific. Its status was never discussed prior to the present paper and order and family allocation (Poecilosclerida: Acarniidae) have remained tentative. It is proposed to allocate it to the order Halichondrida, family Desmoxyidae, on the basis of confused skeletal architecture, possession of acanthose diactines and wispy trichodragmas. The genus is distinguished from other genera of Desmoxyidae by its smooth strongylostyles and by the strongylote nature of the acanthose diactines. The contents of the family Desmoxyidae is discussed and compared with related families.

Kirkpatrick (1900) described from deep waters (90–125 m) off the atoll of Funafuti, Central Pacific, a thinly encrusting sponge with the unusual skeletal structure of a feltwork of spined strongyles with scattered smooth strongyles, combined with frayed trichodragmas. He named the species *Tedania levis* but admitted that it was " . . . only placed in *Tedania* provisionally, . . . should probably come under a new genus near *Tedania* . . . ". De Laubenfels (1936) in his monograph of the orders, families and genera of the Porifera erected a new genus *Julavis* (origin of the name not explained) without having seen the original material. His definition for the new genus was: " . . . two distinct categories of spiny strongyles (sic) for megascleres and raphides for microscleres." This is a misrepresentation of Kirkpatrick's description, as there are smooth and spiny megascleres rather than two spiny types. Since then, as with so many other "paper" genera of de Laubenfels, no further reference was made in the literature on either *Tedania levis* or the genus *Julavis*.

Recently, one of us (HL) collected an orange encrusting sponge off the north coast of Jamaica, with characters closely similar to those of *Tedania levis*. This material is described below as a species new to science and compared to the type specimen of *T. levis* borrowed from the collections of the Natural History Museum, London (BMNH).

In view of the fact that there are now two species answering to the definition of *Julavis*, it is proposed to consider the genus as valid. Its family and order allocation has to be changed from Poecilosclerida: Acarniidae, as proposed by de Laubenfels, to Halichondrida: Desmoxyidae; this will be discussed below.

Julavis jamaicensis, new species
Figs. 1–3

Material examined.—Holotype: Zoological Museum Amsterdam, Porifera collection, reg.no. ZMA POR.11520. Jamaica, off Chalet Caribe, Montego Bay in 20 m depth, dried specimen.

Description.—Thinly encrusting on the

surface of a large dead sclerosponge, *Ceratoporella nicholsoni* (Porifera: Ceratoporellidae). The type specimen was sawed out of the basal skeleton of a large (25 cm diameter) specimen of the sclerosponge (Fig. 1). It is about 1 mm thick, lateral expansion at least 10 × 15 cm. Surface in dry condition smooth, hard, crumbly, difficult to section tangentially. No visible oscules or openings. Colour light orange to beige.

Skeleton (Figs. 2A–B) in dry condition a packed feltwork of confusedly arranged acanthostrongyles with occasional single smooth long spicules in a position perpendicular to the surface. The outermost acanthostrongyles tend to form an irregular palisade with apices pointing outward at different angles. Rarely, the smooth long spicules form bundles. Trichodragmas are scattered throughout the spicule mass. The organic parts are greatly reduced (no doubt due to shrinking). There is no recognizable spongin, but the narrow space between the spicules is definitely fibrous.

Spicules (Figs. 2C–E, 3, Table 1) include acanthostrongyles, strongylostyles and trichodragmas. Acanthostrongyles (Figs. 2C, 3.1–3) are in majority entirely covered by coarse blunt spines; they are somewhat irregularly shaped, often curved, with apices slightly narrower than the shaft. Occasionally they are almost entirely smooth (Fig. 3.2) or smooth asymmetrically at one of the ends (Fig. 3.3); juvenile spicules are finely acanthose, almost smooth, oxea-like (Fig. 2C, middle spicule). Size 127–258 × 8–20 μm. Strongylostyles (Figs. 2D, 3.4) are smooth, style-like but conically rounded at one end and often rather bluntly pointed or stair-stepped at the other. Occasionally the conical end is rhabdose, i.e. abruptly curved. They are rare both in sections and in dissociated spicule mounts and invariably broken. Size up to at least 850 × 4-8 μm. Trichodragmas (Figs. 2E, 3.5–6) form wispy, straight or S-curved bundles of 12–20 raphides. Bundles may be entirely sheathed and then superficially resemble oxea-like spicules (Fig. 3.5). Size 52–152 × 2–8 μm.

Ecology: the sclerosponge encrusted by the new species was collected in a cave.

Comparison with Tedania levis.— The type specimen of *T. levis*, BMNH 1900.10.19.16, is a thin crust of 1.5 mm on a small piece of coralline alga. It has the same appearance and consistency as *Julavis jamaicensis*. Differences between the two species are mostly confined to details of the spicules (Table 1). The acanthostrongyles form the same felted mass as in *J. jamaicensis*, but the uppermost are tangentially arranged (Fig. 4A–B), rather than in a palisade. The acanthostrongyles (Figs. 4C, 5.1–2) are much more strongly curved and distinctly longer and thinner than those of *J. jamaicensis*: 211–340 × 7–14. The long smooth spicules (Figs. 4E, 5.3) closer to typical strongyles, although they also show somewhat unequal ends. Their sizes appear to be somewhat longer: up to 1385 × 4–12 μm. A shorter category of styles reported by Kirkpatrick (245 μm) appears to be foreign. The trichodragmas (Figs. 4D, 5.4–6) are similar but longer than those of *J. jamaicensis*: 144–203 × 3–12 μm.

These skeletal differences in themselves do not form an impressive load of evidence for specific distinctness between the two specimens because specific variation is unknown. However, the wide geographic separation of the recorded specimens supports these small morphological differences and we erect the new species with confidence.

Generic allocation.—De Laubenfels (1936) erected *Julavis* on the basis of the incompatibility of the described characters of *Tedania levis* with those of the genus *Tedania*. It is clear from recent discussions on the contents of *Tedania* and the family Tedaniidae (e.g., in Desqueyoux-Faúndez & van Soest 1996) that de Laubenfels was correct in removing *T. levis* from *Tedania*. The synapomorphy for Tedaniidae, i.e., onychaetes, is lacking in *T. levis*. With two related species known, use of the genus *Julavis* is certainly justified. It remains a rare

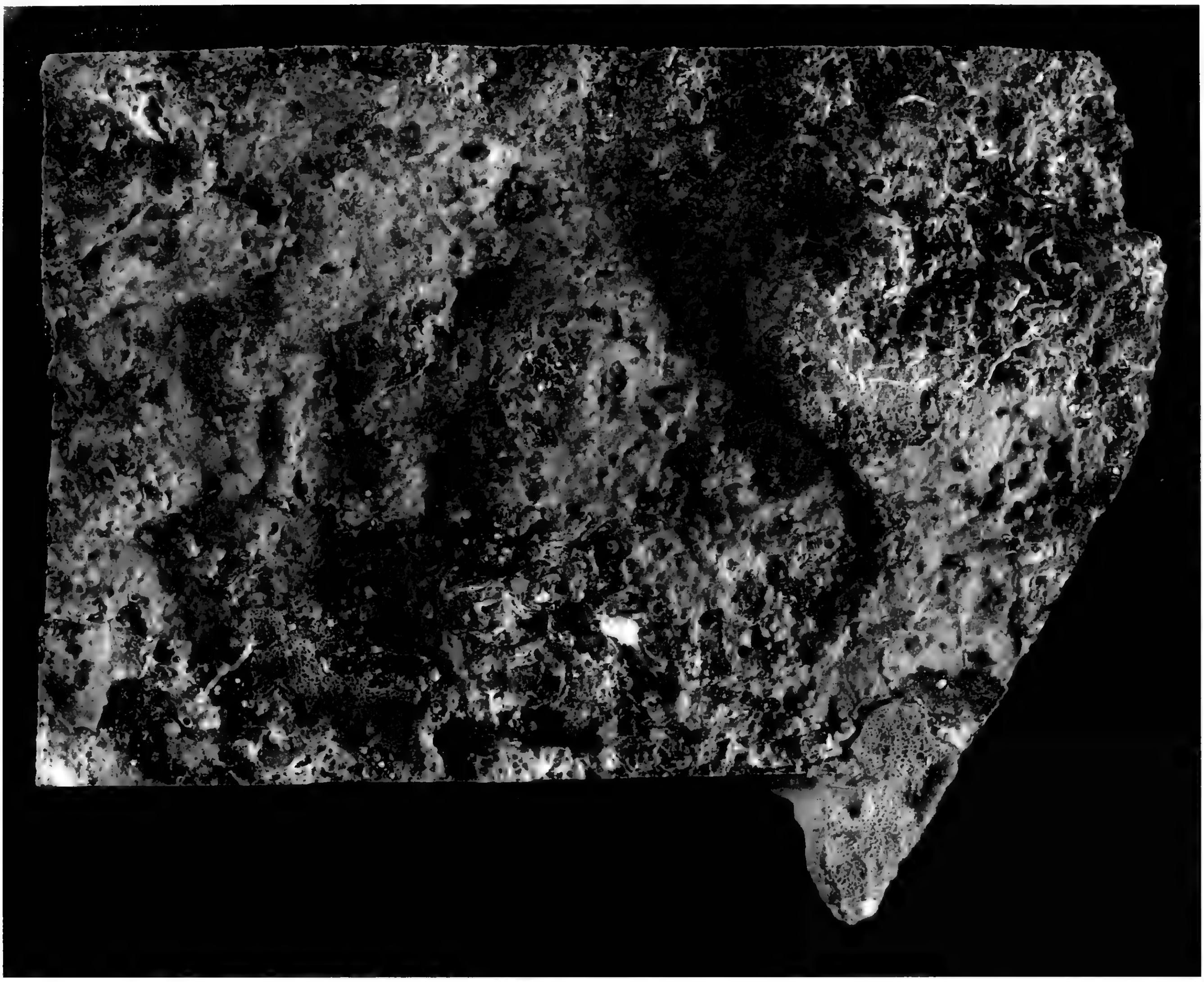

Fig. 1. *Julavis jamaicensis* new species, photo of holotype encrusting *Ceratoporella nicholsoni.*

genus with only two records at opposite sides of the world, perhaps indicating a wider Tethyan distribution.

Family and order allocation.—The major problem with *Julavis* is the family and order allocation. De Laubenfels (1936) assigned *Julavis* to the family Acarniidae, erected for an odd assortment of genera, including among others *Sceptrintus* (now Hadromerida: Latrunculiidae), *Janulum* (Poecilosclerida: Raspailiidae), *Jelissima* (Poecilosclerida: Myxillidae) and *Jones* (Poecilosclerida: Coelosphaeridae). The type genus of the family Acarniidae is *Acarnia* Gray, 1867, erected for type species *Hymeniacidon cliftoni* Bowerbank, 1864, which is a junior synonym of *Clathria frondifera* (Lamarck 1814) (see Hooper & Wiedenmayer 1994: 256). Thus, Acarniidae de Laubenfels, 1936 is a junior synonym of Microcionidae Carter, 1875. *Julavis* needs to be removed from Acarniidae/Microcionidae because it lacks the ectosomal subtylostyles, toxas and palmate isochelae characteristic for this family.

The skeletal architecture and spicule complement would allow allocation to both Poecilosclerida (e.g., family Crellidae) and Halichondrida (e.g., families Desmoxyidae and Halichondriidae).

Crellidae have a surface crust of acanthoxeas or acanthostyles and a choanosomal skeleton consisting of bundles of smooth tornotes, which may be oxea-like, strongly-like or style-like. Normally there are chelate microscleres and short echinating acanthostyles, but these may be absent. Allocation of *Julavis* to Crellidae is not warranted for

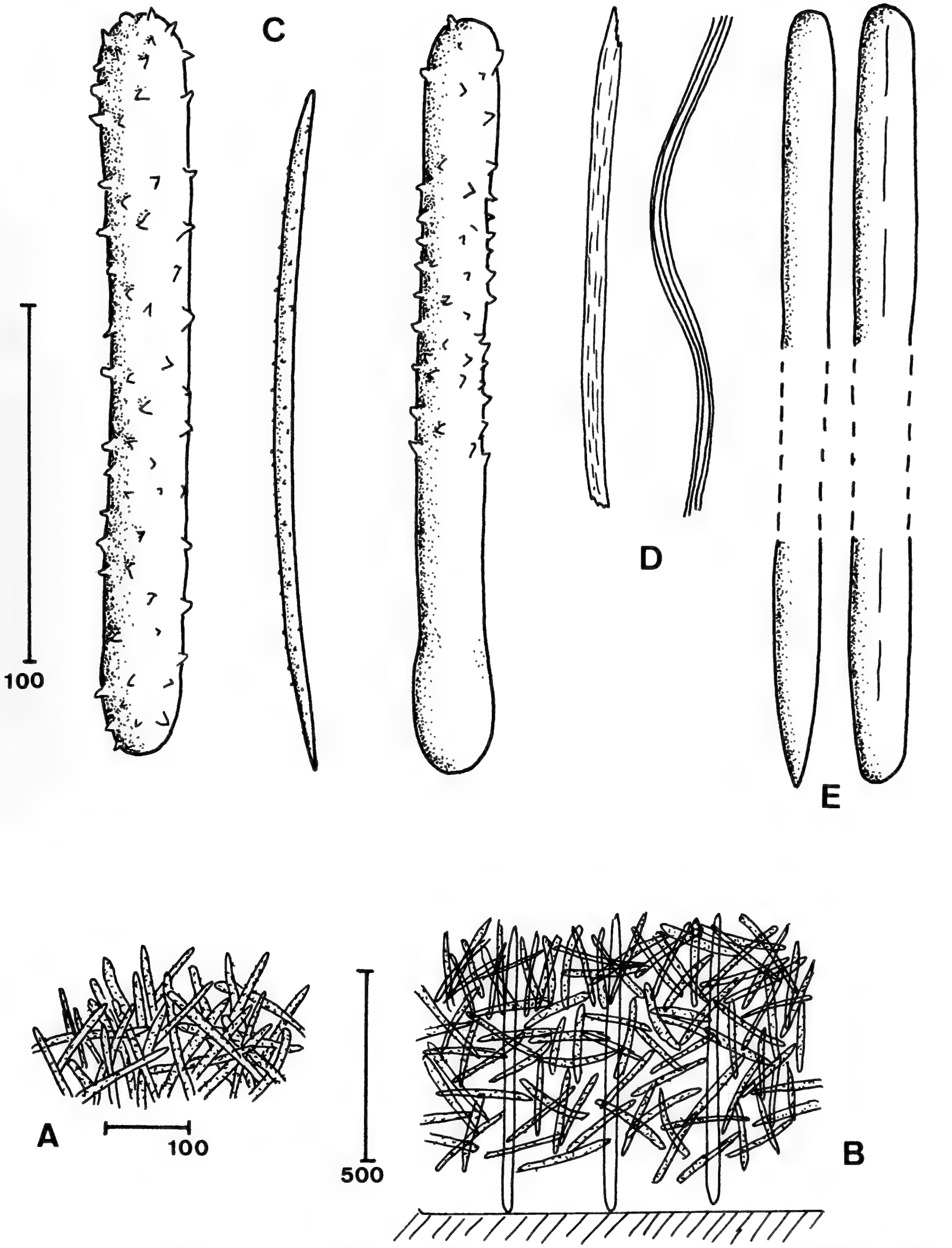

Fig. 2. *Julavis jamaicensis* n. sp., drawings of skeleton and spicules. A, surface view of ectosomal skeleton; B, cross section; C, various growth stages of acanthostrongyles; D, trichodragmas; E, smooth style and strongylote modification.

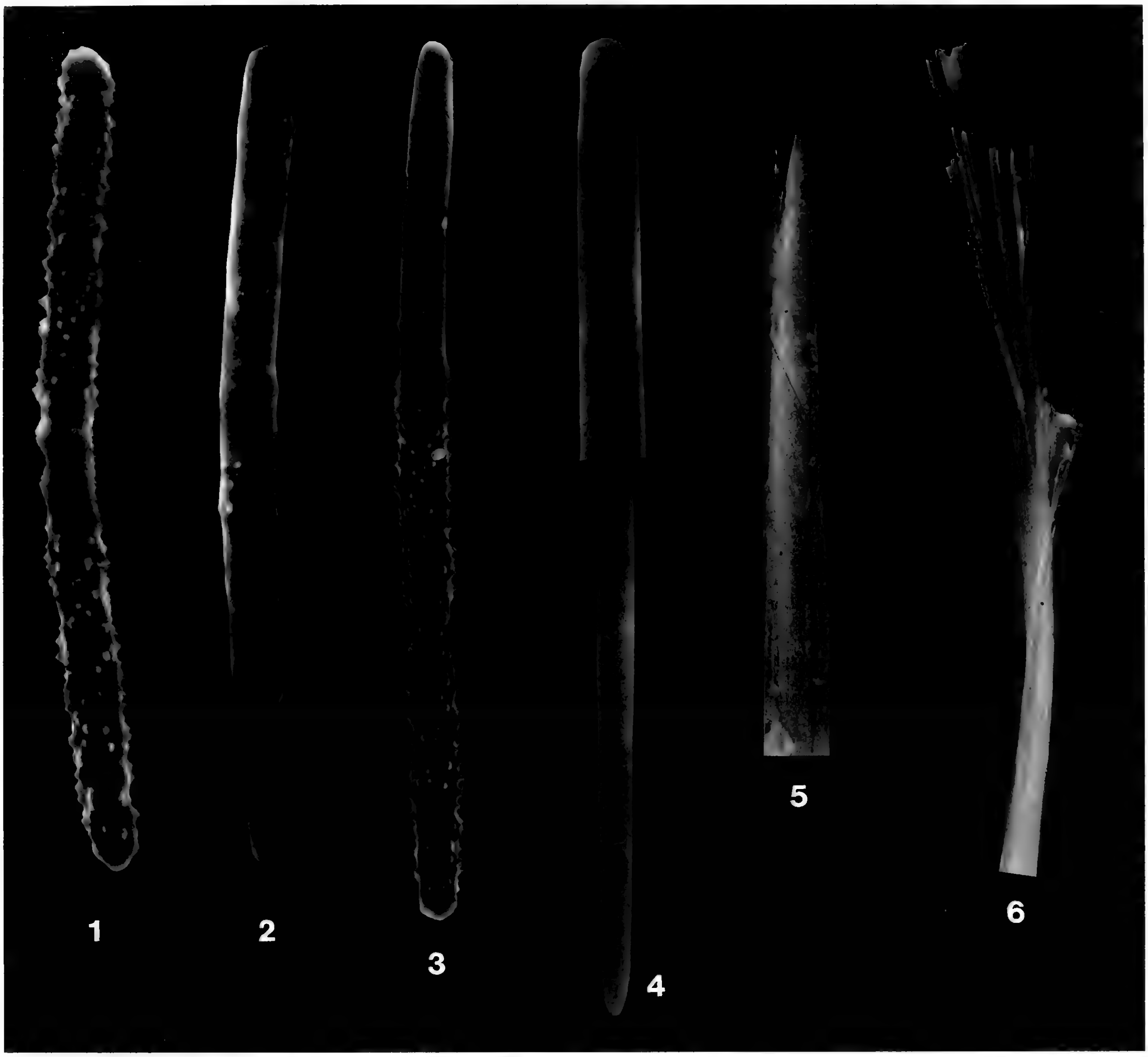

Fig. 3. *Julavis jamaicensis* n. sp., Scanning electronic microscope (SEM) photos of the spicules. 3.1, a fully spined acanthostrongyle (×650); 3.2, virtually smooth "acanthostrongyle" (×650); 3.3, partly smooth, partly spined acanthostrongyle (×650), 3.4, style (×650); 3.5, sheathed trichodragma ×2200); 3.6, irregularly fanned-out trichodragma (×2200).

the following reasons: Crellidae tend to be soft sponges with surface areolae or veinal canals visible; the tangential surface crust is generally thin (single spicule layer) and strictly tangential; the acanthose spicules are never strongyles; the tornotes are seldom longer than 300 μm and never over 600 μm; and, no trichodragmas have been recorded from Crellidae.

Halichondriidae and Desmoxyidae are considered closely related families in a redefined order Halichondrida by van Soest et al. (1990). The generic content of these two families is still in debate: for example, *Ptilocaulis*, assigned to Desmoxyidae by van Soest et al. (1990) on account of its gross morphological similarity to certain *Higginsia* species, was shown to be very close to *Axinella* of the family Axinellidae by Alvarez et al. (1997); the allocation of *Axinyssa* and *Myrmekioderma* to Halichondriidae is disputed by Hooper & Bergquist (1992) and Hooper & Lévi (1993).

Myrmekioderma shares several features with *Julavis*: spined diactinal surface spicules (oxeas in *Myrmekioderma*), smooth

Table 1.—Comparison of spicule types and sizes (μm) of *Julavis levis* (Kirkpatrick 1900) and *J. jamaicensis* n.sp. (ranges, means in italics).

Spicule type	*Julavis levis*	*Julavis jamaicensis*
Acanthostrongyles	211–*280.5*–340 × 7–*11.1*–14	127–*185.2*–258 × 8–*14.1*–20
Strongylostyles*	<1385 × 4–12	<850 × 4–8
Trichodragmas	144–*178.3*–200 × 3–*3.8*–12	52–*108.3*–152 × 2–*3.7*–8

* Most often broken in the spicule slides.

diactinal choanosomal spicules (oxeas in *Myrmekioderma*), and wispy trichodragmas. The two genera are nevertheless considered to be distinct because spination of the surface spicules in *Myrmekioderma* is very fine (and may be occasionally absent) and the choanosomal spicules are arranged in definite tracts. The surface of the known species of *Myrmekioderma* shows a characteristic groove pattern (see van Soest et al. 1990).

A further genus sharing features with *Julavis* is *Heteroxya* Topsent, 1904. Van Soest et al. (1990) tentatively considered it a junior synonym of *Myrmekioderma*, but the evidence for that assumption is weak. The genus is defined as having spined and smooth oxeas in a confused mass, with smaller spined oxeas forming a dense palisade at the surface. No trichodragmas have been reported from the type and only assigned species, *H. corticata* Topsent, 1904. The strongylote and stylote spicules as well as the possession of trichodragmas easily differentiate *Julavis* from *Heteroxya*.

Another genus that needs to be considered is *Higginsia* (Desmoxyidae), which likewise shares with *Julavis* diactinal spined surface spicules (oxeas) over much longer smooth choanosomal spicules. The two genera are considered distinct because the spined oxeas of *Higginsia* have a distinct angular curve in the middle. These spicules often do not form a surface crust but are scattered among the choanosomal megascleres. The choanosomal skeleton consists of well-defined tracts of smooth megascleres.

Julavis links *Higginsia* and *Myrmekioderma* by its possession of coarsely spined diactinal surface spicules (shared with *Higginsia*) and wispy trichodragmas (shared with *Myrmekioderma*). It is sufficiently distinct from both in possessing acanthostrongyles in a thick surface feltwork. Accordingly we propose to include *Julavis* in a rearranged and redefined family Desmoxyidae, which in disagreement with van Soest et al. (1990) receives *Myrmekioderma* and the closely similar *Didiscus* from the family Halichondriidae, and loses *Ptilocaulis* to the family Axinellidae.

Family Desmoxyidae.—Halichondrida with a surface skeleton consisting of spined diactinal spicules (oxeas or strongyles); the choanosomal skeleton is formed either by a confused or perpendicular arrangement of single spicules or interconnected bundles perpendicular to the surface.

Higginsia Higgin, 1877 (jun. syn. *Desmoxya* Hallmann 1917): spined oxeas with abrupt angular curve in the middle; choanosomal skeleton an elaborate system of bundles of megascleres.

Halicnemia Bowerbank, 1866: spined oxeas with abrupt angular curve in the middle; two categories of choanosomal megascleres one of which is erect on the substrate while the other surrounds the first.

Heteroxya Topsent, 1904: Surface skeleton a palisade of smaller spined oxeas, though which perpendicular subectosomal longspined oxeas protrude; choanosomal skeleton a confused mass of smooth and spined oxeas.

Myrmekioderma Ehlers, 1870: surface oxeas rugose or finely spined; choanosomal megascleres in several length categories arranged in a system of interconnected tracts; microscleres wispy or straight trichodrag-

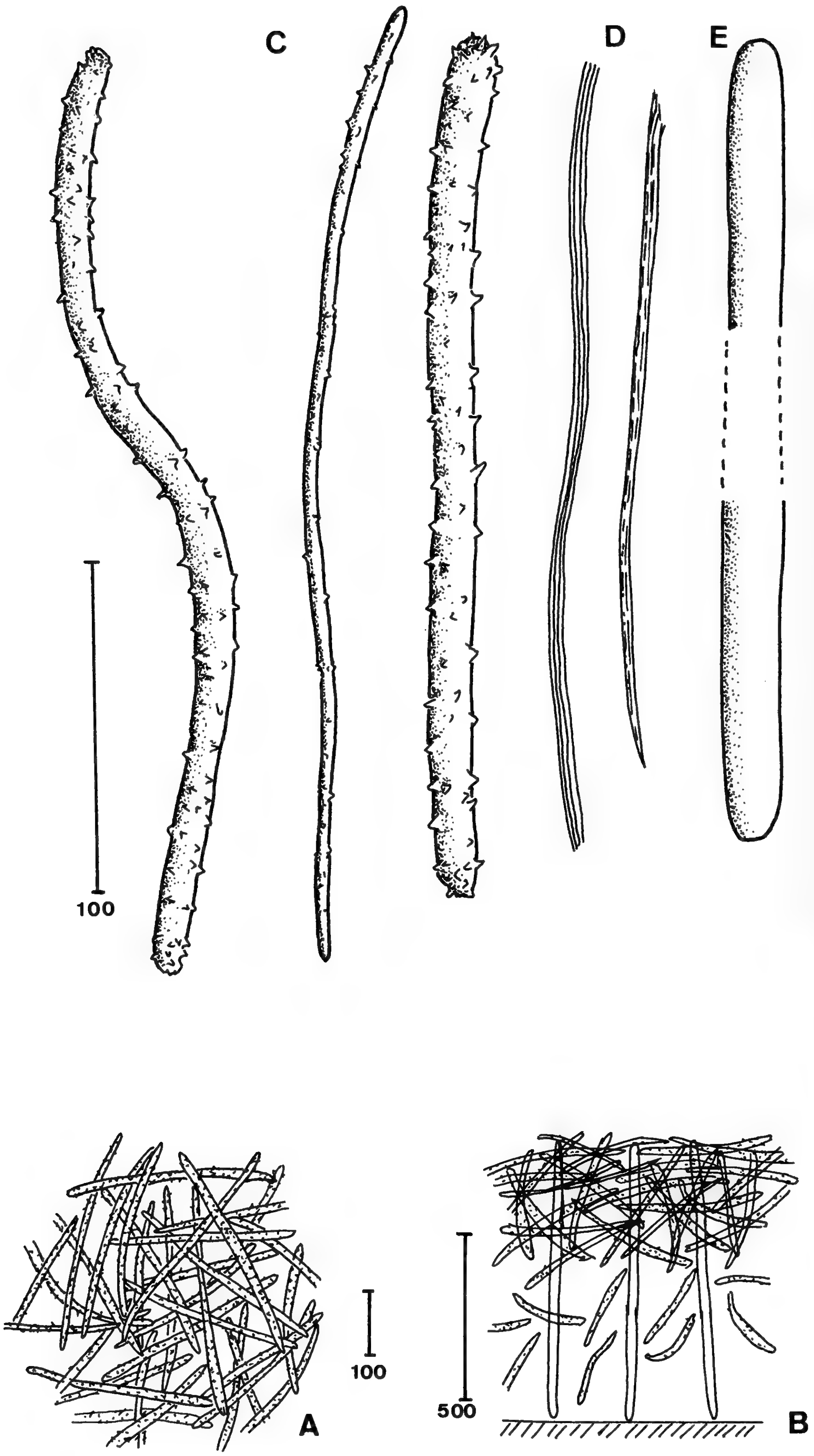

Fig. 4. *Julavis levis* (Kirkpatrick), holotype BMNH 1900.10.19.16, drawing of skeleton and spicules. A, surface view of ectosomal skeleton; B, cross section; C, various growth stages of acanthostrongyles; D, trichodragmas; E, smooth strongyle.

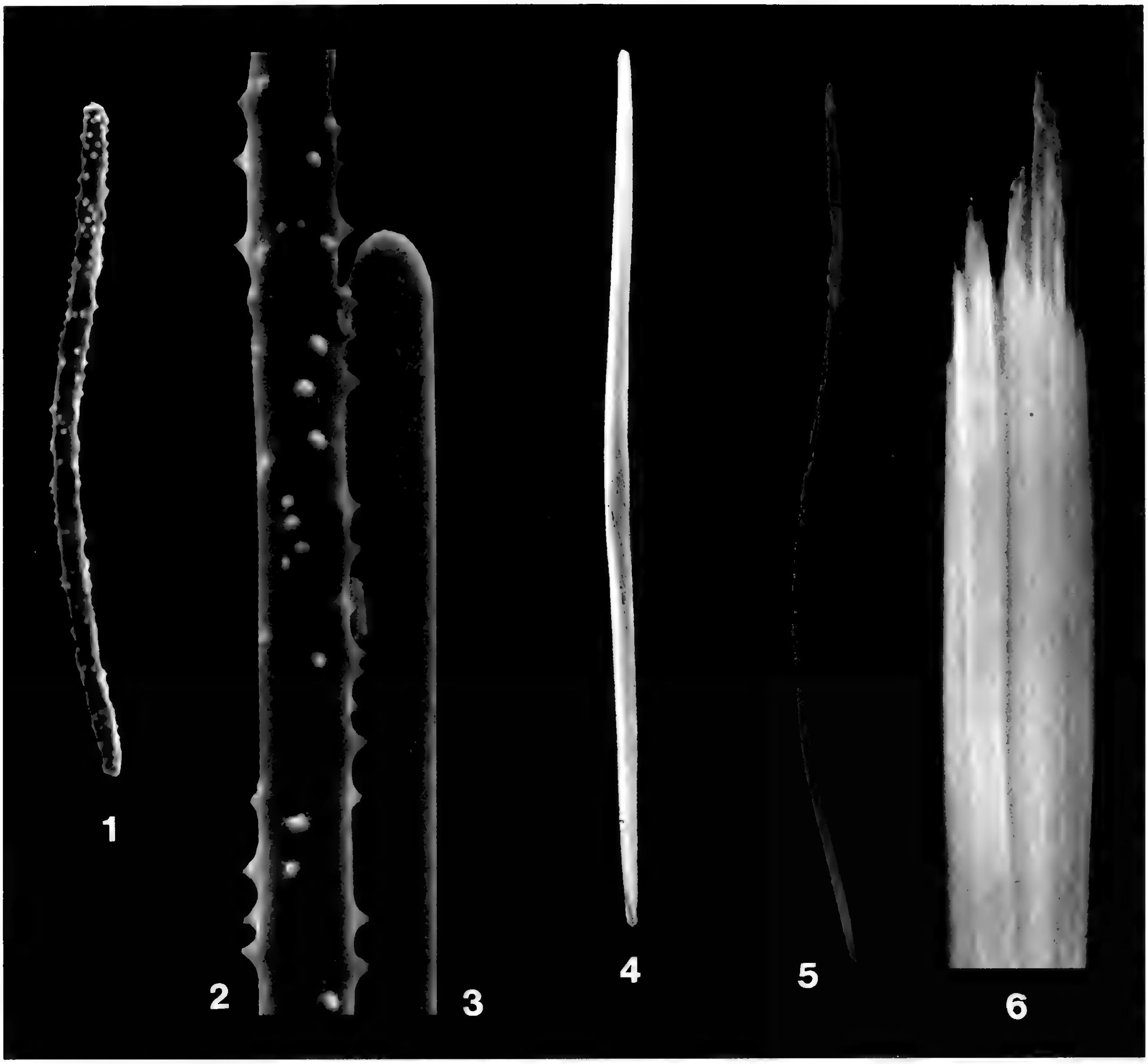

Fig. 5. *Julavis levis* (Kirkpatrick), holotype BMNH 1900.10.19.16, SEM photos of the spicules. 5.1, acanthostrongyle (×300); 5.2, detail of part of acanthostrongyle (×800); 5.3, terminal part of smooth strongyle (×800); 5.4, sheathed trichodragma (×300); 5.5, partly split-open trichodragma (×300); 5.6, detail of trichodragma (×2200).

mas; surface has characteristic sinuous grooves.

Didiscus Dendy, 1922: surface oxeas rugose or finely spined, possessing two unequally sized discs assymmetrically along the shaft; choanosomal megascleres in several length categories arranged in a system of interconnected tracts; surface has characteristic sinuous grooves.

Julavis de Laubenfels, 1936: surface spicules are coarsely spined strongyles forming a thick felted mass at the surface; choanosomal skeleton reduced, consisting of long strongylostyles arranged singly perpendicular to the surface; wispy trichodragmas.

Acknowledgments

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Ms Clare Valentine graciously sent us the specimen of *Tedania levis* on loan. Louis Van der Laan (ZMA) made the habit photograph; Jan Vermeulen (ZMA) made the SEM photos. John Hooper (Brisbane) gave valuable advice.

Literature Cited

Alvarez, B., R. W. M. van Soest, & K. Rützler. 1997. Revision of the Central West Atlantic Axinellidae.—Smithsonian Contributions to Zoology (in press).

Desqueyroux-Faúndez, R., & R. W. M. van Soest. 1996. A review of Iophonidae, Myxillidae and Tedaniidae occurring in the South East Pacific (Porifera: Poecilosclerida).—Revue Suisse de Zoologie 103(1):3–79.

Hooper, J. N. A., & P. R. Bergquist. 1992. Cymbastela, a new genus of lamellate coral reef sponges.—Memoirs of the Queensland Museum 32(1):99–137.

———, & C. Lévi. 1993. Axinellidae from the New Caledonian lagoon (Porifera: Demospongiae).—Invertebrate Zoology 7(6):1395–1472.

———, & F. Wiedenmayer. 1994. Porifera. *in*: A. Wells, ed., Zoological Catalogue of Australia. Volume 12. Melbourne, CSIRO, Australia, 612 pp.

Kirkpatrick, R. 1900. Descriptions of sponges from Funafuti.—Annals and Magazine of Natural History (7)6:345–362.

Laubenfels, M. W. de. 1936. A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera.—(Publications of the Carnegie Institute Washington 467) Publications of the Dry Tortugas Laboratory 30:1–225.

Soest, R. W. M. van, M. C. Diaz, & S. A. Pomponi. 1990. Phylogenetic classification of the Halichondrids (Porifera, Demospongiae).—Beaufortia 40(2):15–62.

Topsent, E. 1904. Spongiaires des Açores.—Résultats des Campagnes Scientifiques du Prince Albert ler de Monaco 25:1–280.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(4):511–519. 1997.

Narella nuttingi, a new gorgonacean octocoral of the family Primnoidae (Anthozoa) from the eastern Pacific

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Abstract.—Specimens originally reported by Nutting (1908) as *Stachyodes dichotoma* Versluys from Albatross explorations in Hawaiian waters are shown to be misidentified and are now described as a new species, *Narella nuttingi.*

In the eastern Pacific, four species of *Narella* have been reported (as *Stachyodes*) from the Hawaiian Islands: *Stachyodes angularis* Nutting, 1908; *S. regularis* Wright & Studer, 1889; *S. bowersi* Nutting, 1908, and *Stachyodes dichotoma* Versluys, 1906 (Nutting 1908).

The species described by Nutting (1908: 576) as *Stachyodes angularis* is referable to the genus *Calyptrophora*, not to *Narella.*

The specimen reported by Nutting (1908: 577) as *S. regularis* Wright & Studer consists of an incomplete terminal branch with remnants of only nine whorls of polyps, but it is adequate to demonstrate that it represents *S. dichotoma* Versluys.

The specimens reported as *S. dichotoma* by Nutting (1908:577) were incorrectly identified. Nutting's (1908) plate 43, fig. 5, captioned "*Stachyodes bowersi* Nutting," does not depict *bowersi*, but the specimen reported as "*Stachyodes dichotoma*" (Nutting 1908:577) from *Albatross* sta. 4013 and retained by Nutting at the State University of Iowa under the name *Calypterinus allmani* Wright & Studer, a species that he did not report from Hawaii. The type specimen of *S. bowersi* (USNM 25377) was not illustrated and does not harbor specimens of the ophiuroid *Ophiocreas*, a specimen of which is clearly shown in Nutting's photograph (1908: pl. 43, fig. 5) and specifically mentioned in the figure explanation (1908:600). In the text (1908:577) Nutting mentions the occurrence of *Ophiocreas* on *S. dichotoma*, not on *S. bowersi*.

Narella Gray, 1870

Narella Gray, 1870:49.—Deichmann, 1936:168.—Bayer, 1956:222; 1961:295 (key only); 1981:937 (key only).

Stachyodes Studer, 1887:49; 1901:40.—Wright & Studer, 1889: xlvii, 53.—Versluys, 1906:86.—Thomson & Henderson, 1906:35.—Kinoshita, 1907:233; 1908: 45.—Thomson & Russell, 1910:142.—Kükenthal, 1912:59; 1915:152; 1919: 452; 1924:308.

Calypterinus Wright & Studer, 1889:xlviii, 54.

Type species.—*Primnoa regularis* Duchassaing & Michelotti, 1860.

Diagnosis.—Primnoidae forming colonies branched pinnately, dichotomously, or trichotomously, rarely unbranched; polyps in pairs or whorls, usually directed basad; sclerites of polyps comprising three or four pairs of large scales surrounding the polyp body but not solidly fused to form rings, and an operculum of 8 roughly triangular scales; coenenchyme with a layer of large scales that may be polygonal, elongate, sometimes tapered and almost fusiform.

Narella nuttingi, new species
Figs. 1–5

Stachyodes dichotoma.—Nutting 1908:577.

Stachyodes bowersi Nutting 1908: pl. 43, fig. 5.

Not *Stachyodes dichotoma* Versluys 1906: 88.

Material examined.—Kauai Island, Hawaii, Hanamaulu warehouse bearing N. 82°45′, W 3.7′, 419–399 fath. (= 767–730 m), bottom temperature 41.0°F, USFC str. *Albatross* sta. 4013, 20 Jun 1902. One nearly complete colony with attached ophiuroid, holotype, USNM 91864 (SEM 2336; Figs. 1, 2). This specimen erroneously illustrated as *Stachyodes bowersi* by Nutting, 1908:pl. 43, fig. 5.

Kauai Island, Hawaii: Ukula Point bearing S. 82°30′, E. 13.1′, 423–438 fath. (= 774–802 m), bottom temperature 41.0°F, USFC str. *Albatross* sta. D-4030, 24 Jun 1902. One colony somewhat broken, paratype, USNM 25376 (SEM 2335; Figs. 4, 5).

Kauai Island, Hawaii: Hanamaulu Warehouse bearing S. 33°, W. 9.5′, 500–385 fath. (915–693 m), bottom temperature 40°F, USFC str. *Albatross* sta. D-3989, 11 Jun 1902. One unbranched terminal branchlet, USNM 22561.

Kauai Island, Hawaii: Hanamaulu Warehouse bearing N. 74°30′, W. 6.6′, 671–957 fath. (1228-1751 m), bottom temperature 38.4°F, USFC str. *Albatross* sta. D-3989, 11 Jun 1902. Detached branches, USNM 25375.

Kauai Island, Hawaii: Ukula Point bearing N. 65°30′, W. 7.4′, 508–557 fath. (= 930–1019 m), bottom temperature 40°F, USFC str. *Albatross* sta. D-4007, 17 Jun 1902. One colony somewhat broken, paratype, USNM 77293 (SEM 2338; Figs. 3, 4).

North of Maui Island, Hawaii: 21°07.0′N, 156°12.7′W, no other particulars as to collection recorded. Three large, somewhat damaged colonies, with ophiuroids attached, USNM 56790.

Cross Seamount: 18°38.7′N, 158°16.8′W, 1420 m, *Pisces V* dive PV238, station CR201 (sample 1), 29 Aug 1993, coll. Scott France and J. Ewann Agenbroad. One incomplete colony with attached ophiuroid, USNM 94451.

Cross Seamount: 18°38.7′N, 158°16.8′W, 1350 m, *Pisces V* dive PV238, station CR203 (sample 1), 29 Aug 1993, coll. Scott France and J. Ewann Agenbroad. One incomplete colony with attached ophiuroid, paratype, USNM 94452 (Fig. 1).

Cross Seamount: 18°38.7′N, 158°16.8′W, 1205 m, *Pisces V* dive PV238, station CR205 (sample 1), 29 Aug 1993, coll. Scott France and J. Ewann Agenbroad. One incomplete colony with attached ophiuroid, USNM 94453.

Diagnosis.—Bushy *Narella* colonies with branching initially verticillate, subsequently becoming dichotomous and approximately uniplanar in the distal branches; 3-5 polyps per whorl; commonly 8-1/2 to 11 (but sometimes as few as 5-6) whorls in 3 cm of branch length; none of the three pairs of body plates adaxially closed; all body plates regularly curved, without keels or crests, their free margins without serrations or sharp projections; one pair of small adaxial buccal scales; apical keel on inner face of opercular scales low, absent from the larger abaxial scales; adaxials narrow, small; cortical sclerites elongate, usually narrow but a few may be wider, without external crests; tentacles with very few minute, flat rods; coenenchyme with a single layer of elongate oval plates, becoming thick and irregular on the large branches, locally with several strong, hemispherical projections longitudinally arranged along the midline.

Description.—The colonies (Fig. 1) are bushy, the branching of the lower parts verticillate with 3 or 4 lateral branches in widely spaced whorls, in the distal branches becoming dichotomous and tending to lie in one plane so the colonies are compressed-flabellate rather than flat fans. The axis is strongly calcified, round, longitudinally striated, with little or no metallic luster or iridescence. Specimens having the proximal part of the trunk preserved show thick secondary deposits of white calcareous material around and above the holdfast.

Polyps are directed basally, up to 3 mm in height (measured parallel with the branch

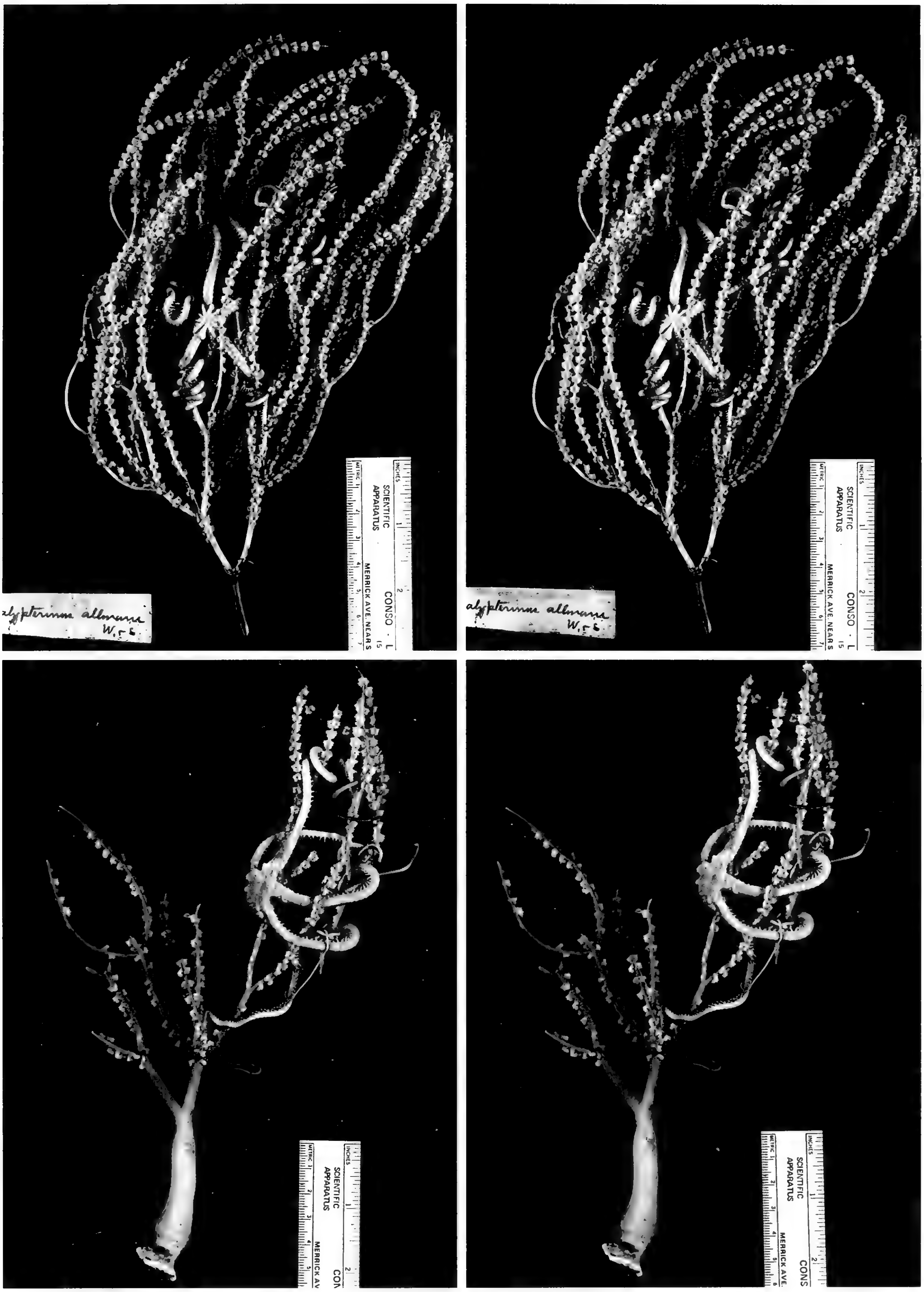

Fig. 1. *Narella nuttingi*, new species. Top, Holotype colony, USNM 91864. Bottom, Paratype colony, USNM 94452.

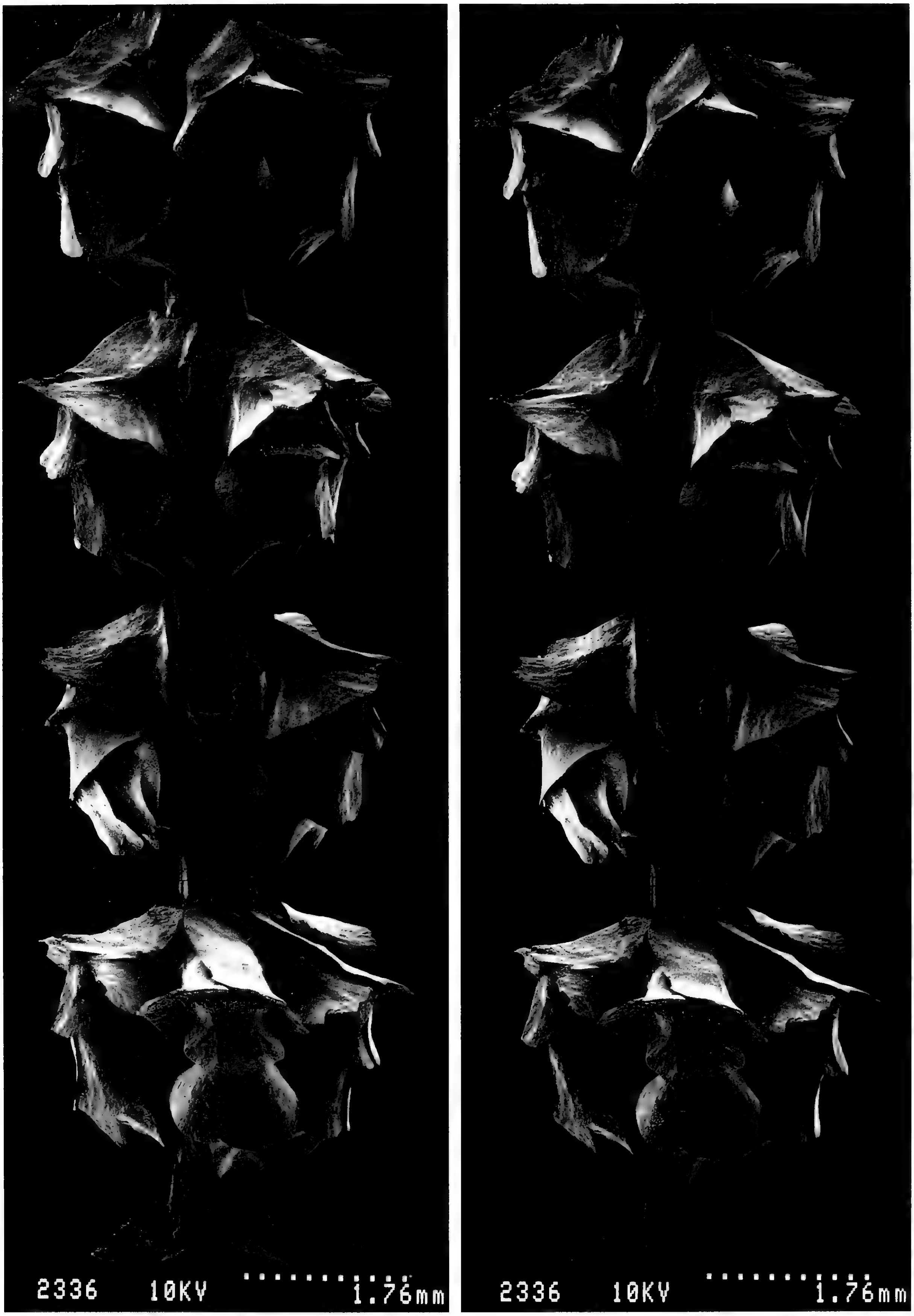

Fig. 2. *Narella nuttingi*, new species. Part of terminal branch of holotype colony, USNM 91684. SEM 2336, stereo pair.

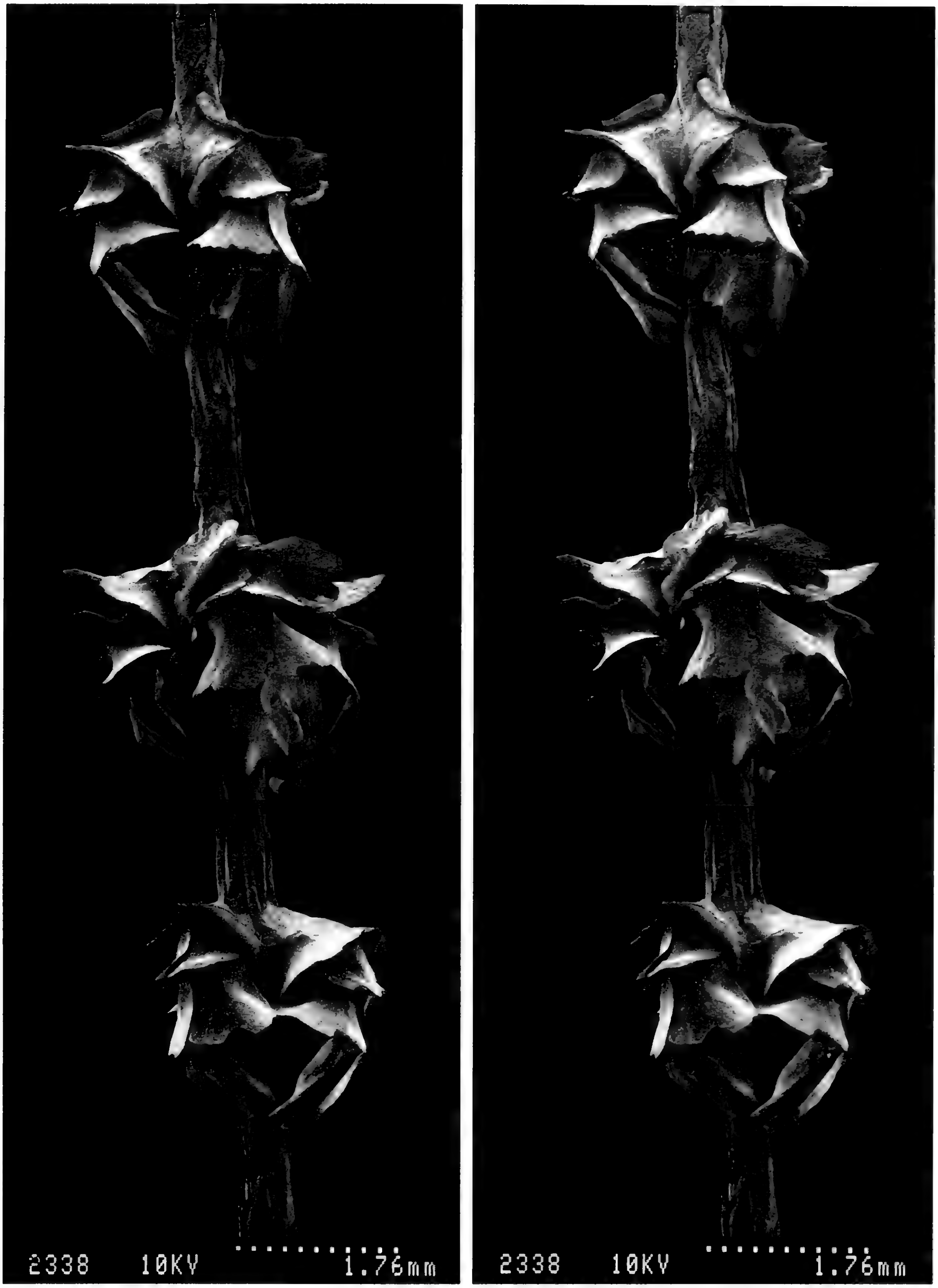

Fig. 3. *Narella nuttingi*, new species. Part of terminal branch of paratype colony, USNM 77293. SEM 2338, stereo pair.

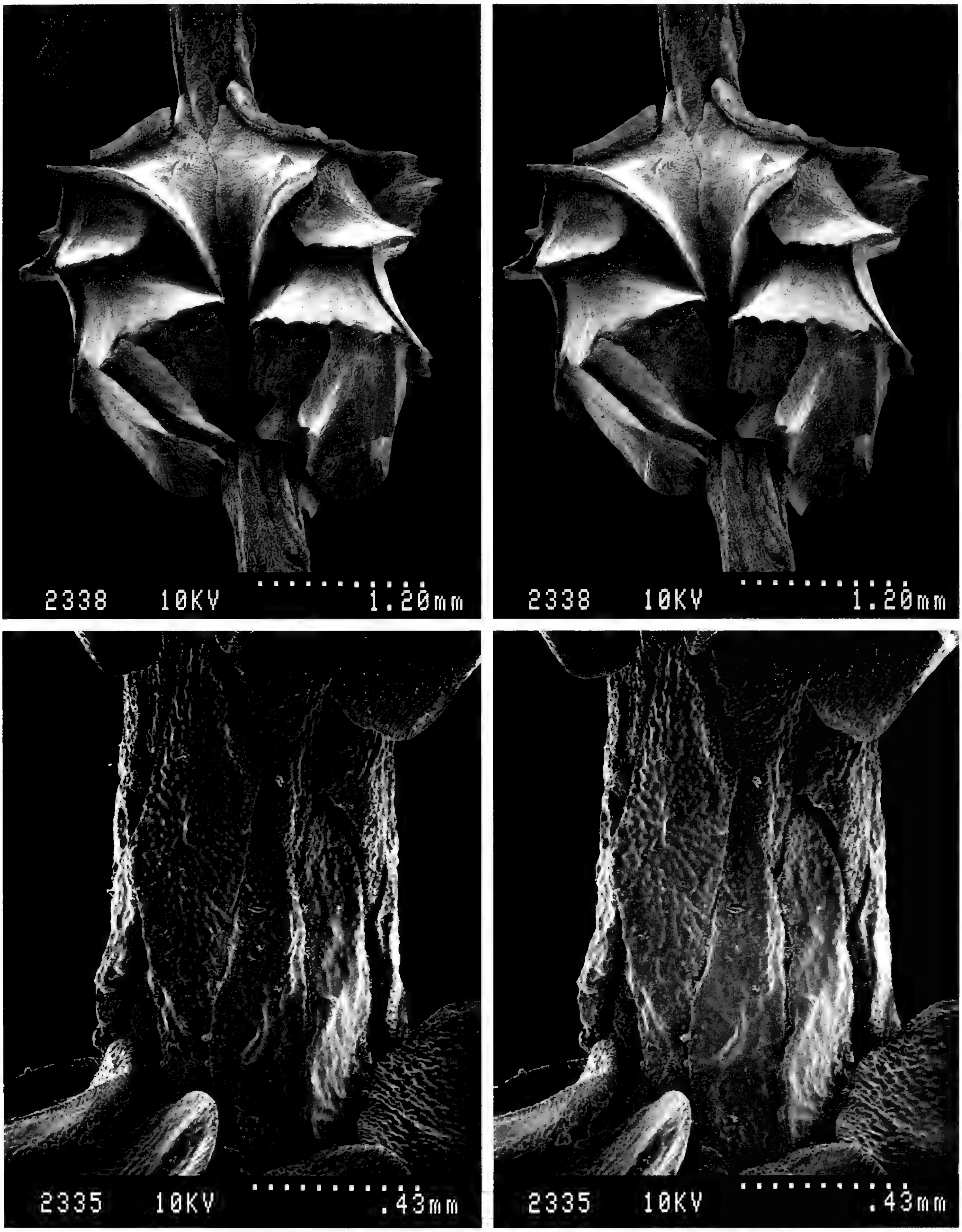

Fig. 4. *Narella nuttingi*, new species. Top, Whorl of polyps of paratype colony, USNM 77293, showing prominent operculum and absence of dorsolateral crest on body scales. SEM 2338. Bottom, Detail of coenenchyme showing elongate, plate-like sclerites; SEM 2335, stereo pairs.

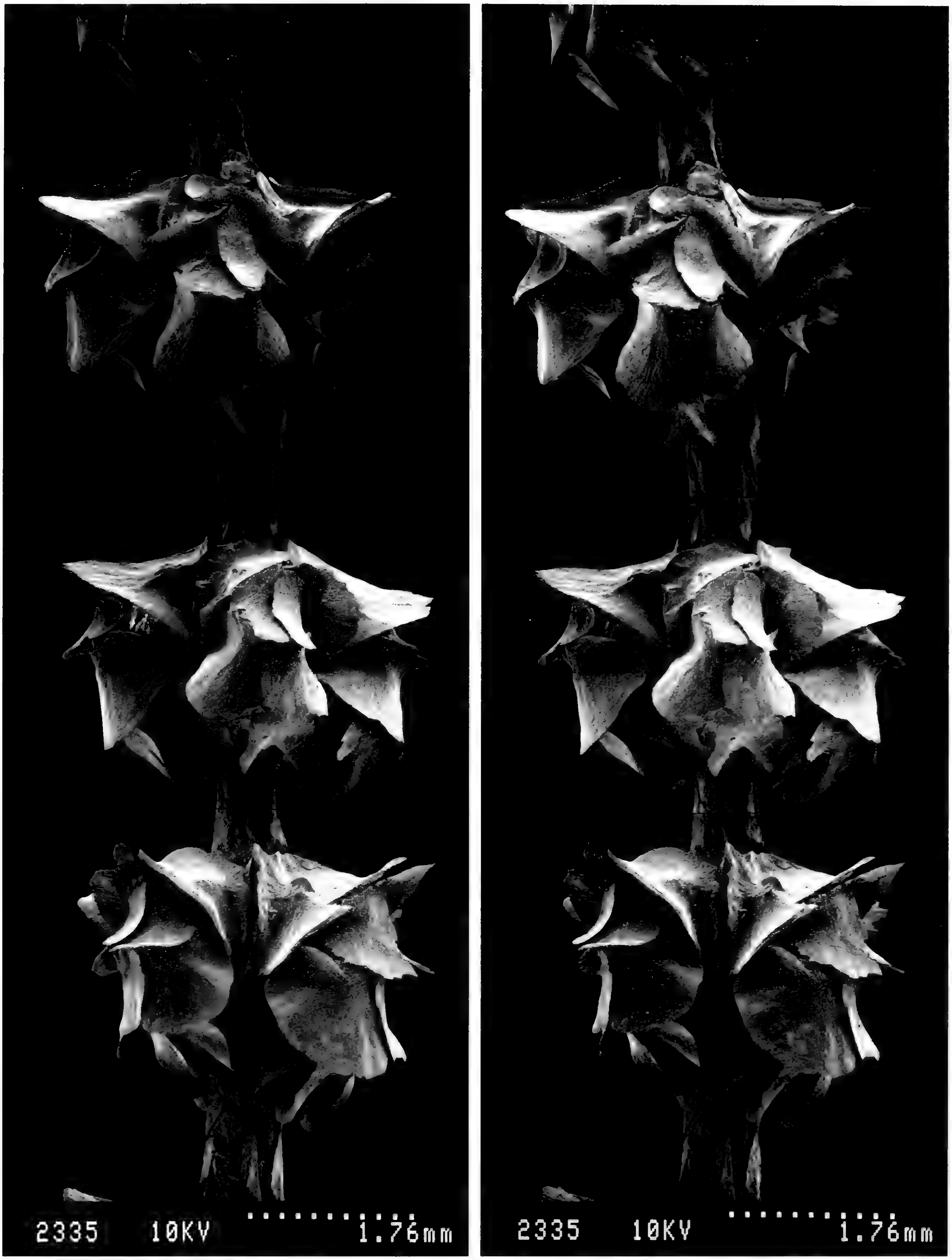

Fig. 5. *Narella nuttingi*, new species. Part of terminal branch of paratype colony, USNM 25376. SEM 2335, stereo pair.

axis), in whorls of 5 on the larger branches, sometimes only 3 near the tips of the terminal branchlets (Figs. 2–5); 8½ to 11 whorls occur in 3 cm of branch length. Polyps with 3 pairs of non-annular body plates, all with uniformly and moderately expanded margins regularly curved and without marginal spines, teeth, or conspicuous serrations. The two basal plates are the largest, regularly curved around the base of the polyp, without a dorsolateral angle or crest, with moderately flared, smooth margins; one of the plates overlaps the other where they meet along the abaxial midline, its thin edge somewhat reflexed. The medial pair of body plates are the smallest, smoothly curved around the body and without dorsolateral crests. The buccal pair have smooth, moderately flared free margins; one pair of small, thin, adaxial buccal scales lie below the adaxial operculars.

The operculum is high, the abaxial scales tall, broad, rounded apically, the outer surface longitudinally concave but without a corresponding well-defined keel on the inner surface; the lateral scales are narrower, more pointed, and have a low keel on the inner surface; the adaxials are narrow, with a low, ridge-like keel. The tentacles have a few minute, irregular flat rods.

The sclerites of the coenenchyme (Fig. 4) are more or less elongate, flat plates with no trace of longitudinal crests or keels even near the polyps, but some of those on the large branches may have several hemispherical projections along the midline.

Etymology.—This species is named for the late Prof. C. C. Nutting, who first unknowingly reported specimens in his report on Hawaiian octocorals collected by USFC steamer *Albatross.*

Variation.—The polyps vary somewhat in size among different colonies, and the spacing of whorls varies locally both within a single colony and among different colonies (compare Figs. 2, 3 and 5).

Distribution.—Eastern Pacific, vicinity of Hawaiian Islands and nearby seamounts, 730–1420 m.

Commensals.—Most colonies have a large ophiuroid, *Asteroschema caudatum* H. L. Clark, entwined among the branches. Nutting (1908:577) reported that colonies examined by him "had coiled around its branches a simple-armed basket fish, probably belonging to the genus *Ophiocreas.*"

Comparisons.—Although the polyps of *N. nuttingi* resemble those of *N. dichotoma* (Versluys) as originally illustrated (Versluys 1906:89, 90), the coenenchymal scales lack the characteristic ridges of that species but instead may have several strong, hemispherical projections along the midline, the adaxial opercular scales are very reduced in size, and branching is not in one plane. *Narella orientalis* (Versluys), which has similar polyps, differs in having broad cortical scales and more strongly developed adaxial opercular scales.

The polyps of *Narella megalepis* (Kinoshita 1908) are generally similar to those of *N. nuttingi*, but the opercular scales have a strong apical keel on the inner surface, the adaxial operculars are broad and well-developed, and the cortical sclerites are thick, irregular polygonal plates; moreover, the overall colonial form is not known because all existing specimens are fragmentary. As originally illustrated (Kinoshita 1908, pl. 3, fig. 21), the branching is dichotomous although it was described as "beinahe federartig." It seems unlikely that the complete colonies would have the openly bushy aspect of *N. nuttingi.* The identity of specimens collected in Japanese waters by USFC str. *Albatross* and reported as *Stachodes megalepis* by Nutting (1912:59) cannot be determined because the specimens were not returned to the U.S. National Museum for permanent storage. It is unlikely that they were *N. megalepis* as Nutting (1912:60) mentioned the presence of worm galleries formed by parasitic annelids, a feature not reported by Kinoshita (1908:47–49) or Utinomi (1979:1015).

Acknowledgments

I am grateful to Dr. Scott C. France and Ms. J. Ewann Agenbroad Berntson, who collected some of the material reported herein. The commensal ophiuroid was identified by Dr. David L. Pawson. The stereographic scanning micrographs illustrating this paper were made by Mr. Walter R. Brown, head of the SEM Laboratory, National Museum of Natural History.

Literature Cited

Bayer, F. M. 1956. Octocorallia. Pp. 163–231, figs. 134–162 *in* R. C. Moore, ed., Treatise on Invertebrate Paleontology Part F. Coelenterata. Lawrence, Kansas: Geological Society of America and University of Kansas Press. xx + 498 pp., 358 figs.

———. 1961. The shallow-water Octocorallia of the West Indian region. A manual for marine biologists.—Studies on the fauna of Curaçao and other Caribbean islands 12:1–373.

———. 1981. Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa.—Proceedings of the Biological Society of Washington 94: 901–947.

Deichmann, E. 1936. The Alcyonaria of the western part of the Atlantic Ocean.—Memoirs of the Museum of Comparative Zoölogy at Harvard College 53:1–317.

Gray, J. E. 1870. Catalogue of the lithophytes or stony corals in the collection of the British Museum. London: British Museum. [i–iv] + 1–51 pp.

Kinoshita, K. 1907. Vorläufige Mitteilung über einige neue japanische Primnoidkorallen.—Annotationes Zoologicae Japonenses 6(3):229–237.

———. 1908. Primnoidae von Japan.—Journal of the College of Science, University of Tokyo 23(12): 1–74, pls. 1–6.

Kükenthal, W. 1912. Die Alcyonaria der deutschen Sudpolar-Expedition 1901-1903.—Deutsche Sudpolar-Expedition 1901–1903, 13. Band. Zoologie 5(3):289–349, pls. 20–23.

———. 1915. System und Stammesgeschichte der Primnoidae.—Zoologischer Anzeiger 46(5): 142–158.

———. 1919. Gorgonaria.—Wissenschaftliche Ergebnisse der deutschen Tiefsee- Expedition auf dem Dampfer "Valdivia" 13(2):1–946, pls. 30–89.

———. 1924. Gorgonaria.—Das Tierreich 47:i–xxviii + 1–478, 209 figs. Berlin and Leipzig, Walter de Gruyter & Co.

Nutting, C. C. 1908. Descriptions of the Alcyonaria collected by the U.S. Bureau of Fisheries steamer Albatross in the vicinity of the Hawaiian Islands in 1902.—Proceedings of the United States National Museum 34:543–601, pls. 41–51.

Studer, Th. 1887. Versuch eines Systemes der Alcyonaria.—Archiv für Naturgeschichte 53(1):1–74, pl. 1.

Thomson, J. A., & W. D. Henderson. 1906. An account of the alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean. Part 1. The Alcyonarians of the deep sea. Calcutta: The Indian Museum. i–xvi + 1–132 pp., pls. 1–10.

———, & E. S. Russell. 1910. Alcyonarians collected on the Percy Sladen Trust Expedition by Mr. J. Stanley Gardiner. Part 1, the Axifera.—Transactions of the Linnean Society of London (2) 13(2):139–164, pls. 6–14.

Utinomi, H. 1979. Redescriptions and illustrations of some primnoid octocorals from Japan.—Proceedings of the Biological Society of Washington 91(4):1008–1025.

Versluys, J. 1906. Die Gorgoniden der Siboga Expedition II. Die Primnoidae. Siboga-Expeditie, Monographie 13a. 1–187 pp., figs. 1–178, pls. 1–10, chart.

Wright, E. P., & Th. Studer. 1889. Report on the Alcyonaria.—Report on the scientific results of the voyage of H. M. S. Challenger during the years 1973–76 under the command of Captain George S. Nares, R. N., F. R. S. and the late Captain Frank Tourle Thomson, R. N. Prepared under the superintendence of the late Sir C. Wyville Thomson, Knt., F. R. S. & c. Regius Professor of Natural History in the University of Edinburgh, director of the civilian scientific staff aboard and now of John Murray, LL. D., Ph. D. & c. one of the naturalists of the expedition. Zoology 31 part 64. i–lxxvii + 1–314 pp., 49 pls.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(4):520–536. 1997.

Annotated list of Veronicellidae from the collections of the Academy of Natural Sciences of Philadelphia and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (Mollusca: Gastropoda: Soleolifera)

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Abstract.—The list of veronicellid slugs presented in this paper is restricted to species identified by criteria previously proposed by the first author. We were able to distinguish 30 species or subspecies, classified in 12 genera. Included are the following: *Belocaulus angustipes*; *Colosius propinquus*; *C. pulcher*; *Diplosolenodes occidentalis*; *D. olivaceus*; *Heterovaginina peruviana*; *Laevicaulis alte* (with new illustrations); *L. natalensis brauni*; *L. stuhlmanni* (with new illustrations); *Latipes cnidicaulus*; *Leidyula dissimilis*; *L. floridana* (with new data and illustration); *L. goodfriendi*; *L. kraussi*; *L. moreleti*; *L. portoricensis*; *L. trichroma*; *Phyllocaulis gayi*; *P. soleiformis*; *Sarasinula dubia*; *S. linguaeformis*; *S. plebeia*; *Simrothula columbiana*; *S. prismatica*; *Vaginulus taunaisii*; *Veronicella bahamensis*; *V. cubensis*; *V. davisi*; *V. sloanei*; *V. tenax*.

The family Veronicellidae Gray, 1840 comprises terrestrial mollusks without shell, commonly called slugs. The distribution is pantropical and over 300 specific names have been registered, most of them synonyms (Hoffmann 1925, Forcart 1953, Thomé 1975a, 1993b).

The phylogenetic position of the Veronicellidae is uncertain. Usually they are classified within the order Soleolifera Simroth, 1890. Some North American authors classify them in the order Systelommatophora Pilsbry, 1948. Others propose placing them in another order of Pulmonates: Archaeopulmonata (Götting 1974). Zilch (1959/60) put the Soleolifera as an Order of the subclass Euthyneura. Colosi (1922) and Hyman (1967) placed the same as an Order of the class Opistobranchia.

Thomé (1993b) discusses the classification status of American Veronicellidae, points out the necessity of embryological and ontogenetic studies, and suggests new groups of characteristics to be analyzed. He comments on the characteristics traditionally used and is of the opinion that there are not enough to determine conclusively the species, and that they do not permit a consistent phylogenetic classification.

The objective of the present work is to identify species of Veronicellidae from two collections through the classical anatomical characteristics proposed by Thomé (1993b). This list is relevant due to the importance of these North American institutions' collections for comparative study of Veronicellidae.

Materials and Methods

The analyzed material belongs to the following Museums: The Academy of Natural Sciences of Philadelphia (ANSP) with 110 lots and 464 specimens; and The National Museum of Natural History, Smithsonian Institution, Washington (USNM) with 97 lots and 272 specimens. Some of these latter lots were intercepted in the United States by US Department of Agriculture (USDA) and bear the occurrence number.

The specimens were dissected according Thomé & Lopes (1973) and the anatomical characteristics used for identification were based on Thomé (1988a, 1993b).

We have included illustrations only for those species where new data made it necessary for their complete description.

The radula and the jaw of some specimens were analyzed by Scanning Electron Microscope (SEM), using the method of Götting (1985).

The synonymy is restricted to main reference works. The occurrences are those cited in Thomé (1993b) with new data from these collections.

Results

Belocaulus angustipes (Heynemann, 1885)

Vaginula angustipes Heynemann, 1885: 275–77.

Belocaulus angustipes; Lopes-Pitoni & Thomé, 1981:586–93; Thomé, 1993b:70.

Occurrence.—Argentina; Brazil: Rio Grande do Sul; Paraguay; Colombia; (introduced: Honduras; U.S.A: Florida, Alabama, Louisiana, Texas).

Examined lots.—ANSP A1438. U.S.A: Florida, Leon County, Tallahassee; L. T. Rose leg; 12 Oct 1967; (Elberta Carte Co. property, East side of the international airport, Dr. Lake Bradford Rd); (3 specimens). USNM 574919. Colombia; 5 Nov 1943; (on *Anthurium* sp., USDA 200372); (1 specimen). USNM 575531. U.S.A: Alabama, Mobile; L. Hubricht leg; Jun 1961; (Mobile Co., Old Church Street, USDA 237188); (3 specimens). USNM 576363. U.S.A: Louisiana, New Orleans; 12 Sep 1962; (on lawn, USDA 244560); (1 specimen). USNM 758251. U.S.A: Louisiana, New Orleans; D. Dundee leg; 1963; (4 specimens). USNM 769131. U.S.A: Texas, Brownsville; D. L. Dunagan leg; 27 Mar 1968; (La Verne's Nursery, USDA 278478); (8 specimens). USNM 769164. U.S.A: Texas, Raymondville; R. Kloepping leg; 11 Apr 1968; (Caldwell Nursery, USDA 278478); (1 specimen). USNM 769169. U.S.A: Texas, Brownsville; 29 Apr 1969; (USDA 288982); (1 specimen). USNM 769170. U.S.A: Texas, Harington; R. Kloepping leg; 12 Apr 1968; (Rainbow Nursery, USDA 278478); (1 specimen). USNM 769175. U.S.A: Texas, Edinburg; W. J. Bone leg; 08 Feb 1968; (Mac's Nursery; Hidalgo Co., USDA 273170); (9 specimens). USNM 769176. U.S.A: Texas, Raymondville; R. Kloepping leg; 30 Jan 1968; (La Verne's Nursery; USDA 273170); (5 specimens). USNM 769178. U.S.A: Texas; W. J. Bone leg; 8 Feb 1968; (McAllen; Waugh Nursery, USDA 273170); (1 specimen). USNM 769180. U.S.A: Texas, San Benito; O. V. Mullins leg; 30 Jan 1968; (Bougainville Nursery, USDA 273170); (6 specimens). USNM 769187. U.S.A: Texas, Brownsville; B. C. Stephenson leg; 30 Jan 1968; (Tropical Nursery; Cameron Co., USDA 273170); (2 specimens). USNM 769196. U.S.A: Texas, Corpus Christi; E. F. Sublett leg; 23 Apr 1968; (Backyard Nursery, Nueces Co., USDA 278478); (1 specimen). USNM 769198. U.S.A: Texas, San Benito; O. V. Mullins leg; 12 Apr 1968; (Brown Lee Farm; Cameron Co., USDA 278478); (6 specimens). USNM 769199. U.S.A: Texas, San Benito; D. L. Dunagan leg; 9 Apr 1968; (Bougainville Nursery, Cameron Co., USDA 278478); (3 specimens). USNM 791487. U.S.A: Florida, Pensacola; J. P. E. Morrison leg; Dec 1961; (1 specimen).

Colosius propinquus (Colosi, 1921)

Vaginula propinqua Colosi, 1921:157; Colosi, 1922:499–500.

Angustipes (Angustipes) pulcher; Kraus, 1953:63 (p.p.).

Occurrence.—Ecuador; U.S.A: Puerto Rico.

Examined lot.—ANSP A1440. Porto Rico: Yauco river, Yaves Lares; H. B. Baker; (8 specimens).

Colosius pulcher (Colosi 1921)

Vaginula pulchra Colosi, 1921:157; Colosi, 1922:496–98; Thomé, 1970b:23–5, 27–9, 31.
Angustipes (Angustipes) pulcher; Kraus, 1953:63 (p.p.).
Colosius pulcher; Thomé, 1993b:72.

Occurrence.—Ecuador; Antilles: Dominican Republic.

Examined lots.—ANSP A1092. St. Domingo; W. M. Gabb leg; (7 specimens). USNM 769142. Ecuador; 18 Mar 1969; (intercepted at Miami on bromeliads); (1 specimen).

Diplosolenodes occidentalis (Guilding 1825)

Onchidium occidentale Guilding, 1825:322.
Diplosolenodes occidentalis; Thomé, 1985: 411–17; 1993b:71.

Occurrence.—Guyana; Venezuela; Colombia; Panama; Costa Rica; El Salvador; Nicaragua; Honduras; Antilles: Dominica, W. I.; Bahamas; U. S. A: Hawaii.

Examined lots.—ANSP A1076. Nicaragua; W. G. Binney leg; (2 specimens). ANSP A1079. Panama: Punta de Piña, R. E. B. Mc Kenney leg; 11 Jan 1907; (1 specimen). ANSP A1080 (=71911). Dominica, W. I.; T. D. A. Cockerell leg; (3 specimens). ANSP A1083. Costa Rica: Rio Surubrer, Bonnefil farms; P. Calvert leg; 16 Oct 1909; (2 specimens). ANSP A1086 (=46583). Colombia: Aracataca; (1 specimen). ANSP A1095 (=57954). Dominican Republic; G. E. & A. H. Verrill leg; 1892; (1 specimen). ANSP A1098 (=140994). Venezuela: Palma Sola; H. B. Baker; 1920; (1 specimen). ANSP A1107a (=45180). A. A. Hinkley leg; 1914; (4 specimens). ANSP A1123. Panama: Flamenco Island, Canal Zone; N. L. H. Krauss leg; 29 Oct 1948; (1 specimen). ANSP A7018. British Guiana, (4°0′ N, 58°0′ W); H. Lang leg; (1 specimen). ANSP A7019. British Guiana, (4°0′ N, 58°0′ W); (2 specimens). ANSP A7022. British Guiana: Georgetown, (6°46′ N, 58°10′W); Lang leg; (1 specimen). USNM 574369. U.S.A: Hawaii, Oahu Island, Ekahanui Gulch; G. S. Starkey leg; 08 May 1945; (from Army Medical Museum, USDA 171519); (1 specimen). USNM 575267. Panama: Cathedral Plaza; J. Zetek leg; (USDA 215629); (1 specimen). USNM 575897b. Honduras; 24 Jan 1961; (intercepted at Charleston on bananas, USDA 234701); (1 specimen). USNM 575973. Bahamas; 20 Oct 1959; (intercepted at Miami on orchids, USDA 227708); (7 specimens). USNM 575975. El Salvador; 15 Jun 1960; (intercepted at Miami on orchids, USDA 231346); (1 specimen). USNM 576190. Nicaragua: Ticuantepe, El Mamon; 20 May 1957; (on plants, USDA 216243); (1 specimen). USNM 805216. Honduras: Bantua; G. W. Van Hyning leg; 03 Oct 1929; (1 specimen).

Diplosolenodes olivaceus (Stearns 1871)

Veronicella olivacea Stearns, 1871:1.
Diplosolenodes olivaceus; Thomé & Lopes-Pitoni, 1976:710–12.

Occurrence.—Nicaragua.

Examined lot.—USNM 39160. Nicaragua: Hacienda Polvón, Departamento de León. J. A. McNiel leg; 1885. (Lectotype).

Heterovaginina peruviana (Kraus 1953)

Vaginina (Heterovaginina) peruviana Kraus, 1953:63–5.
Heterovaginina peruviana; Thomé, 1969: 357.

Occurrence.—Peru.

Examined lot.—USNM 574941. Peru; 01 Feb 1954; (intercepted at New Orleans, on cabbage from Peru, USDA 201313); (1 specimen).

Laevicaulis alte (Férussac 1821)
(Figs 2, 5, 8, 11)

Vaginulus alte Férussac, 1821:14.
Laevicaulis alte; Forcart, 1953:63–8.

Occurrence.—Asia (type locality: Pondichery, India); Oceania; Africa; (introduced?: Bermudas; U.S.A: Texas, Hawaii).

Examined lots.—ANSP A1130/1 (=98631). Bermudas: near Harrington House; S. Brown leg; Jun 1909; (45 specimens). ANSP A1130/2. Bermuda, near Harrington House, Parish; 18 Feb. 1908; (12 specimens). ANSP A10173 (=28314). U.S.A: Texas, Brownsville; 25 Sep 1983; (1515 Flamingo, Cameron Co.); (7 specimens). USNM 187499. U.S.A: Hawaii, Hilo; D. B. Kuhms leg; 17 Aug 1901; (2 specimens). USNM 574368. U.S.A: Hawaii, Oahu Island, Ekahanui Gulch; W. B. Lewellen and W. W. White leg; 31 Jan 1945; (on sewerage system, from Army Medical Museum, USDA 171519); (1 specimen). USNM 574371. U.S.A: Hawaii, Oahu Island, Honolulu; (USDA 171297); (2 specimens). USNM 574943. U.S.A: Hawaii, Midway Island; Lulhilson leg; 13 Nov 1953; (intercepted at Honolulu, on *Poinsettia* in soil from Midway, USDA 200540); (3 specimens). USNM 576340. U.S.A: Hawaii, Oahu Island, Kailua; 1 Aug 1960; (USDA 232396); (1 specimen). USNM 769190. U.S.A: Hawaii; 21 Oct 1968; (intercepted at San Antonio, Texas with shipment of *Achatina fulica* to S. W. State Teachers College, San Marcos, Texas, USDA 278478); (1 specimen).

Laevicaulis natalensis brauni (Simroth 1913)

Vaginula (Annulicaulis) brauni Simroth, 1913:187.
Laevicaulis natalensis brauni; Forcart, 1953:71–4.

Occurrence.—Africa: South Africa.

Examined lot.—ANSP A1106 (=47326). Africa, South Africa: Port Shepstone; H. C. Burnup; (2 specimens).

Laevicaulis stuhlmanni (Simroth 1895)
(Figs 1, 1a, 4, 7, 10)

Vaginula stuhlmanni Simroth, 1895: 61.
Laevicaulis stuhlmanni stuhlmanni; Forcart, 1953:74–6.

Occurrence.—Africa: Zaire.

Examined lots.—ANSP A1137. Rotachuru (?); Dr. J. Beguait; Sep 1914; (2 specimens). ANSP A1138. Belgian Congo (=Zaire); 1919; (3 specimens).

Latipes cnidicaulis (Baker 1926)

Vaginulus (Latipes) cnidicaulis Baker, 1926:29-31; Thomé, 1988c:25-7.
Latipes cnidicaulis; Thomé, 1993b:72.

Occurrence.—Guyana.

Examined lot.—ANSP A7020. (=A5927); Guiana: Kamakusa; H. Lang leg; Jan 1923. (Holotype).

Leidyula dissimilis (Cockerell 1892)

Veronicella dissimilis Cockerell, 1892:134.
Leidyula dissimilis; Thomé, 1988b:808–09; 1993b:71.

Occurrence.—Antilles: Jamaica.

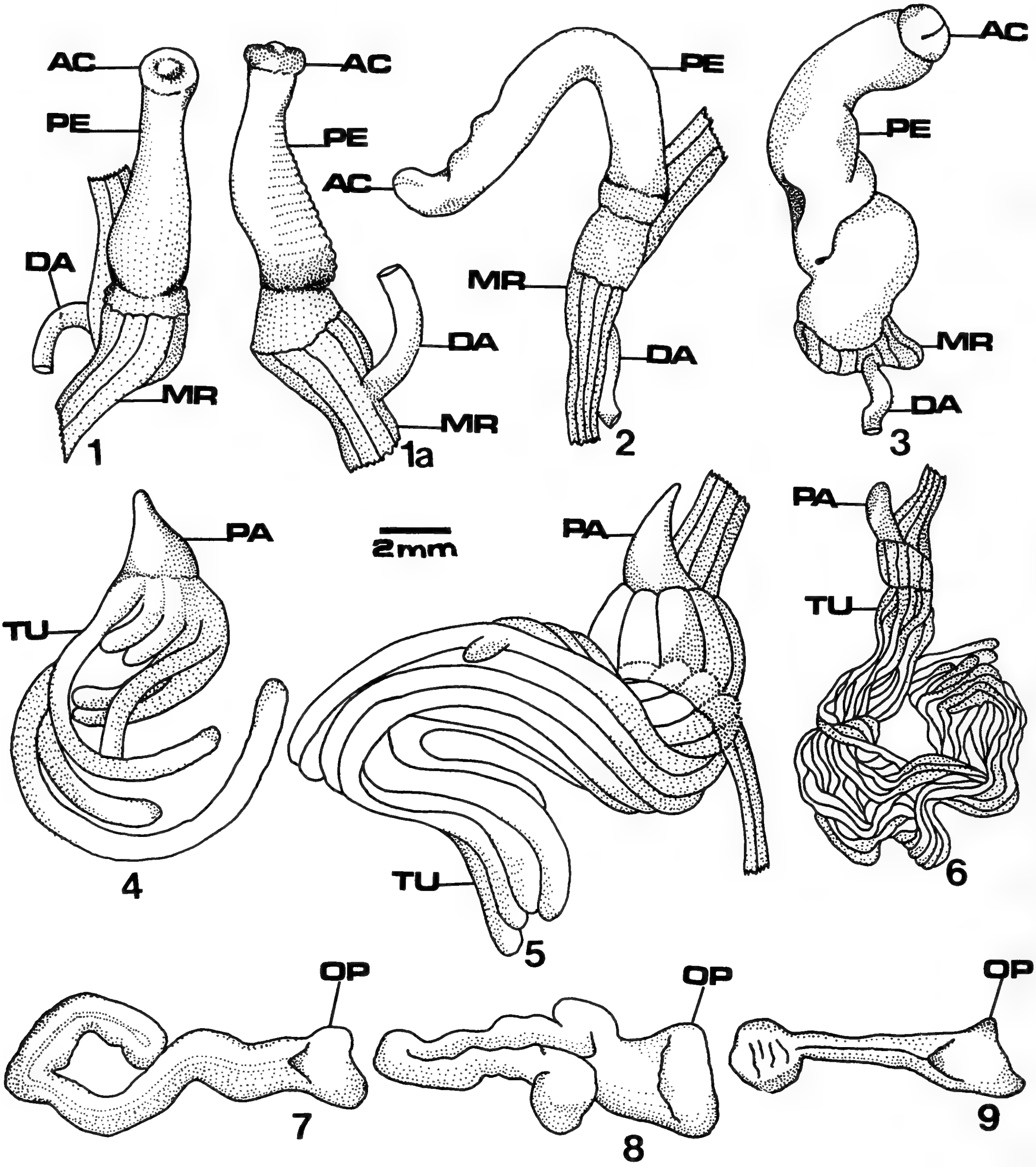
Examined lots.—ANSP A1451. H. B. Baker; 20 Jul 1933; (7 specimens). ANSP A1453. H. B. Baker; 8 Sep 1933; (1 specimen). ANSP A1456. 27 Jun 1933; (3 specimens). ANSP A12219 (=291339a); Jamaica: Somerset; H. B. Baker leg. (Holotype of *Veronicella leptothali* Baker, 1935. ANSP A12220 (=291339b); same data. (6 specimens). (Paratypes of *Veronicella leptothali* Baker, 1935).

Leidyula floridana (Leidy & Binney *in* Binney 1851)
(Figs 3, 6, 9, 12)

Vaginulus floridanus Leidy & Binney *in* Binney, 1851:198, 251.
Leidyula floridana; Baker 1925:167–71; Thomé, 1993b:74.

Occurrence.—Antilles: Dominica W. I.; Cuba. U.S.A: Puerto Rico, Florida, Texas.

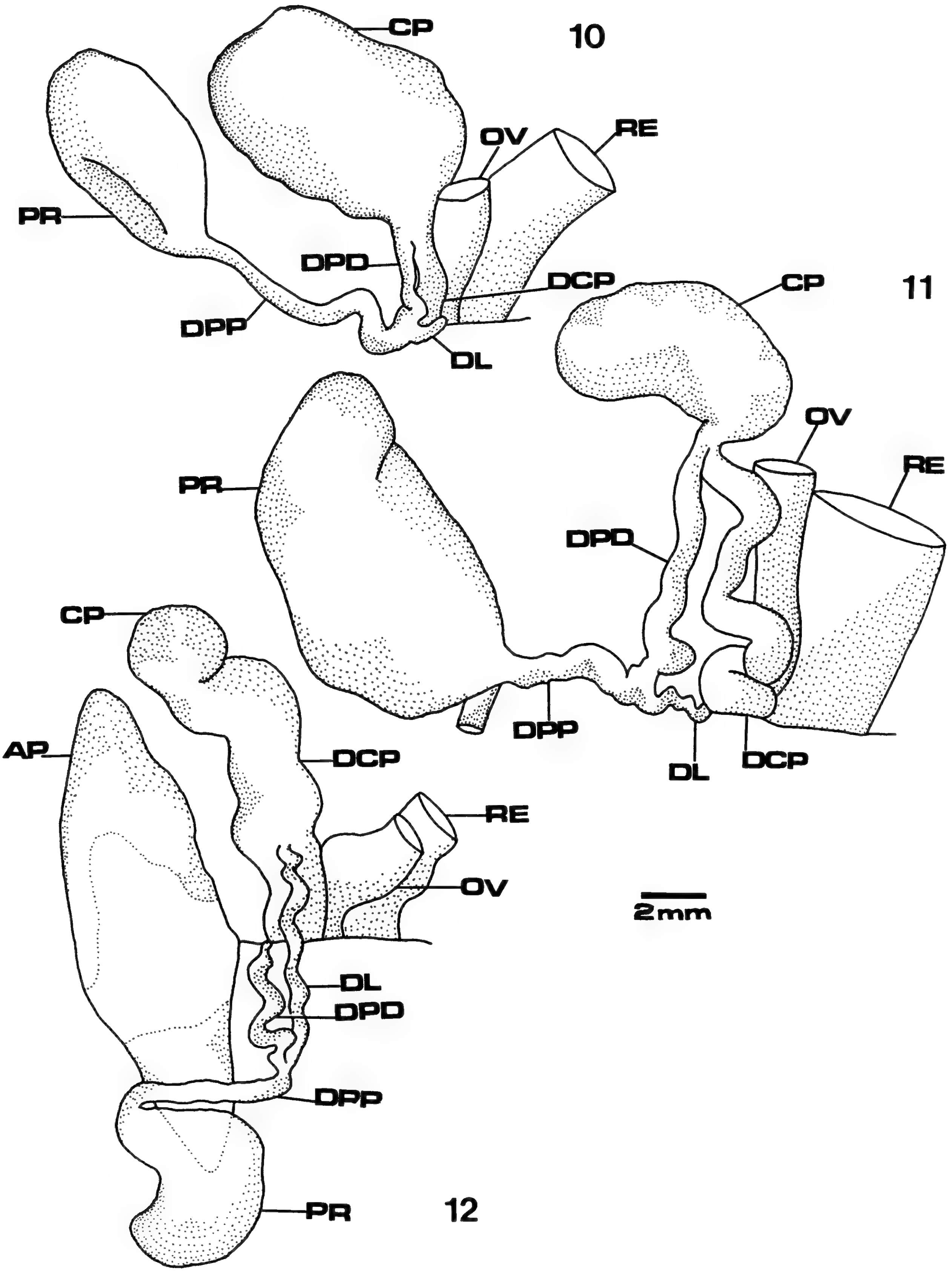
New data.—The jaw presents about 26 flattened laths, sometimes imbricate and of different sizes. The laths have small transverse furrows on the upper third. On some laths the furrows are lengthwise. The midregion of the jaw is larger than the ends (Figs.



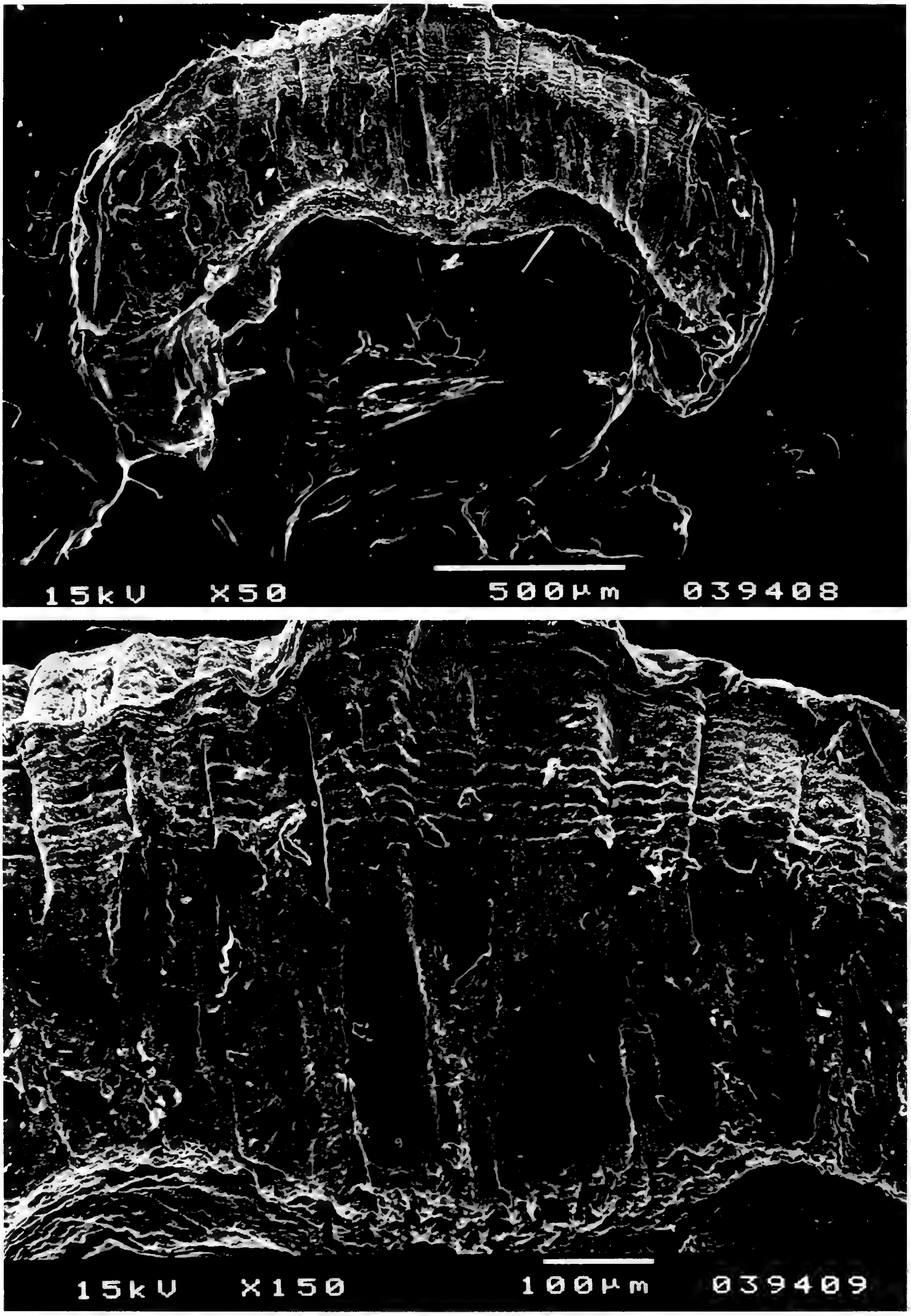
Figs. 1–9. Penis: (1, 1a) *Laevicaulis stuhlmanni;* (2) *L. alte*; (3) *Leidyula floridana*; penial gland; (4) *Laevicaulis stuhlmanni;* (5) *L. alte*; (6) *Leidyula floridana*; pedal gland: (7) *Laevicaulis stuhlmanni;* (8) *L. alte*; (9) *Leidyula floridana*. AC tip of the penis, PE penis, MR retractor muscle, DA anterior deferential duct, PA papilla, TU tubules, OP opening.

13, 14). On 3 radulas examined, there are ca. 94 rows and ca. 95 teeth in each, with an average of about 8.900 teeth (Figs. 15,16). Length, width, and distance from the base to the greatest width for each of 3 rachidian and 3 lateral teeth of the first file on the right was measured (Table 1) and ratios between the means also were calculated (Table 2).

Examined lots.—ANSP A1059 (=154994). U.S.A: Florida, Lignum Vitae Key; H. A. Pilsbry; 28 Mar 1931; (2 specimens). ANSP A1060. U.S.A: Florida, St. Petersburg; (2 specimens). ANSP A1061. Cuba: Matanzas Jumari; H. A. Pilsbry; (6 specimens). ANSP A1067. Cuba: Cienfuegos; H. A. Pilsbry; (2 specimens). ANSP A1068 (=197812). Cuba:



Figs. 10–12. Hermaphroditic region: (10) *Laevicaulis stuhlmanni;* (11) *L. alte*; (12) *Leidyula floridana*. AP accessory purse, CP copulation purse, DCP duct of the copulation purse, OV oviduct, RE rectum, DL joining duct, DPD distal posterior deferential duct, DPP proximal posterior duct deferential duct, PR prostate.



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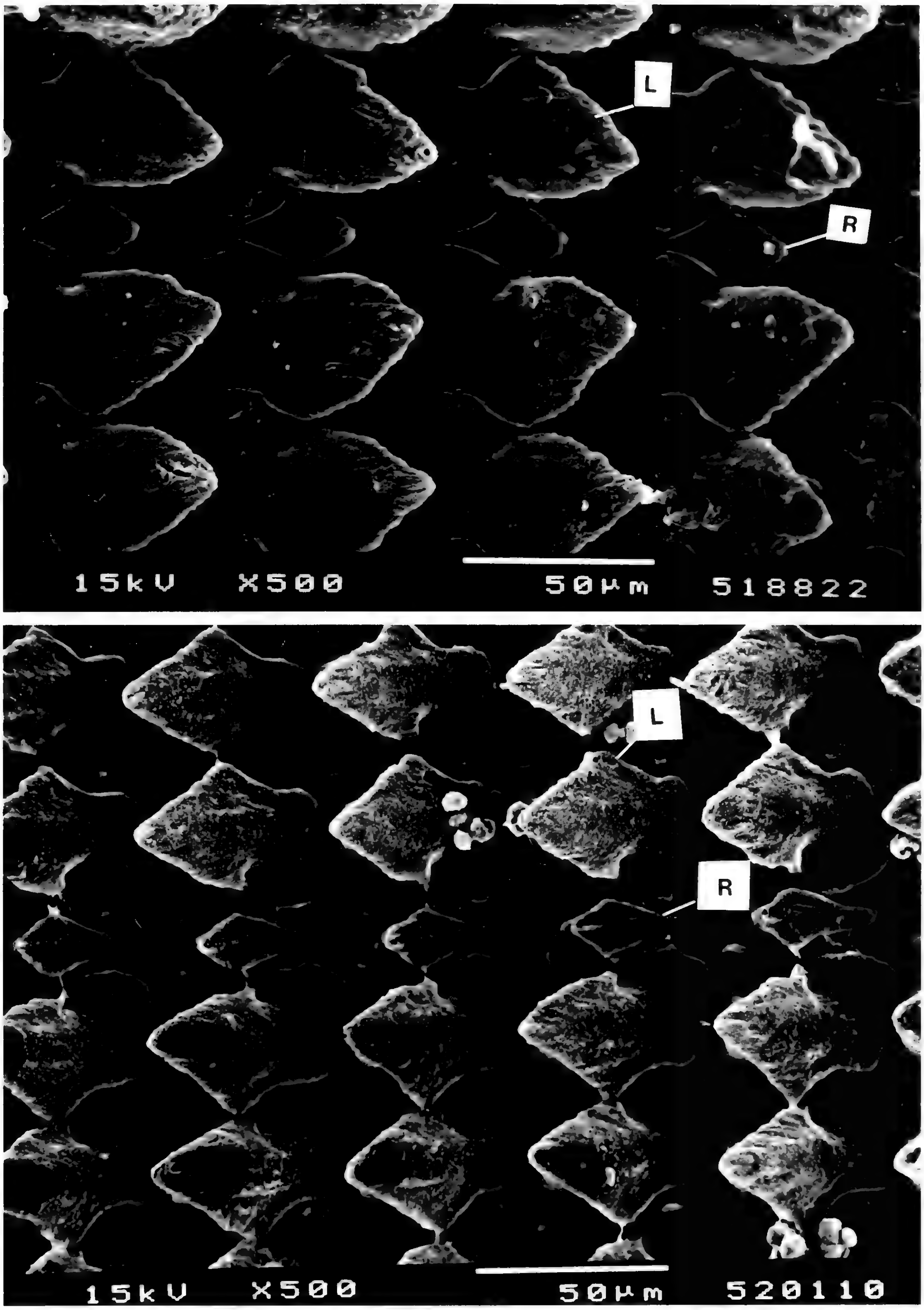
14

Figs. 13–14. *Leidyula floridana.* (13) jaw 50×; (14) median region of the jaw 150×. Paratype USNM 120394.

Cienfuegos; H. A. Pilsbry; (6 miles from Cienfuegos) (9 specimens). ANSP A1069a. Cuba: Zaza del Medio, Prov. Santa Clara; H. A. Pilsbry (2 specimens). ANSP A1071. Cuba: San Juan de Letran; H. A. Pilsbry; (4 specimens). ANSP A1074 (=137807). Cuba: San José, Spiritus; H. A. Pilsbry; (1 specimen). ANSP A1081 (=137803). Cuba: Sancti Spiritus; H. A. Pilsbry; (52 specimens). ANSP A1090 (=63528). U.S.A: Florida, Key



15

16

Figs. 15–16. *Leidyula floridana*. Median region of the radula 500×, (15) paratype USNM 805188; median region of the radula 500×, (16) paratype 805201. L lateral tooth, R rachidian tooth.

Largo; H. C. Manchette leg; (7 specimens). ANSP A1091. U.S.A: Florida, Miami; H. A. Pilsbry; 1899; (5 specimens). ANSP A1093. Cuba: Marianas; M. C. & S. N. Rhoads leg; 1899; (12 specimens). ANSP A1094 (=85610). U.S.A: Florida, Miami; (10 specimens). ANSP A1096 (=91399). U.S.A: Florida, Mond Key; C. B. More. leg; (1 specimen). ANSP A1101 (=93280). U.S.A: Florida, Sugar Loaf Key; H. A. Pilsbry; 1907; (1 specimen). ANSP A1111. U.S.A: Florida, Dry Tortugas; T. Van Hyning leg; (2 speci-

Table 1.—Length, width and distance of the base to the greatest width for each of 3 first lateral teeth and 3 rachidians of *Leidyula floridana,* in μm.

	Laterals			Rachidians		
Lots	Length	Width	Distance	Length	Width	Distance
1094B	49.28	39.93	34.02	33.32	16.93	19.46
	49.10	41.28	35.24	29.91	17.36	20.67
	54.04	39.81	35.59	30.69	17.12	22.73
Mean	50.80	40.34	34.95	31.30	17.13	20.95
805188	69.93	44.65	45.42	40.77	17.85	26.75
	66.30	46.02	42.22	39.71	17.73	27.24
	68.24	44.38	42.85	39.77	18.08	25.26
Mean	68.15	45.01	43.49	40.08	17.88	26.41
1094^{A}	51.73	41.67	5.71	28.87	22.24	20.75
	49.32	43.14	31.53	29.85	18.59	18.71
	55.08	42.85	34.12	29.06	19.00	19.95
Mean	52.04	42.55	33.78	29.26	19.94	19.80
Overall means	56.99	42.63	37.40	33.54	18.31	22.38

Table 2.—Ratios between the averages of the radula teeth of *Leidyula floridana.*

Lots	Q1 = Ll:Rl	Q2 = Lw:Rw	Q3 = Ll:Ld	Q4 = Rl:Rd	Q5 = Ll:Lw	Q6 = Rl:Rw
1094B	1.62	2.35	1.45	1.49	1.25	1.82
805188	1.70	2.51	1.56	1.51	1.51	2.24
1094^{A}	1.77	2.13	1.54	1.47	1.22	1.46
Mean	1.69	2.33	1.51	1.49	1.32	1.84

Ld = lateral distance; Ll = lateral length; Lw = lateral width; Rd = rachidian distance; Rl = rachidian length; Rw = rachidian width.

mens). ANSP A1113 (=185244). U.S.A: Florida, St. Petersburg; (1 specimen). ANSP A1119. U.S.A: Florida, Paradise Key, (18 mi W. of Paradise Key - Dade Co. Florida); O. C. Van Hyning leg; 8 Jul 1930; (1 specimen). ANSP A1129 (=156474). U.S.A: Florida, Collier Co.; O. C. Van Hyning leg; 5 Aug 1930; (1 specimen). ANSP A1159. 12 Jul 1933; (1 specimen). ANSP A1163. U.S.A: Florida; 2 Jul 1936; (1 specimen). ANSP A1439. Puerto Rico: Humanaco, Baker; (5 specimens). ANSP A1448. Sierra Movalos; H. B. Baker; (1 specimen). ANSP A8020. U.S.A: Texas, Corpus Christi; G. M. Davis leg; Aug 1979; (Nueces Co., 27°43′N, 97°25′W) (1 specimen). ANSP A9345. U.S.A: Florida, Lignum Vitae Key; Mar 1931; (24°53′N, 80°42′W); (12 specimens). USNM 120394. U.S.A: Florida, H. H. Bunning leg; (3 specimens). USNM 574579. Puerto Rico: Mayaguez; M. Aviles leg; 23 Jun 1941; (8 specimens). USNM 576488. Dominica, at Clarke Hall; P. Spangler leg; (USDA 249592); (2 specimens). USNM 769159. U.S.A: Texas, Brownsville; D. L. Dunagon leg; 27 Mar 1968; (USDA 278478); (2 specimens). USNM 769168. U.S.A: Texas, Raymondville; R. Kloepping leg; 11 Apr 1968; (USDA 278478); (2 specimens). USNM 769195. U.S.A: Texas, Brownsville; O. V. Mullens leg; 2 Feb 1968; (USDA 273170); (4 specimens). USNM 769197. U.S.A: Texas, Brownsville; 2 May 1967; (USDA 266325) (2 specimens). USNM 805188. Cuba: El Guama; 10 Mar 1900; (1 specimen). USNM 805201. U.S.A: Florida, Monroe County, Pinecrest; J. P. E. Morrison leg; 27 Feb 1966; (1 specimen). USNM 805202. U.S.A: Florida, Monroe County; Pinecrest; ; hl mi W; J. P. E. Morrison leg; 27 Feb 1966; (2 specimens).

Leidyula goodfriendi Thomé, 1994

Leidyula goodfriendi Thomé, 1994:169–72.

Occurrence.—Antilles: Jamaica.

Examined lots.—ANSP A1154. 22 Jun 1933; (2 specimens). ANSP A1161. 1 Aug 1933; (1 specimen).

Leidyula kraussi (Férussac 1823 *in* Férussac & Deshayes, 1820–1851)

Vaginulus kraussii Férussac, 1823:96x *in* Férussac & Deshayes, 1820–1851.

Leidyula kraussi; Thomé, 1990:513–18; 1993b:70.

Occurrence.—Antilles: Haiti; Jamaica; U.S.A

Examined lots.—ANSP A?? (=62126). Jamaica: Bog Walk; J. Fox leg; 1891; (5 specimens). ANSP A1115. Jamaica: Port Antonio; Wm. J. Fox; 1891; (2 specimens). ANSP A1133 (=85633). Haiti; C. J. Simpson leg; (1 specimen). ANSP A1153. 24 Aug 1933; (1 specimen). ANSP A1148 (=62130). Jamaica: Bog Walk; Wm. J. Fox.; 1891; (1 specimen). ANSP A1150. 25 Aug 1933; (3 specimens). ANSP A1152. 26 Jun 1933; (1 specimen). ANSP A1160. 7 Jul 1933; (1 specimen).

Leidyula moreleti (Fischer 1871)

Vaginula moreleti Fischer, 1871:168–69, 175.
Leidyula moreleti; Thomé, 1971:32–4, 1993b:71.

Occurrence.—Colombia; Nicaragua; Honduras; Guatemala; Mexico; U.S.A: Florida; Antilles: Cuba.

Examined lots.—ANSP A1054 (=63941). U.S.A: Florida, Cape Romano; (1 specimen). ANSP A1066. Mexico: Vera Cruz; H. B. Baker; (Custotolapam farm); (43 specimens). ANSP A1107b (=45180). Guatemala; A. A. Hinkley leg; 1914; (4 specimens). ANSP A1110. Cuba: Nueva Gerona, Isle of Pines; G. W. H. Soelnei leg; 18 Jun 1917; (3 specimens). ANSP A1112. Mexico: Mecos; A. A. Hinkley; (1 specimen). ANSP A1117 (=45670). Guatemala: Livingston, A. A. Hinkley; (2 specimens). ANSP A1135 (=45188). Guatemala: Jacola; A. A. Hinkley leg; 12 Feb 1917; (3 specimens). ANSP A1146 (=61309). Mexico: Tabasco; (1 specimen). ANSP A9344. Mexico: Campeche, Peninsula Yucatan; 28 Jul 1932; (18°50′N, 91°20′W); (2 specimens). USNM 120395. Nicaragua: Polvon; W. G. Binney leg; 1890; (1 specimen). USNM 574589. Mexico; 12 Dec 1949; (intercepted at Brownsville, Texas, USDA 185542); (1 specimen). USNM 574940. Colombia; 1945; (on plants, USDA 202348); (1 specimen). USNM 575079. Colombia: Bello; C. Carmona leg; 10 Feb 1956; (on vegetables, USDA 209666); (3 specimens). USNM 575194. Mexico: San Luis Potosi, Tamazunchale; 30 Jul 1957; (intercepted in Laredo, Texas, on orchid plants, USDA 215961); (1 specimen). USNM 576004. Honduras; 27 Sep 1961; (in seed corn, USDA 241044); (7 specimens). USNM 620158. Mexico: San Luis Potosi, Huichihuayan; (on orchid plants, USDA 212287); (1 specimen). USNM 769137. Mexico; 8 Apr 1967; (intercepted at Brownsville, Texas on orchids, USDA 266325); (1 specimen).

Leidyula portoricensis (Semper 1885)

Vaginula portoricensis Semper 1885:302
Leidyula portoricensis; Thomé 1975b:18; Thomé & Mansur 1990:534–35.

Occurrence.—Antilles: Puerto Rico, U.S.A.

Examined lots.—ANSP A1439. Porto Rico: Rio Humanaco; H. B. Baker; (2 specimens). ANSP A1442. Porto Rico: Montoro; H. B. Baker; (1 specimen). ANSP A1447. Sa Valuera; H. B. Baker; (2 specimens).

Leidyula trichroma Baker, 1935

Veronicella (Leidyula) kraussii trichroma Backer, 1935:84, 88.
Leidyula trichoma; Thomé, 1988c:32–33.

Occurrence.—Antilles: Jamaica.

Examined lots.—ANSP A1058. Jamaica: Catadupa station, Montego Bay, St. James; H. B. Baker leg; (holotype); ANSP A12218. Same data (paratype).

Phyllocaulis gayi (Fischer 1871)

Vaginula gayi Fischer, 1871:172.
Phyllocaulis gayi; Thomé, 1976:71–5; 1993b:70.

Occurrence.—Chile; (introduced?: Mexico).

Examined lot.—USNM 805195. Chile: Valdivia; E. P. Reed leg; (2 specimens).

Phyllocaulis soleiformis (Orbigny 1835)

Vaginulus soleiformis Orbigny, 1835:2.
Phyllocaulis soleiformis; Thomé, 1976:75–6; 1993b:70.

Occurrence.—Argentina; Uruguay; Brazil: Rio Grande do Sul.

Examined lots.—ANSP A1085 (=69656). Uruguay: Maldonado; W. H. Rush leg; (1 specimen). USNM 576353. Argentina: 30 Km E of Azul; Lord and Jellison leg; May 1962; (USDA 245400); (1 specimen).

Sarasinula dubia (Semper 1885)

Vaginula dubia Semper, 1885:296; Thomé, 1972:252–53.
Sarasinula dubia; Thomé, 1993b:71.

Occurrence.—Brazil: Rio Grande do Sul, São Paulo; Venezuela; Colombia; Honduras; Mexico; U.S.A: Florida, Texas; Antilles: Trinidad and Tobago; Dominica, W.I.; Dominican Republic; Haiti; French Polynesia: Society Islands, Tahiti.

Examined lots.—USNM 769177. U.S.A: Texas, Raymondville; O. V. Mullens leg; 2 Feb 1968; (Willacy Co., Caldwell Nursery, USDA 273170); (3 specimens). USNM 574646. Dominican Republic: Santiago de los Caballeros; J. Jimines leg; 1951; (USDA 190012); (2 specimens). USNM 574676. Trinidad and Tobago: Trinidad, (British W. Indies); 1951; (USDA 191870); (4 specimens). USNM 575465. Haiti; 2 Dec 1958; (intercepted at New York, on *Caladium* plants, USDA 224155); (1 specimen). USNM 575897a. Honduras; 24 Jan 1961; (intercepted at Charleston on bananas, USDA 234701); (2 specimens). USNM 576001. U.S.A: Florida, Miami; 13 Sep 1961; (on the tree *Persea americana*, USDA 239104); (1 specimen). USNM 576337. Honduras: La Lima; 28 Oct 1958; (on a banana plantation, USDA 234081); (8 specimens). USNM 769138. U.S.A: Texas, Brownsville, (on with general nursery plants, USDA 273170); (10 specimens). USNM 769157. U.S.A: Texas, Brownsville; D. L. Dunagan leg; 16 Apr 1968; (Neal Robinson's Nursery, USDA 278478); (7 specimens). USNM 769163. U.S.A: Texas, Raymondville; R. D. Kloepping leg; 11 Apr 1968; (Caldwell Nursery, USDA 278478); (3 specimens). USNM 769177. U.S.A: Texas, Raymondville; O. V. Mullens leg; 2 Feb 1968; (Willacy Co., Caldwell Nursery, USDA 273170); (3 specimens). USNM 769179. U.S.A: Texas, Brownsville; D. L. Dunagan leg; 26 Mar 1968; (Pan American Nursery, USDA 278478); (2 specimens). USNM 805184. Society Islands: Tahiti; 28 Sep 1899; (2 specimens). USNM 805204. Dominica; Portsmouth; 4 Aug 1929; (E side of watershed); (14 specimens).

Sarasinula linguaeformis (Semper 1885)

Vaginula linguaeformis Semper, 1885:307-08; Thomé, 1973:35–6.
Sarasinula linguaeformis; Thomé, 1993b: 71.

Occurrence.—Brazil: from São Paulo, Minas Gerais to the Northeast, Amazonas; Paraguay; Peru; Guyana.

Examined lots.—ANSP A7021. British Guiana: Georgetown, (6°46′N, 58°10′W); H. Lang; (specimens had been dried out and treated with tri-sodium phosphate, upgraded to 70% ETOH); (2 specimens). USNM 381391. Paraguay; Felippone leg; (4 specimens). USNM 769152. Peru; 17 Jan 1969; (intercepted at Miami on bromeliads, USDA 278478); (1 specimen). USNM 805252. Brazil: Lassance, MG; D. M. Cochran leg; 22 Mar 1935; (Marthyin Corn, USDA 132173); (6 specimens).

Sarasinula plebeia (Fischer 1868)

Vaginulus plebeius Fischer, 1868:145; Thomé, 1971:34–6.
Sarasinula plebeia; Thomé, 1993b:71.

Occurrence.—Chile; Brazil: from Rio Grande do Sul to Paraíba; Venezuela; Colombia; Costa Rica; El Salvador; Honduras; Guatemala; Mexico, U. S. A: Puerto Rico, Florida, Texas; Antilles: St. Lucia; Dominica, W. I.; Virgin Islands; Dominican Republic; Jamaica; Cuba. Also cited to Australia; Asia; Africa.

Examined lots.—ANSP A9346. Venezuela: Carabobo State, Campo Alegre, (4 miles east of Caracas); (00021548, 10°35′N, 66°52′W, EDP, 21548); (26 specimens). USNM 574451. Venezuela: Sucre, Cariaco; G. Marcuzzi leg; Sep 1948; (USDA 180965); (3 specimens). USNM 574834. Virgin Islands: Saint Thomas; 1952; (USDA 195560); (2 specimens). USNM 574838. Virgin Islands: Saint John; 4 Aug 1952; (USDA 195744); (8 specimens). USNM 574942. Dominican Republic; 7 Jan 1954; (USDA 201313); (1 specimen). USNM 575265. Costa Rica; 2 Oct 1957; (USDA 216763); (1 specimen). USNM 575366. Venezuela: Anzoatequi, San Tome; T. Briceno leg; (USDA 216763); (1 specimen). USNM 576341. Costa Rica; 1960; (USDA 231087); (1 specimen). USNM 578214. Costa Rica: Golfito; M. Kosztarali leg; 21 Feb 1970; (USDA 295099); (1 specimen). USNM 768944. Nicaragua; 10 Nov 1969; (intercepted at Miami on bromeliads, USDA 283854); (1 specimen). USNM 768945. El Salvador: Santa Tecla; 3 Jun 1969; (intercepted at Miami on weeds, USDA 283854); (4 specimens). USNM 768946. Mexico; V. C. Fort leg; 23 Oct 1969; (intercepted at Fort Laredo, Texas, on orchids); (2 specimens). USNM 769135. El Salvador; 8 Jan 1968; (intercepted at New Orleans on orchids, USDA 273170); (1 specimen). USNM 769143. Puerto Rico: Bayamon; 16 Sep 1966; (intercepted at San Juan on Saint Augustine grass, USDA 266325); (1 specimen). USNM 769156. Puerto Rico: Cupey Alto; 23 Oct 1968; (intercepted at San Juan on *Dossaena* leaf, USDA 278478); (1 specimen). USNM 769186. U.S.A: Texas; W. J. Bone leg; 8 Feb 1968; (McAllen, Hidalgo Co., Waugh Nursery, USDA 273170); (1 specimen). USNM 805203. Honduras; H. E. Ostmark and C. Evers leg; 13 Aug 1962; (on bananas, USDA 243607); (5 specimens). USNM 805204. Dominica: Portsmouth; 4 Aug 1929; (E side of watershed); (14 specimens). USNM 805235. Unknown (St. Lucia?); 10 Aug 1929; (1 specimen).

Simrothula columbiana (Simroth 1914)

Vaginula columbiana Simroth, 1914:300–03; Thomé, 1970a:76–8; 1979:144–45.
Simrothula columbiana; Thomé, 1993b:72.

Occurrence.—Colombia.

Examined lot.—ANSP A1441. (?) Cabo Rojo, (R33, Cabo Rojo); H. B. Baker; (1 specimen).

Simrothula prismatica (Simroth 1914)

Vaginula prismatica Simroth, 1914:314–16; Thomé, 1972:261–63.
Simrothula prismatica; Thomé, 1993b:72.

Occurrence.—Colombia.

Examined lot.—USNM 575078. Colombia: Bello. C. Carmona; 10 Feb 1956; (USDA 209666); (2 specimens).

Vaginulus taunaisii Férussac, 1821

Vaginulus taunaisii Férussac, 1821:13.
Vaginulus taunayi; Thomé, 1971:36–9; 1993b:72.

Occurrence.—Brazil: Rio de Janeiro.

Examined lot.—USNM 805194. Brazil: Rio de Janeiro, Niemeyer Avenue; 7 Feb 1935; (1 specimen).

Veronicella bahamensis Dall, 1905

Veronicella schivelyae bahamensis Dall, 1905:446.
Veronicella bahamensis; Thomé & Lopes-Pitoni, 1976:712–13; Thomé, 1993b:72.

Occurrence.—Bahamas.

Examined lot.—USNM 180415. Bahamas: Little Abaco; O. Bryant leg; (lectotype); USNM 180738. Bahamas: Nassau, Johnson Place; O. Bryant leg; 6 Jul 1904; (3 specimens).

Veronicella cubensis (Pfeiffer 1840)

Onchidium cubense Pfeiffer, 1840:250.
Veronicella cubensis; Thomé, 1993a:113–21; 1993b:70

Occurrence.—Antilles: Dominica, W.I.; Dominican Republic; Haiti; Cuba; Bahamas; U.S.A. Puerto Rico, Louisiana, Hawaii.

Examined lots.—ANSP A1083. Cuba: Havana, La Salud; H. A. Pilsbry; 1904; (5 specimens). ANSP A1443. Araciba river; H. B. Baker; (4 specimens). ANSP A1446. Catano; H. B. Baker; (1 specimen). ANSP A1741. Cuba: Punto Angre; (2 specimens). USNM 575898. Bahamas: Andros Island; 11 Feb 1961; (intercepted at Port Everglades, on bananas plantation); (1 specimen). USNM 576360. Puerto Rico; 17 Oct 1962; (on plants); (1 specimen). USNM 709075. Dominica; T. M. Clarke and J. F. G. leg; 13 Jan 1965; (at Clarke Hall); (1 specimen). USNM 769160. U.S.A: Louisiana, New Orleans; 29 Jun 1970; (on sidewalk near Tuoro Hospital); (1 specimen). USNM 805193. Haiti: Furcy; A. Curtiss; 20 Jun 1944; (with eggs); (1 specimen).

Veronicella davisi Thomé, Santos & Pedott, 1996

Veronicella davisi Thomé, Santos & Pedott, 1996:265–74.

Occurrence.—Antilles: Jamaica; Cuba.

Examined lots.—ANSP A1065a. Cuba: Majagua; H. A. Pilsbry (Holotype); ANSP A1065. Same data; (6 specimens) (Paratypes); ANSP A1069. Cuba: Prov. Santa Clara, Zaza del Medio; H. A. Pilsbry; (6 specimens). ANSP A1072. Jamaica; J. B. Henderson; (1 specimen). ANSP A1073 (=137804). Cuba: Trinidad; H. A. Pilsbry; (5 specimens). ANSP A1075. Cuba, 15 Km South of Sancti Spiritus; H. A. Pilsbry; (2 specimens). ANSP A1077. (=137806). Cuba: Trinidad; H. A. Pilsbry; (1 specimen). ANSP A1155. J. 5. Som.; 22 Jun 1933; (1 specimen). ANSP A1156. 20 Jul 1933; (1 specimen). ANSP A1157. 7 Jul 1933; (1 specimen). ANSP A1158. 22 Jun 1933; (1 specimen). ANSP A1748. J. 5. Som.; 22 Jun 1933; (2 specimens).

Veronicella sloanei (Cuvier 1817)

Onchidium sloanei Cuvier, 1817:411.
Veronicella sloanei; Thomé, 1988a:13–35; 1993b:70.

Occurrence.—Colombia: Isla de Providencia; Nicaragua; Bermudas; Bahamas; (U.S.A: Massachusetts—introduced?); Antilles: Barbados; Jamaica; Cayman Islands.

Examined lots.—ANSP A1070. Grand Cayman; 17 Apr 1929; (Sta 4; Pinchat Exped); (2 specimens). ANSP A1078. Isabel, Old Providence Id; 1929; (Pine Hot Exped); (1 specimen). ANSP A1104 (=57956). Nicaragua: Machuca; Dr. J. F. Bransford; (1 specimen). ANSP A1108. Bermuda: Frascati Hotel; A. Gulick; (3 specimens). ANSP A1109. Jamaica: Kingston Bath; T. D. A. Cockerell; (7 specimens). ANSP A1114. Jamaica: Kingston; T. D. A. Cockerell; May 1892; (1 specimen). ANSP A1118. Jamaica: Kingston; T. D. A. Cockerell; (1 specimen). ANSP A1120. Grand Cayman; 1929; (Pinchat Exped); (1 specimen). ANSP A1124. Jamaica: Kingston; T. D. A. Cockerell; (2 specimens). ANSP A1125. Jamaica: Kingston; T. D. A. Cockerell; (1 specimen). ANSP A1126. Jamaica: Kingston; T. D. A. Cockerell; (1 specimen). ANSP A1130 (=98631). Bermuda: near Harrington House; S. Brown; Jun 1909; (1 specimen). ANSP A1144 (=65396). Jamaica; J. B. Henderson Jr.; (2 specimen). ANSP A1145. Jamaica: Port Antonio; W. J. Fox; 1891; (4 specimens). ANSP A1149 (=69360). Nantucket (introduced ?); Dr. B. Sharp; Aug 1896; (on bananas); (1 specimen). ANSP A1437 (=60964). Bermudas: St. George; Heilprind Expedition leg; 1888. (Holotype of *Vaginulus schivelyae* Pilsbry, 1890). ANSP A1452. H. B. Baker; 5 Sep 1933; (3 specimens). ANSP A1455. H. B. Baker; 5 Jul 1933; (1 specimen). ANSP A1747. J. 33 .H.; 20 Aug 1933; (15 specimens). ANSP A1748. Bahamas; Mich. Goodrich; 21 Aug 1933; (1 specimen). USNM 574916. Jamaica; (British West Indies); 24 Jul 1953; (intercepted at Miami, Florida, on orchids, USDA 199469); (1 specimen). USNM 791486. Jamaica; (1 specimen). USNM 805186. Jamaica: Kingston; C. R. Orcutt leg; 29 Aug 1927; (2 specimens). USNM 805190. Jamaica: Saint Thomas, Antully Parish; C. R. Orcutt leg; Aug 1927; (3 specimens). USNM 805192. Jamaica: Antully; C. R. Orcutt leg; (10 specimens).

Veronicella tenax Baker, 1931

Veronicella (*Tenacipes*) *tenax* Baker, 1931: 131–34.

Veronicella tenax; Thomé, 1988c:30–2; 1993b:72.

Occurrence.—Antilles: Antigua and Barbuda; Cuba.

Examined lot.—ANSP A12221 (=291340a). Cuba: Enseñada de San Vicente, Cueva de Tiburón, Pinar del Rio; H. P. Pilsbry leg; 1928; (Holotype). ANSP A12222 (=291340b). same data; (2 specimens); (Paratypes). ANSP A1164. Antigua; A. P. Brown; (5 specimens).

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Literature Cited

Baker, H. B. 1925. North American Veronicellidae.—Proceedings of the Academy of Natural Sciences of Philadelphia 77:157–184.

———. 1926. Veronicellidae from British Guiana.—Proceedings of the Academy of Natural Sciences of Philadelphia 78:29–34.

———. 1931. Notes on West Indian Veronicellidae.—Nautilus 44:131–137.

———. 1935. Jamaican land snails, 3.—Nautilus 48: 83–88.

Binney, A. 1851. The terrestrial air-breathing Mollusks of the United States, and adjacent territories of North America. Augustus A. Gould, Boston, 2v.

Cockerell, T. D. A. 1892. Mollusca 10. *Veronicella dissimilis* n. sp.—Journal of the Institute Jamaica 1:134.

Colosi, G. 1921. Diagnosi di Vaginulidi (Gasteropodi terrestri).—Atti dela Società italiana de Scienzia Naturali del Museo Civile di Storia Naturale, Milano 60:156–160.

———. 1922. Contributo alla conoscenza anatomica e sistematica dei Vaginulidi Sud-Americani.—Anales del Museo Nacional de Historia Natural de Buenos Aires Tomo XXXI:475–517.

Cuvier, G. 1817. Mémoires pour servir à l'histoire et à l'anatomie des Mollusques. Chez Deterville Libr., Paris, 492 pp.

Dall, W. H. 1905. Report on Land and Fresh-water shells collected in the Bahamas in 1904, by Mr. Owen Bryant and others.—Smithsonian Miscellaneous Collections 47:433–452.

Férussac, D. de. 1821. Tableux systématiques des animaux mollusques. Deuxième partie: tableau de la famille des Limaces. Chez Arthus-Bertrand, Libraire-éditeur, Paris, 27pp.

———, & G. P. Deshayes. 1820–1851. Histoire Naturelle Générale et Particulière des Mollusques terrestres et Fluviatiles tant des espéces que l'on trouve aujourd'hui vivantes, que des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels que présentent ces animaux et leurs coquilles. Chez J.-B. Baillière, Paris, 4v.

Fischer, P. 1868. Diagnoses de deux Limaciens de la Nouvelle Calédonie.—Journal de Conchyliologie 16:145–146.

———. 1871. Révision des espèces du Genere *Vaginula* Férussac.—Nouvelles Archives du Muséum d'Histoire Naturelle, Paris 7:147–175.

Forcart, L. 1953. The Veronicellidae of Africa (Mollusca, Pulmonata).—Anales du Musée Royal du Congo Belge, Tervuren, Serie in 8, Sciences Zoologiques, 23:1–110.

Götting, K.-J. 1974. Malakozoologie. Grundriss der Weitierkunde. Gustav Fischer, Stuttgart, 320pp.

———. 1985. Kiefer und Radula in der Gattung *Phyllocaulis* Colosi (Pulmonata; Soleolifera; Veronicellidae).—Archiv für Molluskenkunde 116(⅓):47–56.

Guilding, L. 1825. Description of a new Species of *Onchidium*.—Transactions of the Linnean Society of London 14:322–324.

Herrmannsen, A.N. 1849. Indicis Generum Malacozoorum primordia. Sumptibus & Typis Theodori Fischeri, Cassel, v. 2, 717pp.

Heynemann, D. F. 1885. Die nackten Landpulmonaten des Erdbodens.—Jahrbücher der Deutschen malakozoologischen Gesellschaft 12:236–330.

Hoffmann, H. 1925. Die Vaginuliden. Ein Beitrag zur Kenntnis ihre Biologie, Anatomie, Systematik, geographischen Verbreitung und Phylogenie. (Fauna et Anatomia ceylanica, III, Nr. 1).—Jenaische Zeitschrift für Naturwissenschaft, Jena 61 (NF 54) (1–2):1–374.

Hyman, L. H. 1967. The Invertebrates: Mollusca I.: McGraw Hill Book Co., New York 6:791pp.

International Code of Zoological Nomenclature, third edition. 1985. International Trust for Zoological Nomenclature, London, 338pp.

Jaeger, E. C. 1978. A source-book of Biological names and terms, third edition, sixth printing. Charles C. Thomas publisher, Springfield, Ill., 323pp.

Kennard, A. S. 1942a. The Histoire and Prodrome of Férussac, part I.—Proceedings of the Malacological Society of London 25:12–17.

———. 1942b. The Histoire and Prodrome of Férussac, part II–III.—Proceedings of the Malacological Society of London 25:105–118.

Kraus, O. 1953. Vaginulidae aus Peru.—Archiv für Molluskenkunde 82:63–65.

Lopes-Pitoni. V. L., & J. W. Thomé. 1981. Revisão do gênero *Belocaulus* Hoffmann, 1925 (Mollusca, Veronicellidae).—Revista Brasileira de Biologia, Rio de Janeiro 41(3):585–593.

Martens, E. von 1867. Die Preussische Expedition nach Ost- Asien. Nach amtlichen Quellen. Zoologischer Theil, II. Band: die Landschnecken. Verlag der Königlichen Geheimen Ober-Hofbuchdrückerei, Berlin, xxi+447p.

Neave, S. A. 1940. Nomenclatur Zoologicus. A list of the names of Genera and Subgenera in Zoology from the tenth edition of Linnaeus 1758 to the end of 1935. The Zoological Society of London, 4 v. V. 4:Q–Z and supplement, 758pp.

Orbigny, A. d'. 1835. Synopsis terrestrium et fluviatilium molluscorum, in suo per American meridionalem itinere, ab A. d'Orbigny, collectorum.—Magazin du Zoologie, Paris 5:1–44.

Pfeiffer, L. 1840. Übersicht der im Januar, Februar und März 1839 auf Cuba gesammelten Mollusken.—Archiv für Naturgeschichte 6(1):250–261.

Pilsbry, H. A. 1890. New and little known american Mollusks, n° 3.—Proceedings of the Academy of Natural Sciences of Philadelphia 42:296–302.

Semper, C. 1885. Reisen im Archipel der Philippinen. C. W. Kreidel's Verlag, Wiesbaden. II Theil, 3. Band: Landmollusken, 7. Heft, pp. 291–327.

Simroth, H. 1895. Über die von Herrn Dr. Stuhlmann im Innern von Ostafrika gesammelten Nacktschnecken.—Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig (1892–1894), 19/21:51–66.

———. 1913. Über die von Herrn Prof. Voeltzkow auf Madagaskar und in Ostafrika erbeuteten Vaginuliden, nebst verwandtem Material von ganz Afrika. *in* A. Voeltzkow, Reise in Ostafrika in den Jahren 1903–1905, mit Mitteln der Hermann und Elise geb. Heckmann Wentzel-Stiftung ausgeführt. Wissenschaftliche Ergebnisse. E. Schweizerbärt'sche Verlagsbuchhandlung, Nägele & Dr. Sproesser, Stuttgart, 3. Band: Systematische Arbeiten, 3. Heft, pp. 127–216.

———. 1914. Beitrag zur Kentniss der Nacktschnecken Columbiens. Zugleich eine Übersicht über die neotropische Nacktschnecken-Fauna überhaupt. (*in* Voyage d'Exploration Scientifique en Colombie).—Mémoires de la Societé Neuchâteloise des Sciences Naturelles 5:270–341.

Stearns, R. E. C. 1871. Description of a new species of *Veronicella* from Nicaragua.—Conchological Memoranda 8:1.

Thomé, J. W. 1969. Erneute Beschreibung neotropischer Veronicellidae-Typen (Mollusca; Gastropoda): II. Arten aus der Sammlung des Senckenberg-Museums in Frankfurt a.M.—Archiv für Molluskenkunde 99(5/6):331–363.

———. 1970a. Redescrição dos tipos de Veronicellidae (Mollusca; Gastropoda) neotropicais: III. Espécies depositadas no "II. Zoologisches Institut und Museum der Universität" de Göttingen.—Iheringia, Porto Alegre, Série Zoologia (38):73–88.

———. 1970b. Redescrição dos Tipos de Veronicellidae (Mollusca; Gastropoda) neotropicais: V. Espécies depoditadas no "Museo ed Istituto di Zoologia Sistematica della Universitá", de Turim, Itália.—Iheringia, Porto Alegre, Série Zoologia (39):19–31.

———. 1971. Redescrição dos tipos de Veronicellidae (Mollusca; Gastropoda) neotropicais: VII. Espécies depositadas no "Muséum National d'Histoire Naturelle", Paris, França.—Iheringia, Porto Alegre, Série Zoologia (40):27–52.

———. 1972. Redescrição dos tipos de Veronicellidae (Mollusca; Gastropoda) Neotropicais. VIII. Espécies depositadas no "Institut für Spezielle Zoologie und Zoologisches Museum" de Berlim.—Arquivos de Zoologia, São Paulo 21(5): 235–281.

———. 1973. Erneute Beschreibung neotropischer Veronicellidae-Typen (Mollusca; Gastropoda) VI. Arten aus der Sammlung des Universitets Zoologiske Museum in Kopenhagen.—Steenstrupia 4:31–50.

———. 1975a. Estado atual da sistemática dos veronicelídeos americanos (Mollusca; Gastropoda).—Arquivos do Museu Nacional, Rio de Janeiro 55:157–165.

———. 1975b. Os gêneros da família Veronicellidae nas Américas (Mollusca; Gastropoda).—Iheringia, Porto Alegre, Série Zoologia (48):3–56.

———. 1976. Revisão do gênero *Phyllocaulis* Colosi, 1922 (Mollusca; Veronicellidae).—Iheringia, Porto Alegre, Série Zoologia (49):67–90.

———. 1979. A redescription of Types of six Species of neotropical Veronicellidae (Mollusca; Gastropoda) in the British Museum (Natural History).—Bulletin of the British Museum (Natural History), Zoology 35(2):135–147.

———. 1985. Redescrição dos tipos de Veronicellidae (Mollusca; Gastropoda) neotropicais. X. Os tipos de *Diplosolenodes occidentalis* (Guilding, 1825) no British Museum (Natural History), Londres.—Revista Brasileira de Zoologia, São Paulo 2(6):411–417.

———. 1988a. Recaracterização de *Veronicella sloanei* (Cuvier, 1817) (Mollusca; Gastropoda; Veronicellidae).—Iheringia, Porto Alegre, Série Zoologia (67):13–35.

———. 1988b. Lista das Veronicellidae (Mollusca; Gastropoda) da Jamaica.—Revista Brasileira de Biologia, Rio de Janeiro 48(4):807–810.

———. 1988c. Redescrição dos tipos de Veronicellidae (Mollusca; Gastropoda) neotropicais: XI. Espécies na "Academy of Natural Sciences", Philadelphia.—Iheringia, Porto Alegre, Série Zoologia (69):25–40.

———. 1990. Recaracterização de *Leidyula kraussi* (Férussac 1823) (Mollusca; Gastropoda; Veronicellidae).—Revista Brasileira de Biologia, Rio de Janeiro 50(2):513–518.

———. 1993a. Erneute Beschreibung von *Veronicella cubensis* (Pfeiffer 1840) (Gastropoda; Veronicellidae).—Archiv für Molluskenkunde 122: 113–121.

———. 1993b. Estado atual da sistemática dos Veronicellidae (Mollusca; Gastropoda) americanos, com comentários sobre sua importância econômica, ambiental e na saúde.—Biociências, Porto Alegre 1(1):61–75.

———. (1993) 1994. Nova *Leidyula* Baker da Jamaica (Mollusca; Soleolifera; Veronicellidae).—Revista Brasileira de Zoologia, São Paulo 10(1):169–172.

———, & V.L.R. Lopes. 1973. Aulas Práticas de Zoologia, I. Dissecação de um molusco gastrópode desprovido de concha.—Iheringia, Porto Alegre, série Divulgação (3):34–45.

———, & V.L. Lopes-Pitoni. 1976. Redescrição dos tipos de Veronicellidae (Mollusca; Gastropoda): espécies no "National Museum of Natural History, Smithsonian Institution", Washington, E.U.A.—Revista Brasileira de Biologia, Rio de Janeiro 36(3):709–714.

———, & G. G. Mansur. 1990. Recaracterização de *Leidyula portoricensis* (Semper, 1885) (Veronicellidae; Gastropoda). In: REUNIÃO ANUAL DA SBPC, 42, 08/13-07-90, Porto Alegre. Anais (Communicações) . . . SBPC, São Paulo 567pp. pp. 534–35. (Suplemento de Ciência e Cultura).

———, P. H. dos Santos, & L. Pedott. (1995) 1996. Nova espécie de *Veronicella* Blainville, 1817 (Mollusca; Gastropoda; Soleolifera) da América Central.—Biociências, Porto Alegre 3(2):265–274.

Zilch, A. 1959/1960. Gastropoda, Teil 2: Euthyneura. In: Schindewolf, O. H. (org.). Handbuch der Paläozoologie. Gebrüder Bornträger,. Berlin, 6: 834pp.

Appendix

On the spelling and date of *Vaginulus taunaisii* Férussac, 1821 (Veronicellidae; Soleolifera; Gastropoda; Mollusca).—A number of differences continue to exist among malacologists regarding the spelling and date of the name proposed more than a century ago by the Frenchmen, d'Audebard de Férussac (father and son). Even now, through correspondence, an argument on the subject has been put forth by a well-known colleague. I do not pretend to have found the full solution, but I hope to contribute to clarification of the controversy with a view to achieving a consensus.

The generic name *Vaginulus* was proposed by Férussac in 1821 (p. 6,9,13). In my opinion it is a valid name, with correct, latinized, original spelling, although use of the masculine suffix (from the Latin: *vagina* + *ulus*, *ula*, *ulum* = diminutive) (Jaeger 1978: 275) may be considered unsuitable, but not wrong. The spelling is in conformity with the International Code of Zoological Nomenclature (ICZN) 1985, art. 11(b)(i), 32 (c)(ii), table 2 on P. 207.

To replace *Vaginulus*, the generic name *Vaginula* was proposed by Berthold, 1827, according to Neave (1940:625). Fischer (1871:148) also suggested changing it due to error (fautif) and among others, Deshayes (1930) himself, *in* Férussac & Deshayes 1820-1851: 96^{6} and even Hoffman (1925:172) insisted on the substitution, without justifying their position. Nevertheless, it should be considered an unjustified emendation (ICZN 1985, art. 33 (b) (iii) and, therefore, *Vaginula* Berthold, 1827 (non *Vaginula* Sowerby, 1820 (Hoffmann, 1925:172); *Vaginula* Risso, 1826 (Neave 1940: 625) must be considered a junior objective synonym.

The specific name *taunaisii* (Férussac 1821:13, and Férussac 1821 and 1823, *in* Férussac & Deshayes 1820–1851, pl. 8A, fig. 7, pl. 8B, fig. 1–2, and p. 96^{q-r}) is said to be an homage to the Frenchman, Taunay (son), whose modern patronym appears to have been erroneously latinized. Fischer (1871:170) and Hoffman (1925:173), amongs others, have already proposed the correct spelling as *taunayi* (ICZN 1985, art. 11, (h) (i)

(3), 31 (a) (i) and (ii)). The original species name, *taunaisii*, has been used by very few authors, the most recent of these being Martens (1867). In spite of this, taking into consideration the opinions of editors and consultants, and based on art. 32 (c) (ii) of the ICZN (1985), I propose a return to the original spelling of the specific name, with the specific name *taunayi* becoming an "incorrect subsequent spelling" (art. 33 (c) ICZN 1985).

Regarding the date of the confusing publication of the Férussacs, the most solid work of dating by external evidence must be that of Kennard (1942a, 1942b), who accepts the date of 17 July 1822 for the pages containing the original description of *Vaginulus* and *V. taunaisii*. Nevertheless, the date on the cover of the Férussac work is January 1821 (janvier 1821) and in the second edition of the great work of Férussac & Deshayes (1820–1851), page 96[1] (edited by Deshayes in 1830) is it expressly stated that the disputed work of Férussac was published in June of 1821 (juin 1821), and therefore distributed with six months delay, but not more than a year and a half, as Kennard figured. Also Herrmannsen (1849), Fischer (1871), and Hoffmann (1925), among others, mention the date of 1821 as valid for the taxa in question, which also appears to me to be valid external evidence.

The species *Vaginulus taunaisii (=taunayi)* Férussac, 1821 has been well redescribed (Thomé 1971:36–39, 41, fig, 15–17, 22), and the genus recharacterized (Thomé 1975b:7–9, 28–32), which should now be considered monotypic. Thus the argument has little significance for the stability and universality of the taxa, for there are no taxonomic implications for their determination and classification. This is also true with reference to the maintenance of the family name, which should be Veronicellidae, as has been demonstrated by Thomé (1979:138–141).

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Revision of the scaleworm genus *Eulagisca* McIntosh (Polychaeta: Polynoidae) with the erection of the subfamily Eulagiscinae and the new genus *Pareulagisca*

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Abstract.—A new subfamily of Polynoidae, *Eulagiscinae*, is established for *Eulagisca* McIntosh, to include the type species *E. corrientis*, *E. gigantea* Monro, *E. puschkini* Averincev, and two new species, *E. uschakovi* and *E. macnabi*, all from the Antarctic and Subantarctic regions, and the new genus *Pareulagisca* for *P. panamensis* (Hartman), new combination, from the central Pacific Panama region.

McIntosh (1885) described *Eulagisca corrientis* from deep water in the South Atlantic and South Indian Oceans. Monro (1939) described some large polynoids from the deep Antarctic as *E. gigantea.* Hartman (1939) added *E. panamensis* from shallow water of Pacific Panama, and Averincev (1972) added *E. puschkini* from shallow water in the Antarctic Davis Sea. The prostomia resemble those of the members of the subfamilies Lepidonotinae Willey, 1902 and Lepidastheniinae Pettibone, 1989, by having the lateral antennae inserted on anterior extensions, on the same level as the ceratophore of the median antenna, or subterminally, without distinct ceratophores. The parapodia differ from those of both subfamilies by having the notopodia and neuropodia well developed, with projecting digitiform acicular lobes, rather than projecting acicular lobes lacking. The elytra of some specimens, identified as *E. gigantea*, and some new material, showed some differences and are referred to two new species: *E. uschakovi* and *E. macnabi.*

Some distinctive characters of species of *Eulagisca*, and not shown by *E. panamensis*, referred herein to the new genus *Pareulagisca*, include the following: long palps of the prostomium with six longitudinal rows of papillae; prominent conical facial tubercle on the upper lip, ventral to the ceratophore of the median antenna; tentaculophores of segment I, lateral to the prostomium, with projecting digitiform acicular lobe and group of long setae; and 15 pairs of elytra (16 pairs in *P. panamensis*).

In addition to the collections in the National Museum of Natural History, Smithsonian Institution (USNM), the specimens covered herein are deposited in the following Museums: Natural History Museum, London (BMNH); Natural History Museum of Los Angeles County (LACM-AHF): Zoological Institute Academy of Sciences, Leningrad (ZIASL); Zoological Museum, Hamburg (ZMH): Zoologisk Museum, Universitet i Oslo (ZMUO).

Family Polynoidae Kinberg, 1856
Eulagiscinae, new subfamily

Diagnosis.—Body elongate, with segments moderate in number (up to 41). Elytra and bulbous elytrophores 15 (*Eulagisca*) or 16 (*Pareulagisca*) pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32 (33). Elytra large, oval, with or without papillae, microtubercles, macrotubercles and globular vesicles or papillae. Dorsal cirri, on non-elytrigerous segments, with cylindrical cirrophores posterodorsal to notopodia, with distal styles; dorsal tubercles, in line with elytrophores, bulbous or indistinct. Prostomium bilobed, with paired palps and three antennae; median antenna with large ceratophore in anterior notch of prostomium, with distal style; lateral antennae inserted terminally or subterminally on anterior extensions of prostomium, without distinct ceratophores; two pairs of eyes. First or tentacular segment not visible dorsally; tentaculophores lateral to prostomium, each with dorsal and ventral tentacular cirri, similar to median antenna, with or without digitiform acicular lobe and numerous or single setae; with or without distinct facial tubercle on upper lip. Second or buccal segment with nuchal fold, first pair of elytra and elytrophores, biramous parapodia, and ventral buccal cirri, longer than following ventral cirri. Biramous parapodia with both noto- and neuropodia with prominent projecting digitiform acicular lobes and numerous noto- and neurosetae. Notosetae of one kind, stout (*Eulagisca*) or two kinds: stout and slender, capillary (*Pareulagisca*). Ventral cirri short, tapering. Pharynx with two pairs of jaws and eleven pairs of dorsal and ventral papillae (not examined in *Pareulagisca*). Pygidium with pair of anal cirri.

Remarks.—The prostomia of the Eulagiscinae agree with the Lepidastheniinae and the Lepidonotinae in having the lateral antennae inserted terminally or subterminally, without distinct ceratophores, and disagreeing with the Harmothoinae having distinct ceratophores and inserted ventrally. The nuchal folds on the second or buccal segment in Eulagiscinae are distinctive. The biramous parapodia, with both rami having prominent digitiform acicular lobes and numerous noto- and neurosetae in Eulagiscinae, differ from the other subfamilies.

Key to the Genera and Species of the Subfamily Eulagiscinae

1. Elytra 16 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 33. Elytra without tubercles and border or surface papillae (Fig. 5G). Prostomium with long palps, without 6 longitudinal rows of papillae (Fig. 5A). Tentaculophore of segment I without projecting acicular lobe, with single seta (Fig. 5A); facial tubercle weakly developed. Notosetae of two kinds: 1) stout, acicular, smooth or with faint spinous rows (Fig. 5D); and 2) slender, capillary, smooth or with few spines (Fig. 5E) .... *Pareulagisca*, n.gen.: *P. panamensis* (Hartman 1939), n. comb. (Fig. 5A–G)
– Elytra 15 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32. Elytra variable. Prostomium with long palps with 6 longitudinal rows of papillae (Fig. 2A) Tentaculophores of segment I with projecting digitiform acicular lobe and group of long setae; with prominent conical facial tubercle (Fig. 2A). Notosetae of one kind, stout, with long spinous regions, tapering to blunt tips (Figs. 1C, 2C, 3C, 4D) .... *Eulagisca* McIntosh 1885....... 2
2. Neurosetae tapering to sharp tips (Fig. 3D; Averincev 1972, pl. 13:9–11). 3
– Neurosetae tapering to slightly hooked tips (Figs. 1D, 2D, 4E) 4
3. Elytra with sharply pointed tubercles and globular vesicles with few to numerous terminal spines (Fig. 3E) .... *E. uschakovi*, new species (Fig. 3A–E).
– Elytra without border or surface papillae; with numerous microtubercles on anterior part (Averincev 1972, pl. 13:8) .... *E. puschkini* Averincev, 1972 (pl. 13:8–12).
4. Elytra with border papillae (Figs. 1E, 4F) 5
– Elytra without border papillae; surfaces with conical microtubercles, larger conical tubercles, and globular vesicles (Fig. 2F) .... *E. gigantea* Monro, 1939 (Fig. 2A–F)
5. Surface of elytra with conical papillae on anterior part (Fig. 1E) .... *E. corrientis* McIntosh, 1885 (Fig. 1A–E)
– Surface of elytra with conical microtubercles and larger spiny tubercles (Fig. 4F) .... *E. macnabi*, new species (Fig. 4A–F).

Genus *Eulagisca* McIntosh, 1885

Type species.—*Eulagisca corrientis* McIntosh, 1885, by monotypy. Gender, feminine.

Diagnosis.—Body rather large, wide, flattened, slightly tapering anteriorly and more so posteriorly, with segments up to 41. Elytra and bulbous elytrophores 15 pairs, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32. Elytra large, covering dorsum, easily detached, with or without microtubercles, macrotubercles, bulbous vescicles, and fringes of papillae. Dorsal cirri with cylindrical cirrophores and long styles on non-elytrigerous segments; dorsal tubercles bulbous. Prostomium bilobed, with paired long palps each with six longitudinal rows of papillae, and three antennae; median antenna with ceratophore in anterior notch of prostomium, with long style; lateral antennae inserted on anterior extensions of prostomium, on same level as median antenna, without distinct ceratophores; eyes 2 pairs, large, laterally on middle of prostomium, nearly contiguous. First or tentacular segment indistinct dorsally; tentaculophores lateral to prostomium, each with projecting digitiform acicular lobe, group of setae, and long dorsal and ventral tentacular cirri. Prominent conical facial tubercle ventral to ceratophore of median antenna. Second segment with semilunar nuchal pad and nuchal fold covering posterior part of prostomium, first pair of elytrophores, biramous parapodia, and long ventral buccal cirri lateral to ventral mouth. Parapodia biramous, with numerous golden setae. Notopodia well developed, with prominent digitiform acicular lobes; neuropodia with long digitiform presetal acicular lobes and shorter rounded postsetal lobes. Notosetae numerous, stouter than neurosetae, with long spinous regions, tapering to blunt tips; neurosetae more numerous and finer than notosetae, with long spinous regions, tapering to rather long bare tips. Ventral cirri short, subulate. Pharynx with two pairs of chitinous jaws and 11 pairs of dorsal and ventral papillae. Pygidium with pair of anal cirri. Nephridial papillae short, cylindrical, beginning on segment VI.

Remarks.—As indicated by Benham (1921:45), McIntosh's choice of *Eulagisca* for *E. corrientis* was a poor one, since it differs in so many ways from *Lagisca*, including the type of the prostomium, parapodia, and elytra.

Eulagisca corrientis McIntosh, 1885
Fig. 1

Eulagisca corrientis McIntosh, 1885:91, Fig. 1, pl. 13:fig. 4, pl. 7A:figs. 3, 4,

Not *Eulagisca corrientis.*—Benham, 1921: 43, pl. 6:figs. 36–38, pl. 7:figs. 39–42.

[?] *Eulagisca corrientis.*—Monro, 1930:48, fig. 11a–e (no elytra); 1936:90 (no elytra).

Not *Harmothoe corrientis* (?).—Augener, 1932:19. (= *Harmothoe* sp.).

Not *Eulagisca corrientis.*—Stiller, 1996:30, pl. 4:figs. 1–5.

Material examined.—South Atlantic: off east coast of South America, south of Buenas Aires, 37°17′S, 53°52′W, 1097 m, green sand, *Challenger* Sta. 320, 14 Feb 1876, syntype (BMNH 1885.12.1.71). South Indian Ocean: Between Kerguelen and Heard Islands, 52°04′S, 71°22′E, 274 m, coarse gravel, *Challenger* Sta. 150, 2 Feb 1874, syntype (BMNH 1885.12.1.83).

Remarks.—The species is somewhat doubtful, since it was based on two syntypes, a smaller complete specimen but without elytra, from *Challenger* Sta. 320, and an anterior fragment of a larger specimen with two elytra, from Sta. 150. There is a possibility that the two syntypes belong to different species but the type material does not allow one to clarify this point. Monro (1930:48) examined McIntosh's type specimens and referred some specimens from off the South Shetlands to *E. corrientis*, but without elytra and thus doubtful. Monro (1936:90) added a record from off the Falkland Islands, but the specimen also lacked elytra. Stiller (1996:30) added *E. corrientis* from the eastern Weddell Sea. It does not agree with the two syntypes in the BMNH.

The specimens described as *E. corrientis* by Benham (1921:43) appear to be a mixture of *Eulagisca* species and need to be reexamined. The specimen that Augener (1932:19) questionably referred to *Harmothoe corrientis* was examined from the Olso Museum (ZMUO); it is in poor condition, the prostomium is harmothoid and different from that of *Eulagisca*; it is referred to *Harmothoe* sp.

Description.—Incomplete syntype with 19 segments, 29+ mm long and 24 mm wide with setae. Smaller complete syntype with 35 segments, 34 mm long and 16 mm wide with setae. Dorsum with brown pigmentation. Elytra and bulbous elytrophores 15 pairs, in usual arrangement (McIntosh 1885: pl. 13, fig. 4). Elytra subreniform, surface with soft conical papillae and long delicate clavate papillae near posterior and lateral borders (Fig. 1E). Dorsal cirri with cylindrical cirrophores and papillate styles extending beyond setae; dorsal tubercles nodular.

Bilobed prostomium wider than long, with long papillate palps and three antennae; median antenna with large ceratophore in anterior notch, with style missing; lateral antennae inserted on anterior extensions of prostomium, with rather long styles with subterminal enlargements and filamentous tips; two pairs of large closely approximated eyes on lateral sides; tentaculophores lateral to palps and prostomium, each with projecting digitiform acicular lobe and four setae directed anteriorly, and dorsal and ventral tentacular cirri, similar to lateral antennae; prominent conical facial tubercle ventral to ceratophore of median antenna (Fig. 1A; McIntosh 1885: pl. 13, fig. 4). Segment II with large semilunar nuchal fold, first pair of large elytrophores, biramous parapodia and long ventral buccal cirri (Fig. 1A; McIntosh: pl. 13 fig. 4).

Biramous parapodia with notopodia and neuropodia about equal in size, both with projecting acicular lobes; notopodia rounded basally, with projecting acicular lobes on lower sides; neuropodia subconical with projecting presetal acicular lobes and shorter rounded postsetal lobes (Fig. 1B; McIntosh 1885: fig. 1). Notosetae numerous, forming radiating bundle of four lengths, slightly stouter than neurosetae, short, slightly curved and longer, straight, with long spinous regions, tapering to short bare tips (Fig. 1C; McIntosh 1885: pl. 7A fig. 3). Neurosetae numerous, forming fan-shaped bundle, with long spinous regions, tapering to slightly hooked bare tips; upper ones more slender and upper few with delicate secondary tooth (Fig. 1D; McIntosh 1885: pl. 7A fig. 4). Ventral cirri slender, with few papillae, tapering, extending slightly beyond basal part of neuropodia (McIntosh 1885: fig. 1).

Distribution.—South Atlantic and South Indian Oceans, in 274–1097 meters.

Eulagisca gigantea Monro, 1939
Fig. 2

Eulagisca gigantea Monro, 1939:103 (part), Fig. 4a–d, f–h (not e), Sta. 30 only.—Uschakov, 1962:174 (part), Sta. 283, pl. 9E, G, H (not F); 1966:174 (part), Sta. 282, pl. 9E, G, H (not F) (English translation).—Hartman, 1967:21 (part, not Sta. 1003).—Not Averincev, 1972:131 (=*E. uschakovi*, new species).—Not Desbruyères, 1976:85, pl. 1: figs. a–c (=*Eulagisca*, new species?).—Hartmann-Schröder & Rosenfeldt, 1990: 91 (part), pl. 1:3–5 (not 1, 2).—Not Stiller, 1996:30, pl. 10:figs. 1–5. (=*E. uschakovi*, new species).

Material examined.—Antarctic: Off Princess Elizabeth Land, 66°48′S, 71°24′E, 540 m, British, Australian, New Zealand, Antarctic Research Expedition Sta. 30, 27 Dec 1929, lectotype (BMNH 1941.3.3.16, largest of three syntypes of *E. gigantea*).

Drake Passage, between South America and Antarctica, 56°06′S, 66°19′W, 384–494 m, *Eltanin* Sta. 740, 18 Sep 1963, 1 specimen (USNM 57466, ident. by Hartman 1967). South Shetland Islands, 61°25′S, 56°30′W, 300 m, *Eltanin* Sta. 993, 13 Mar 1964, 1 specimen (USNM 57467, ident. by

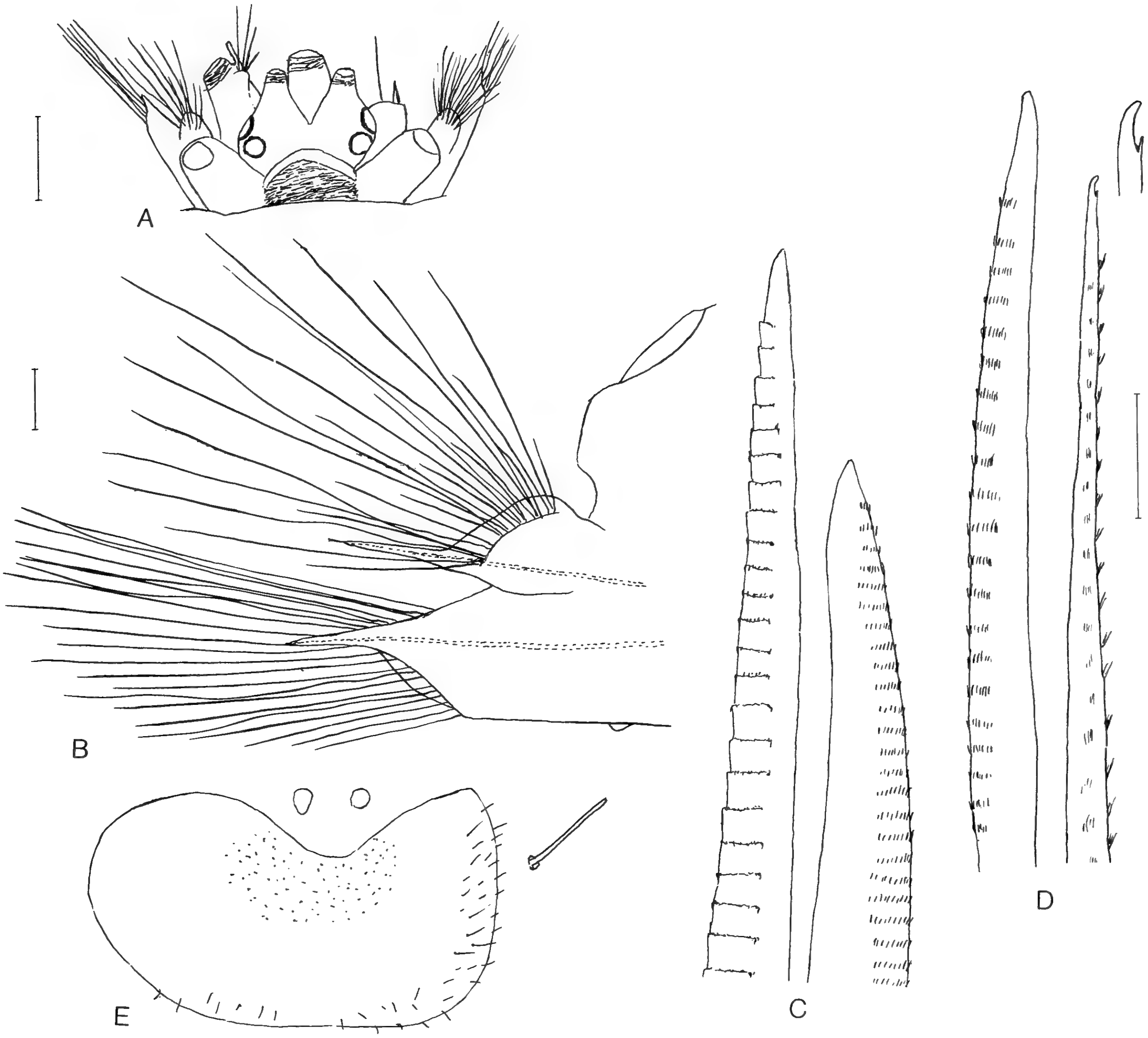

Fig. 1. *Eulagisca corrientis*, A–D, syntype from Sta. 320 (BMNH 1885.12.1.71): E, syntype from Sta. 150 (BMNH 1885.12.1.83): A, Dorsal view of anterior end, right tentaculophore damaged; missing: styles of median and lateral antennae, palps, and tentacular cirri; B, Right elytrigerous parapodium, anterior view, aciculae dotted, style of ventral cirrus missing; C, Tips of long and short notosetae; D, Middle and upper neurosetae, with detail of tip, E, Right elytron, with detail of papillae. Scales = 1.0 mm for A; 0.5 mm for B; 0.1 mm for C,D; E (not to scale).

Hartman 1967). South Orkney Islands, 60°50′S, 42°55′W, 298–302 m, *Eltanin* Sta. 1082, 14 Apr 1964, 1 specimen (USNM 57469, ident. by Hartman 1967). 59°53′S, 32°19′W, 523–671 m, *Islas Orcada* Cruise 1876, USARP Sta. 130, 25 Feb. 1976, 1 specimen (USNM 74575).

Remarks.—The type material of *Eulagisca gigantea* Monro (1939) consists of three syntypes. They proved to be a mixture of at least two species. The largest syntype from Sta. 30, with the elytral tubercles and vesicles as on Fig. 4c, d and not Fig. 4e by Monro (1939), was selected as the lectotype. The next largest syntype from Sta. 107, with elytral tubercles as shown on Fig. 4e, was selected as the holotype of *E uschakovi*, new species. The smallest syntype from Sta. 39, which lacked elytra, was selected as a paratype of *E. uschakovi*, based on the similarity of the neurosetae.

The two specimens from the Continental plateau off Kerguelen, in 172–262 m, described and figured by Desbruyères (1976) as *E. gigantea*, differ: the elytra have a well-developed lateral fringe of long papillae and the surface is covered with conical spiny vesicles (pl. 1A–C), thus differing from *E. gigantea*, and probably indicating a new species. The specimens were not available for examination to complete the description.

One of the specimens from Elephant Island, Antarctica, in 280–432 m, referred to *E gigantea* by Hartmann-Schröder and Rosenfeldt (1990:91, pl. 1; 3–5, not 1, 2), agree with *E. gigantea*, based on the photos of the elytra; the other specimen is referred to *E. uschakovi*, new species. Stiller (1996: 30, pl. 10:figs. 1–5) reported *E. gigantea* from the eastern Weddell Sea. Based on the description and figures, it is added to *E. uschakovi*, new species.

Additional records of *E. gigantea*, with elytra lacking, are omitted. They must be referred to *Eulagisca* sp.

Description.—Lectotype with 38 segments, 148 mm long, 44 mm wide with setae. Specimen from South Shetland Island (USNM 57467) 68 mm long, 46 mm wide with setae, 38 segments. Specimen from South Orkney Island (USNM 57469) 155 mm long, 94 mm wide with setae, 38 segments. Body large, flattened, with long parapodia (parapodia and setae longer than body width). Body colorless except for traces of brown transverse bands, with golden setae.

Fifteen pairs of elytra, on bulbous elytrophores, large, thick, subreniform, covering dorsum, darker along posterior border, without border papillae (Fig. 2F; Monro 1939: fig. 4b). Surface of anterior part of elytra with numerous conical microtubercles, middle part with larger sharply pointed conical tubercles and posterior part with curved conical tubercles (rarely 2-pronged), some smaller spines, and soft globular vesicles, dotted yellowish distally (Fig. 2F; Monro 1939: fig. 4c, d, not e; Uschakov, 1966: pl. 9E, not F). Dorsal cirri with cylindrical cirrophores, bulbous on posterior basal parts, with styles extending to end of neurosetae, with short clavate papillae. Dorsal tubercles bulbous, posterior ones on segments 33–38 projecting posteriorly.

Bilobed prostomium wider than long, median antenna with large ceratophore in anterior notch, with style missing (probably long, similar to but longer than lateral antennae); lateral antennae inserted on anterior extensions of prostomium, without distinct ceratophores, with styles rather long, finely papillated, with subterminal enlargements and filamentous tips; palps long, stout, tapering, with six longitudinal rows of papillae; two pairs of rather large eyes with lenses on posterior half of prostomium; tentaculophores (segment I) lateral and anterior to prostomium, with prominent digitiform acicular lobes, group of long setae (up to 10) directed anteriorly, and long dorsal and ventral tentacular cirri, similar to but longer than lateral antennae; with prominent conical facial tubercle below ceratophore of median antenna (=subtentacular cirrus by Monro) (Fig. 2A; Monro 1939: fig. 4a). Segment II with prominent semilunar nuchal pad and conical fleshy nuchal fold covering posterior part of prostomium (latter may be pulled back), first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, inserted basally, similar to tentacular cirri (Fig. 2A; Monro 1939: fig. 4a).

Biramous parapodia with small subconical notopodia with projecting acicular lobes; larger neuropodia with subtriangular presetal acicular lobes and shorter subconical postsetal lobes (Fig. 2B; Monro 1939: fig. 4f). Notosetae numerous, forming radiating bundle, about as stout as neurosetae, of three lengths, some shorter, curved, some about as long as neurosetae, stout, acicular, with long spinous regions, tapering to bare entire tips (Fig. 2B, C; Monro 1939: fig. 4g; Uschakov 1962: pl. 9G). Neurosetae numerous, forming fan-shaped bundle, with long spinous regions and rather long, slightly hooked entire bare tips; upper ones more slender, with longer spinous regions (Fig. 2D, E; Monro 1939: fig. 4h; Uschakov

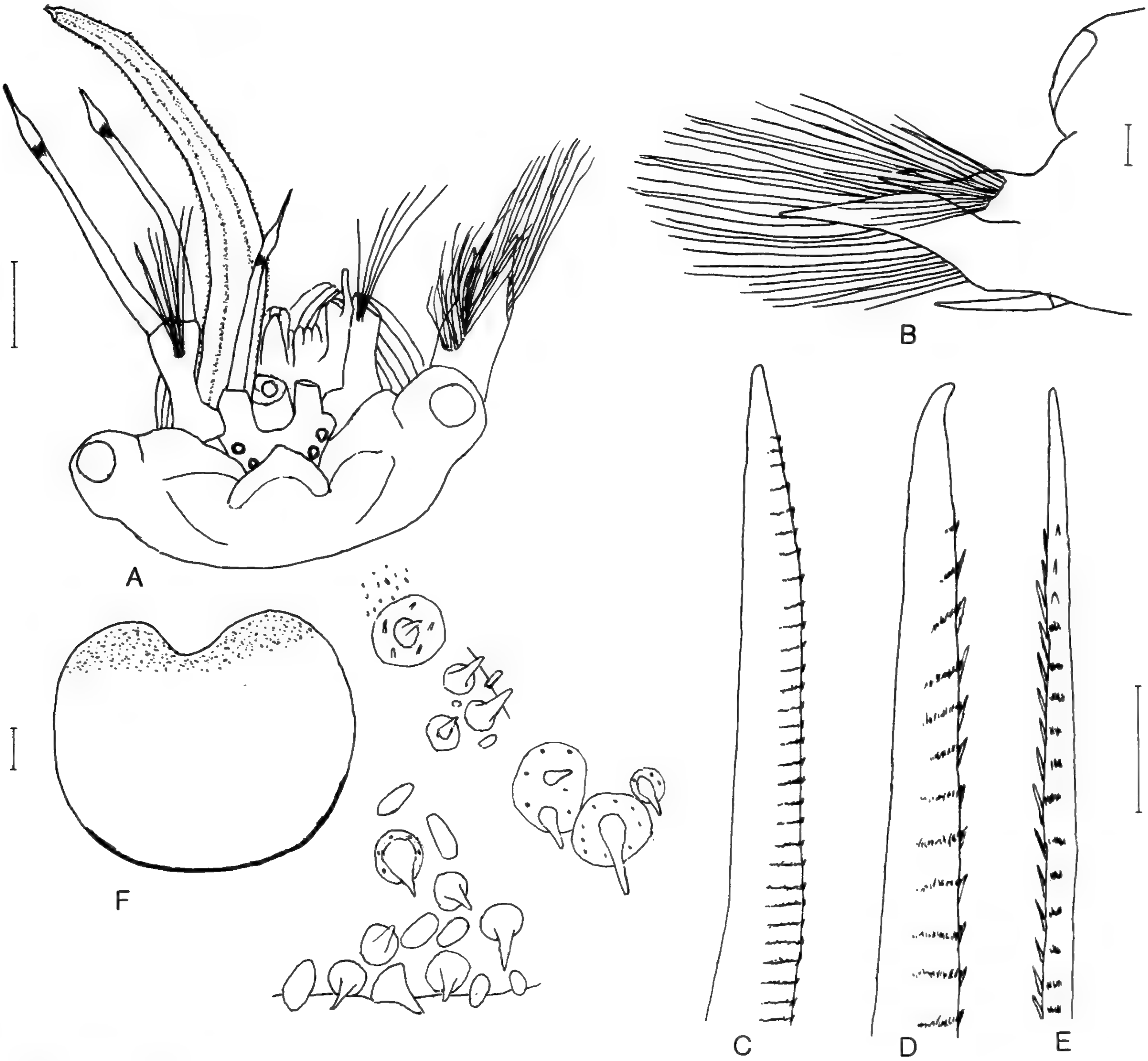

Fig. 2. *Eulagisca gigantea*, A. Specimen from South Shetland Island (USNM 57467); B–F, lectotype (BMNH 1941.3.3.16): A, Dorsal view of anterior end, pharynx partially extended; missing; right palp, median and right lateral antennae, right dorsal and ventral tentacular cirri, left parapodium of segment 2 not shown; B, Right elytrigerous parapodium, anterior view; C, Notoseta from same; D, Middle neuroseta from same; E, Upper neuroseta from same; F, Elytron, with detail of microtubercles, larger tubercles, and soft globular vesicles. Scales = 2.0 mm for A; 2.0 mm for B; 0.1 mm for C–E; 5.0 mm for F.

1966: pl. 9H). Ventral cirri short, subulate, extending slightly beyond basal part of neuropodia (Fig. 2B).

Distribution.—Antarctic, Off Princess Elizabeth Land, Davis Sea, Drake Passage, Scotia Sea, South Shetlands, South Orkneys, in 200–900 meters.

Eulagisca uschakovi, new species
Fig. 3

Eulagisca gigantea Monro, 1939:103 (part: Sta. 39 & 107, Fig. 4e only).—Uschakov, 1962:174 (part: Sta. 232, pl. 9F only; 1966:174 (part: Sta. 232, pl. 9F only (English translation).—Hartman, 1967:21 (part: Sta. 1003 only).—Averincev, 1972: 131, pl. 13:1–7.—Hartmann-Schröder & Rosenfeldt, 1990:91 (part, pl. 1:1, 2, not 3–5). Not Monro, 1939 (lectotype).—Stiller, 1996:30, pl. 10: figs. 1–5.

Material examined.—Antarctic: Off MacRobertson Land, 66°45′S, 62°63′E, 219 m, British, Australian, New Zealand Antarctic Research Expedition Sta. 107, 16 Feb

1931, holotype (BMNH 1941.3.3.18, as next longest syntype of *E. gigantea*). Off Enderby Land, 66°10′S, 49°41′E, 300 m, B.A.N.A.R.E. Sta. 39, 17 Feb 1930, paratype (BMNH 1941.3.3.17, as smallest syntype of *E. gigantea*).

Bransfield Strait, 62°41′S, 54°43′W, 210-220 m, *Eltanin* Sta. 1003, 15 Mar 1964, paratype (USNM 57468, as *E. gigantea* by Hartman, 1967). Off Palmer Archipelago, 62°09′S, 57°49′W, 220-229 m, *Eastwind* Sta. 66, 19 Feb 1966, 2 paratypes (USNM 35289). Scotia Sea, 61°19′S, 44°26′W, 274–280 m, *Islas Orcada* Sta. 123, 22 Feb 1976, 1 specimen (USNM 74576).

Ross Sea, 75°50′S, 173°08′W, 476 m, *Eltanin* Sta. 38, 31 Jan 1968, 2 paratypes (USNM 58350).

Types.—Holotype (BMNH 1941.3.318, next largest syntype of *E. gigantea*): 110 mm long, 70 mm wide with setae, 39 segments, with elytra. Paratype (BMNH 1941.3.3.17, smallest syntype of *E. gigantea*): 56 mm long, 36 mm wide with setae, 37 segments, without elytra but neurosetae agree with holotype. Two paratypes from Ross Sea (USNM 58350): 140–190 mm long, 85–100 mm wide with setae, 39 segments, with elytra. Paratype from Palmer Archipelago (USNM 58351): 81 mm long, 48 mm wide with setae, 38 segments, with elytra (figured).

Description.—Body brownish on mid-dorsum, on bases of elytrophores and dorsal tubercles. Dorsum with ciliated bands (ca 14 per segment), continuing on elytrophores and dorsal tubercles (Averincev 1972: pl. 13:1).

Elytra large, thin (compared with *E. gigantea*), subreniform, splashed with brownish pigmentation; surfaces with numerous microtubercles on anterior part, sharply pointed tubercles on middle part, and posterior part with additional globular vesicles with few to numerous terminal spines, and some papillae but no thick fringe (Fig. 3E; Monro 1939; fig. 4e; Uschakov 1962; pl. 9F; Averincev 1972: pl. 13.5; Hartmann-Schröder & Rosenfeldt 1990: pl. 1:1, 2; Stiller 1996, pl. 10 fig. 3). Dorsal cirri with large cylindrical cirrophores, inflated basally, with long papillate styles extending beyond setae; dorsal tubercles nodular (Fig. 3B; Averincev 1972: pl. 13:2).

Bilobed prostomium wider than long; median antenna with large ceratophore in anterior notch, with long, finely papillated style with subterminal enlargement and filamentous tip; lateral antennae inserted on anterior extensions of prostomium, without distinct ceratophores, styles similar to but shorter than median antenna; palps long, stout, tapering, with six longitudinal rows of papillae; two pairs of rather large eyes on posterior half of prostomium; tentaculophores (segment I) lateral and anterior to prostomium, with digitiform acicular lobes, group of long setae directed anteriorly, and long dorsal and ventral tentacular cirri, similar to but longer than antennae; with prominent conical facial tubercle below ceratophore of median antenna (Fig. 3A; Averincev 1972:pl. 13:1; Stiller 1996:pl. 10, fig. 1). Segment II with prominent semilunar nuchal pad and conical nuchal fold covering posterior part of prostomium, first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, inserted basally, similar to tentacular cirri (Fig. 3A; Averincev 1972:pl. 13:1; Stiller 1996: pl. 10, fig. 1).

Biramous parapodia with smaller and shorter notopodia and larger neuropodia, both with projecting digitiform acicular lobes (Fig. 3B). Notosetae numerous, short to longer, slightly stouter than neurosetae, with long spinous regions and short bare tapered tips (Fig. 3C; Averincev 1972: pl. 13:4; Stiller 1996: pl. 10, fig. 4). Neurosetae numerous, with long spinous regions, all tapering to long, slender, bare, pointed tips (Fig. 3D; Averincev 1972: pl. 13:3; Stiller 1996: pl. 10, fig. 5). Ventral cirri short, tapered, papillate (Fig. 3B).

Etymology.—The species is named for the late P. V. Uschakov, in recognition of his vast contributions to the study of the Polychaeta.

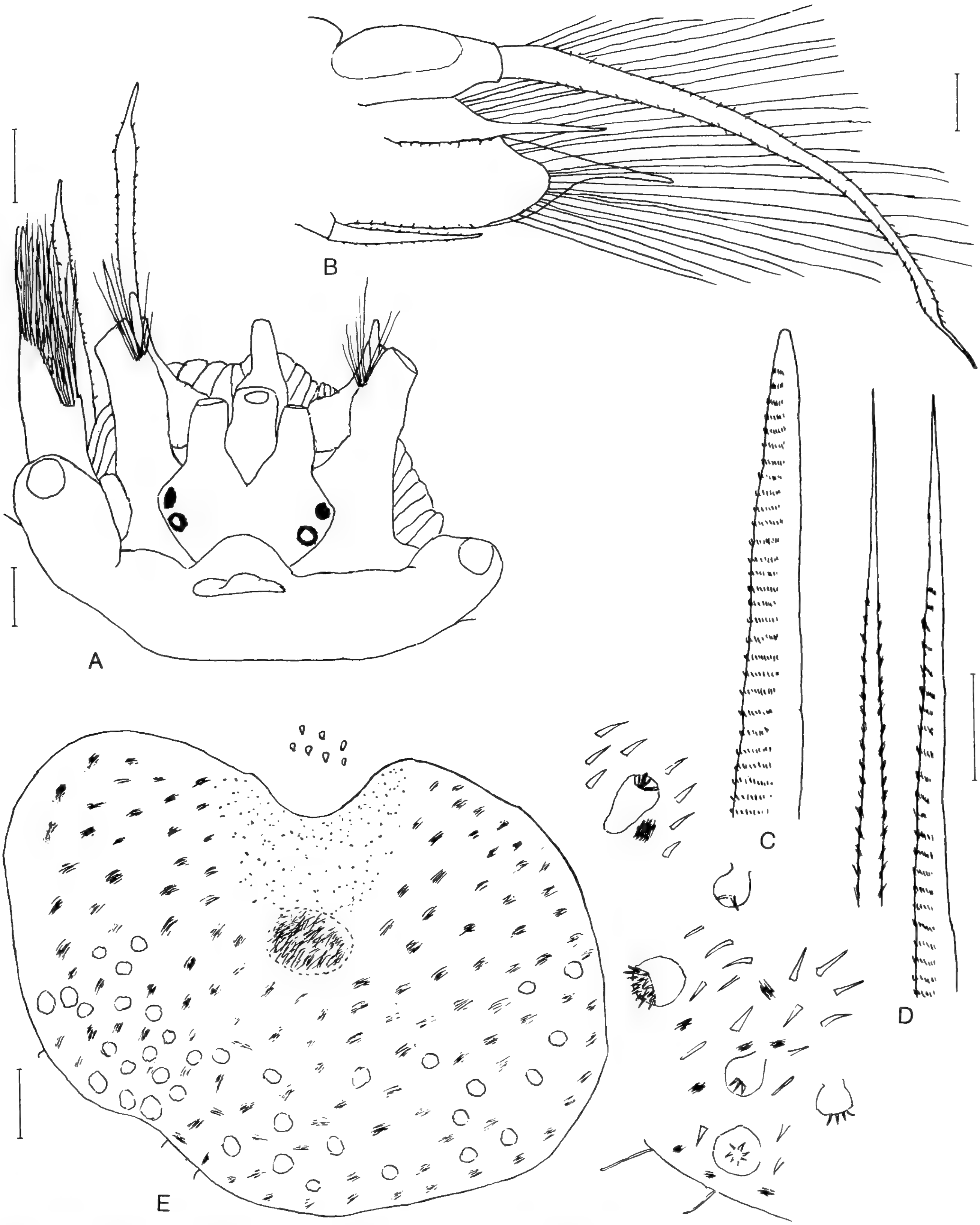

Fig. 3. *Eulagisca uschakovi*, new species, A–D, paratype (BMNH 1941.3.3.17); E, paratype (USNM 58351): A, Dorsal view of anterior end, pharynx partially extended; missing: palps, styles of median and lateral antennae, dorsal and ventral tentacular cirri, except left one; segment 2 with nuchal fold partially folded back, right parapodium not shown: B, Right cirrigerous parapodium, posterior view; C, Tip of notoseta; D, Tips of two neurosetae; E, Right elytron, with detail of microtubercles, sharply pointed tubercles, spinous globular vesicles, and papillae. Scales = 1.0 mm for A; 1.0 mm for B; 0.1 mm for C, D; 2.0 mm for E.

Remarks.—The polynoids from the Davis Sea in 11–920 m, referred by Averincev (1972:131, pl. 13:1–7) to *Eulagisca gigantea,* were not available for examination. The description and figures agree with *E. uschakovi.* One of the specimens from Elephant Island (Antarctica) in 280-437 m, referred to *E. gigantea* by Hartmann-Schröder and Rosenfeldt (1990:91, pl. 1:1, 2, not 3–5), also agree with *E. uschakovi.*

The elytra of *E. uschakovi* differ from the other species of *Eulagisca* in having sharply pointed tubercles and globular vesicles with few to numerous terminal spines. The neurosetae of *E. uschakovi* agree with *E. puschkini* Averincev by having neurosetae tapering to sharp tips, rather than ending in slightly hooked blunt tips, as in the other species of *Eulagisca.* This also applies to the record of *E. gigantea* by Stiller (1996, pl. 10:figs. 3, 5) from the eastern Weddell Sea.

Distribution.—Antarctic, off MacRobertson Land, off Enderby Land, Davis Sea, Bransfield Strait, off Palmer Archipelago, Scotia Sea, Elephant Island, South Orkneys, Ross Sea, Weddell Sea, in 10–920 meters.

Eulagisca macnabi, new species
Fig. 4

Material examined.—Antarctic: Off South Orkneys, 61°00′S, 44°58′W, 283–329 m, *Eastwind,* Sta. 29, 11 Feb 1966, D. L. Pawson and D. F. Squires, coll., holotype (USNM 58352).

Description.—Holotype 62+ mm long, 38 mm wide with setae, segments 24, plus small regenerating posterior end. Body flattened, with long parapodia (about as long as body width); dorsum with transverse ciliated bands (ca 10 per segment) extending on bases of elytrophores and dorsal tubercles (Fig. 4A–C).

Elytra large, subreniform, covering dorsum, with fringes of long border papillae laterally, posteriorly and medially; surfaces splotched with brownish pigmentation, conical microtubercles on anterior part, small to larger spiny tubercles posteriorly and medially, some rounded tubercles with medial filamentous extensions (Fig. 4F). Dorsal cirri with cylindrical cirrophores with glandular bulbous lobes on anterior and posterior sides and distal brown bands; styles missing; dorsal tubercles nodular (Fig. 4C).

Bilobed prostomium with large ceratophore of median antenna in anterior notch, style missing; lateral antennae inserted on anterior extensions of prostomium, with long papillate styles and filamentous tips; two pairs of lateral eyes moderate in size; palps long, tapering, with six longitudinal rows of papillae; tentaculophores lateral to prostomium and palps, each with projecting digitiform acicular lobe, missing dorsal and ventral tentacular cirri, and bundle of long setae (ca. 14); conical facial tubercle ventral to ceratophore of median antenna; dark brown bands on ceratophore of median antenna, lateral extensions of prostomium for lateral antennae, and tentaculophores (Fig. 4A). Segment II with semilunar nuchal pad and subconical nuchal fold, partially pulled back, first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, similar to lateral antennae (Fig. 4A).

Biramous parapodia with prominent projecting digitiform acicular lobes on both rami. Notopodium smaller than neuropodium, rounded, with projecting acicular lobe on lower side; larger neuropodium with subconical presetal acicular lobe and shorter subconical postsetal lobe (Fig. 4B, C). Notosetae numerous, forming radiating bundle of three lengths, stouter than neurosetae, acicular, with spinous rows and rather long bare tips (Fig. 4B, D). Neurosetae numerous, forming fan-shaped bundle, with long spinous regions, upper ones more slender, all with rather long, slightly hooked bare tips (Fig. 4B, E). Ventral cirri short, tapered, papillate (Fig. 4B, C). Nephridial papillae beginning on segment VI.

Etymology.—The species is named for the late Dr. James A. Macnab, a dedicated and inspirational teacher.

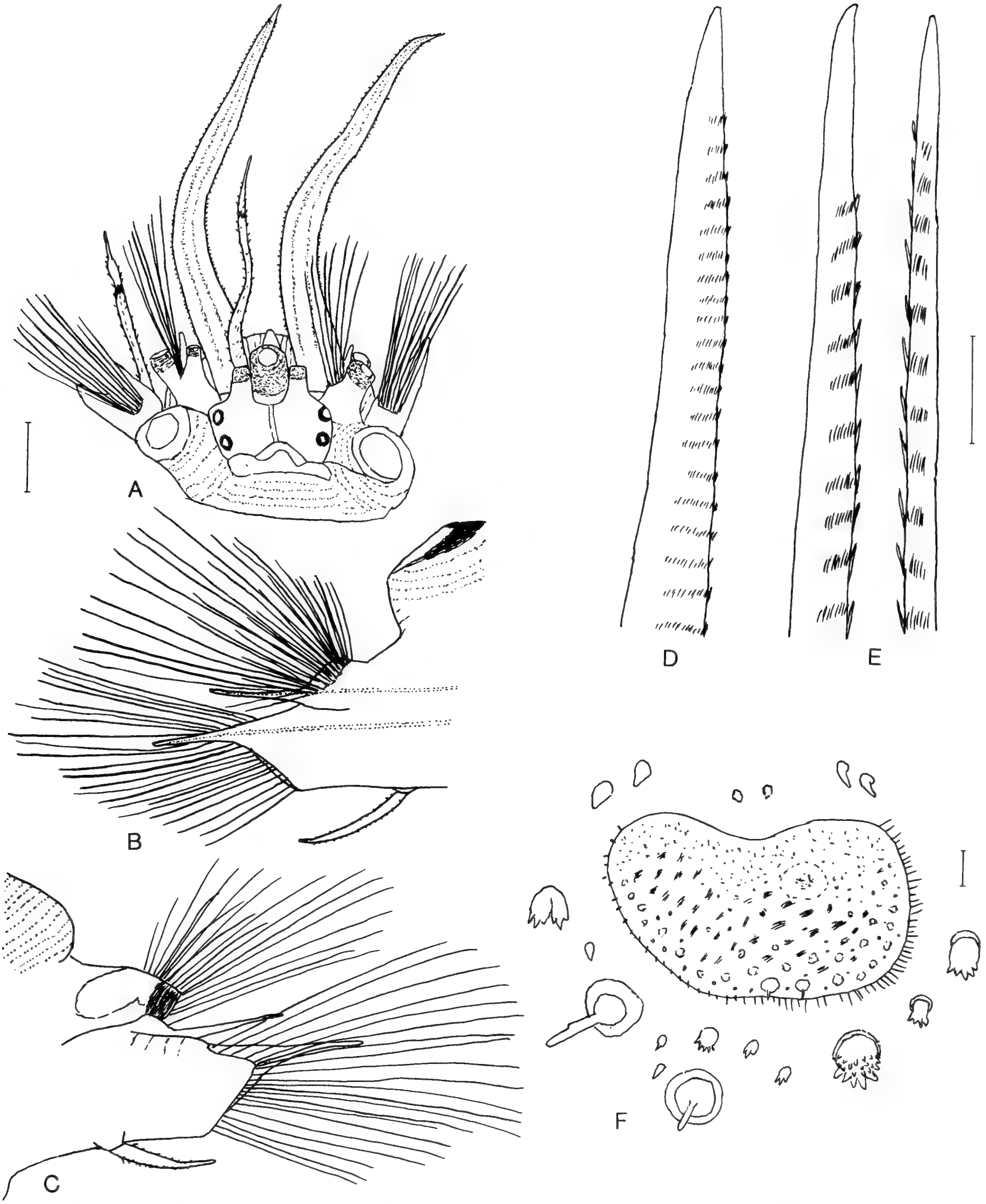

Fig. 4. *Eulagisca macnabi*, new species, holotype (USNM 58352): A, Dorsal view of anterior end, missing: styles of median and right lateral antennae, right and left dorsal and ventral tentacular cirri, right ventral buccal cirrus, and elytra; nuchal fold partially pulled back; B, Right elytrigerous parapodium, anterior view, aciculae dotted; C, Right cirrigerous parapodium, posterior view, style of dorsal cirrus missing; D, Notoseta from same; E, Middle and upper neurosetae from same; F, Right elytron, with detail of microtubercles, spiny vesicles, and papillae. Scales = 2.0 mm for A-C; 0.1 mm for D, E; 2.0 mm for F.

Distribution.—Antarctic, South Orkneys, 300 meters.

Remarks.—The elytra of *E. macnabi* differ from the other species of *Eulagisca* by the well developed border fringes of papillae and the surface spiny tubercles.

Eulagisca puschkini Averincev, 1972

Eulagisca puschkini Averincev, 1972:131, pl. 13:8–12.

Remarks.—A single specimen was collected by aqualung in the Davis Sea, in 32 meters, on rocky bottom, among sponges and hydroids (Type deposited in ZIASL). The type was not available for examination. The following was reported by Averincev.

The large specimen is 175 mm long, 55 mm wide without setae, and 85 mm wide with setae, number of segments ?. The anterior end, including the prostomium, palps, tentaculophores, facial tubercle, nuchal fold, and pharynx, agree with *Eulagisca gigantea*. The elytra differ from the other species of *Eulagisca* by lacking border and surface papillae, by having numerous microtubercles on the anterior part, with a red-brown iridescent spot on the medial half (pl. 13:8). The biramous parapodia have large digitiform processes with inner aciculae. The notosetae are thicker than the neurosetae, with transverse spinous rows and short bare tips (pl. 13:12). The neurosetae have subdistal spinous rows and end in tapered bare tips, and few with small secondary tooth (pl. 13:9–11).

The elytra of *E. puschkini* differ from other members of *Eulagisca* by lacking border papillae, surface tubercles and vesicles, and with only numerous microtubercles on the anterior half. The neurosetae of *E. puschkini*, with tapered bare tips, agree with those of *E. uschakovi* new species.

Distribution.—Antarctic, Davis Sea, in 12 meters.

Pareulagisca, new genus

Type species.—*Eulagisca panamensis* Hartman, 1939. Gender: feminine.

Diagnosis.—Body subrectangular, tapering slightly anteriorly and posteriorly, with segments up to 37. Elytra and bulbous elytrophores 16 pairs, on segments 2, 4, 5, alternate segments to 23, 26, 29, 32, 33. Elytra large, covering dorsum, smooth, without tubercles or papillae. Dorsal cirri on non-elytrigerous segments, with cylindrical cirrophores, bulbous basally, with papillate styles extending to tips of setae; dorsal tubercles slightly bulbous. Prostomium bilobed, with two long finely papillate palps and three papillate antennae; ceratophore of median antenna large, in anterior notch of prostomium, lateral antennae inserted on anterior extensions of prostomium subterminal to ceratophore of median antenna; two pairs of lateral eyes, moderate in size. Tentaculophores of segment I lateral to prostomium, each with single seta, without projecting acicular lobe (as in *Eulagisca*), and papillate dorsal and ventral tentacular cirri; facial tubercle weakly developed. Second or buccal segment with thick, fleshy nuchal fold, first pair of elytrophores, biramous parapodia, and long ventral buccal cirri, lateral to ventral mouth. Parapodia biramous, noto- and neuropodia about equal in length, both subconical with projecting acicular lobes. Numerous notosetae forming radiating bundles, nearly as long as neurosetae, of two kinds: stout, acicular (about as stout as neurosetae), smooth or with faint spinous rows; slender, capillary, smooth or with few spines. Numerous neurosetae stout, with long spinous regions and long, bare, slightly hooked entire tips, with or without minute secondary tooth. Ventral cirri short, tapered, papillate. Pygidium with pair of papillate anal cirri. Nephridial papillae beginning on segment IV.

Etymology.—*Pareulagisca* from Greek *para* = near + *Eulagisca* in allusion to the similarity of the two genera.

Pareulagisca panamensis (Hartman 1939), new combination

Fig. 5

Eulagisca panamensis Hartman, 1939:31, pl. 3:figs. 38–42.

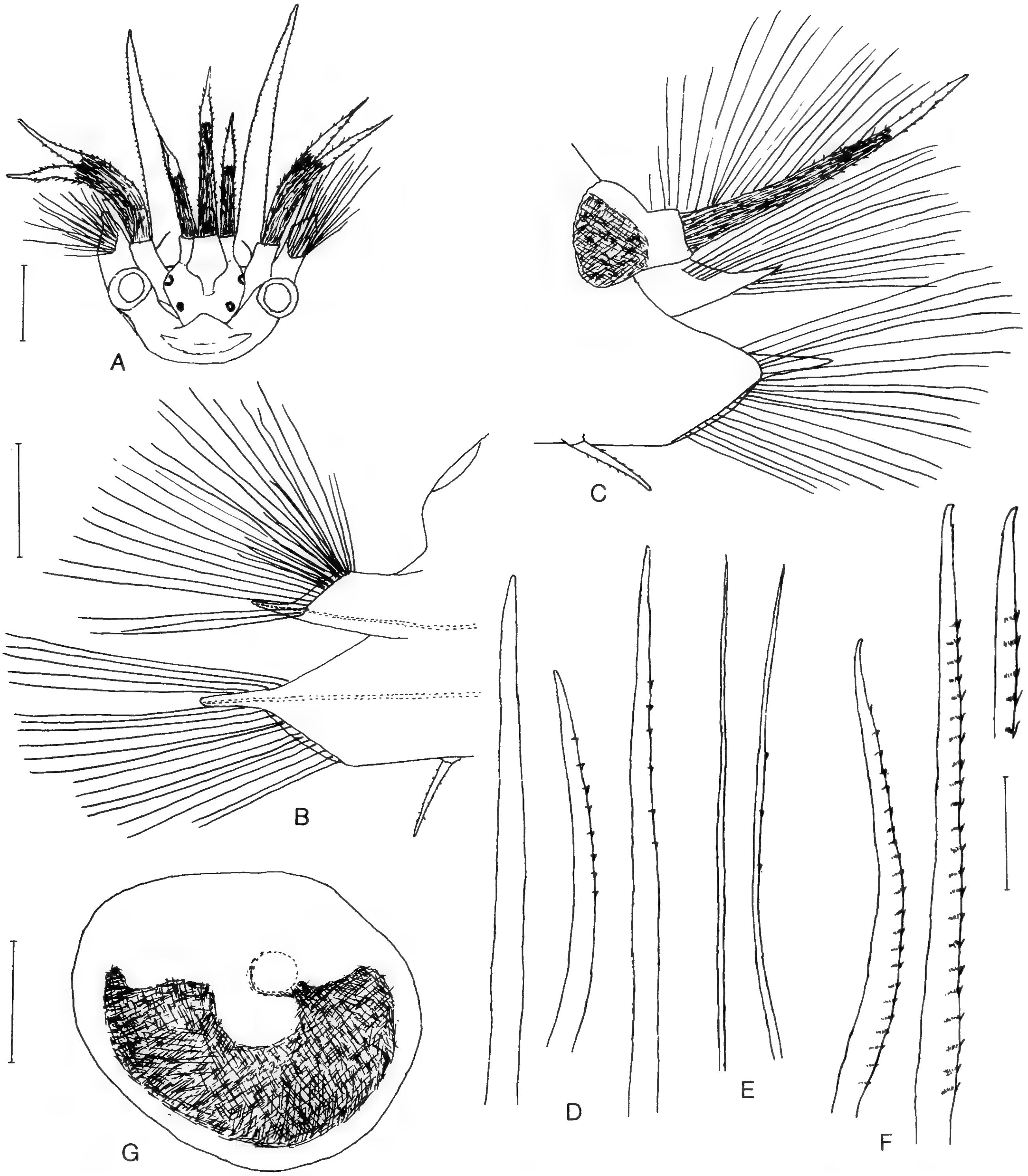

Fig. 5. *Pareulagisca panamensis*, holotype of *Eulagisca panamensis* (LACM-AHF 10): A, Dorsal view of anterior end; B, Right elytrigerous parapodium, anterior view, aciculae dotted; C, Right cirrigerous parapodium, posterior view; D, Three stout notosetae from same; E, Two slender, capillary notosetae from same; F, Lower and upper neurosetae from same; G, Right elytron. Scales = 2.0 mm for A; 1.0 mm for B, C; 0.1 mm for D–F; 2.0 mm for G.

Material examined.—Pacific: Panama, Piñas Bay, 07°34′N, 78°12′W, shore, rock, *Velero* Sta. 436, 28 Jan 1935, holotype (LACM-AHF 10).

Description.—Holotype 42 mm long, 15 mm wide with setae, 37 segments. Body subrectangular, flattened, tapering slightly anteriorly and posteriorly. Elytra and bulbous elytrophores 16 pairs (not 15, as indicated by Hartman) on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32, 33, dorsal cirri present on posterior four segments. Elytra large, covering dorsum, fleshy, smooth, without tubercles or papillae, with rust-colored semilunar pigmentation on posterior half (Fig. 5G; Hartman 1939, pl. 3:fig. 42). Dorsal cirri with cylindrical cirrophores, bulbous basally, and long styles extending to about tips of setae, with short papillae on distal half and brown pigmentation on basal three-fourths; dorsal tubercles slightly bulbous (Fig. 5C; Hartman 1939: pl. 3, fig. 39).

Bilobed prostomium suboval, without cephalic peaks; ceratophore of median antenna in anterior notch of prostomium, very large, with long papillated style enlarged subdistally, with filamentous tip; lateral antennae inserted on anterior extensions of prostomium, subterminal to large ceratophore of median antenna, with shorter styles; palps long, thick, tapered, finely papillated; two pairs of eyes moderate in size; tentaculophores lateral to prostomium, each with single seta, dorsal and ventral tentacular cirri, similar to median antenna; facial tubercle indistinct (Fig. 5A). Second or buccal segment with triangular nuchal fold, first pair of bulbous elytrophores, biramous parapodia, and long ventral buccal cirri, similar to tentacular cirri (Fig. 5A).

Notopodia of biramous parapodia almost as long as neuropodia, subconical, with projecting acicular lobes on lower sides; neuropodia subconical, with longer presetal acicular lobes and shorter, rounded postsetal lobes (Fig. 5B, C; Hartman 1939: pl. 3, fig. 39). Notosetae numerous, forming radiating bundle of two kinds: acicular, about as stout as neurosetae, mostly smooth and shorter, curved, with 6–12 widely-spaced spinous rows (Fig. 5D: Hartman 1939: pl. 3, fig. 40); and slender, tapering to pointed and capillary tips, smooth or with few widely-spaced spines (Fig. 5E). Neurosetae numerous, forming fan-shaped bundle, lower shorter to upper longer, with long spinous regions and rather long bare, slightly hooked entire tips, upper few with minute secondary tooth (Fig. 5F; Hartman 1939: pl. 3, figs. 38, 41). Ventral cirri short, tapered, with short papillae (Fig. 5B, C).

Table 1.—Comparison of characters for *Eulagisca* and *Pareulagisca*.

	Eulagisca	*Pareulagisca*
Elytra	15 pairs	16 pairs
Palp	6 longitudinal rows of papillae	without longitudinal rows of papillae
Tentaculophore	with projecting acicular lobe and group of long setae	without projecting acicular lobe and single seta
Notosetae	of one kind, long, spinous rows, tapering to blunt tips	of 2 kinds: 1) stout, acicular 2) slender, capillary

Distribution.—Central Pacific Ocean, Panama, intertidal.

Remarks.—*Pareulogisca panamensis* is unusual in having 16 pairs of elytra, instead of the more common 15 pairs, and in having two distinct types of notosetae: stout and slender, capillary. The large size of the ceratophore of the median antenna is also unusual.

Pareulagisca differs from *Eulagisca* as shown in Table 1.

Literature Cited

Augener, H. 1932. Antarktische und Antiboreale Polychaeten nebst einer Hirundinee.—Scientific results of the Norwegian Antarctic Expedition 1927–28. Det Norske Videnskaps-Akademii Oslo, Pp. 1–88.

Averincev, V. G. 1972. [Benthic polychaete worms of the Errantia from the Antarctic and Subantarctic in the material of the Soviet Antarctic Expeditions].—Akademiia Nauk SSSR Zoologicheskii Institut 5:88–293. [In Russian]

Benham, W. B. 1921. Polychaeta. Australian Antarctic Expedition 1911–14, Under the leadership of Sir Douglas Mawson, D.Sc.B.E.—Scientific Reports, Series C. Zoology & Botany 6(3):1–128.

Desbruyères, D. 1976. Bionomie benthique du plateau continental de l'archipel des Iles Kerguelen-Macrofaune 3. Contribution a l'étude des Polynoidae (Annelides Polychètes) des Terres australes et Antarctiques Françaises.—CMFRA Prospections en Océnographie Biologique et

Bionomie Benthique aux abords des Iles Kerguelen et Crozet No. 39:83–96.

Hartman, O. 1939. Polychaetous annelids. Part I. Aphroditidae to Pisionidae.—Allan Hancock Pacific Expeditions 7(1):1–156.

———. 1967. Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* cruises, chiefly from Antarctic Seas.—Allan Hancock Monographs in Marine Biology 2:1–387.

Hartmann-Schröder G. 1986. Die Polychaeten 56 Reise der "Meteor" zu den South Shetland-Inseln (Antarktis).—Mitteilungen aus dem hamburgishchen zoologischen Museum und Institut 83: 71–100.

———, & P. Rosenfeldt. 1990. Dis Polychaeten der "Walther Herwig" Reise 68/1 nach Elephant Island (Antarktis) 1985 Teil 1: Aphroditidae bis Cirratulidae.—Mitteilungen aus dem Hamburgishchen zoologischen Museum und Institut 87: 89–122.

Kinberg, J. G. H. 1856. Nye slagter och arter af Annelider.—Ofversigt af Konglia Vetenkaps-Akademiens Förhandlingar, Stockholm 12:381–388.

McIntosh, W. C. 1885. Annelida Polychaeta.—Report on the Scientific Results of the Voyage of *H. M. S. Challenger* . . . 1873–76 . . . Zoology 12(34):1–554.

Monro, C. C. A. 1930. Polychaete worms.—Discovery Reports 2:1–222.

———. 1936. Polychaete worms. II.—Discovery Reports 12:59–198.

———. 1939. Polychaeta.—Reports British Australian and New Zealand Antarctic Research Expedition, 1929–1931, series B 4(4):87–156.

Pettibone, M. H. 1989. A new species of *Benhamipolynoe*, (Polychaeta:Polynoidae:Lepidastheniinae) from Australia, associated with the unattached stylasterid coral *Conopora adeta*.—Proceedings of the Biological Society of Washington 102:300–304.

Stiller, M. 1996. [Distribution and biology of the Aphroditides and Polynoids (Polychaeta) in the eastern Weddell Sea and the Lazarev Sea (Antarctica).].—Reports on Polar Research, No. 185 Heft Nr. 185/1996:1–200. [in German]

Uschakov, P. V. 1962. [Polychaetous Annelids of the Families Phyllodocidae and Aphroditidae from the Antarctic and Subantarctic Waters.—Biological Results of Soviet Antarctic Expedition (1955–1958).] Issledovaniia fauny morei Zoologicheskii Institut Akameniia Nauk SSSR, I(IX):129–189. [in Russian]

———. 1966. English translation of 1962 by Israel Program Scientific Translations, 131–188.

Willey, A. 1902. Polychaeta.—Report on the Collections of Natural History made in the Antarctic Regions during the Voyage of the "Southern Cross" 12:262–283.

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Protodrilus gelderi, a new species of infralittoral, interstitial polychaete from Massachusetts Bay

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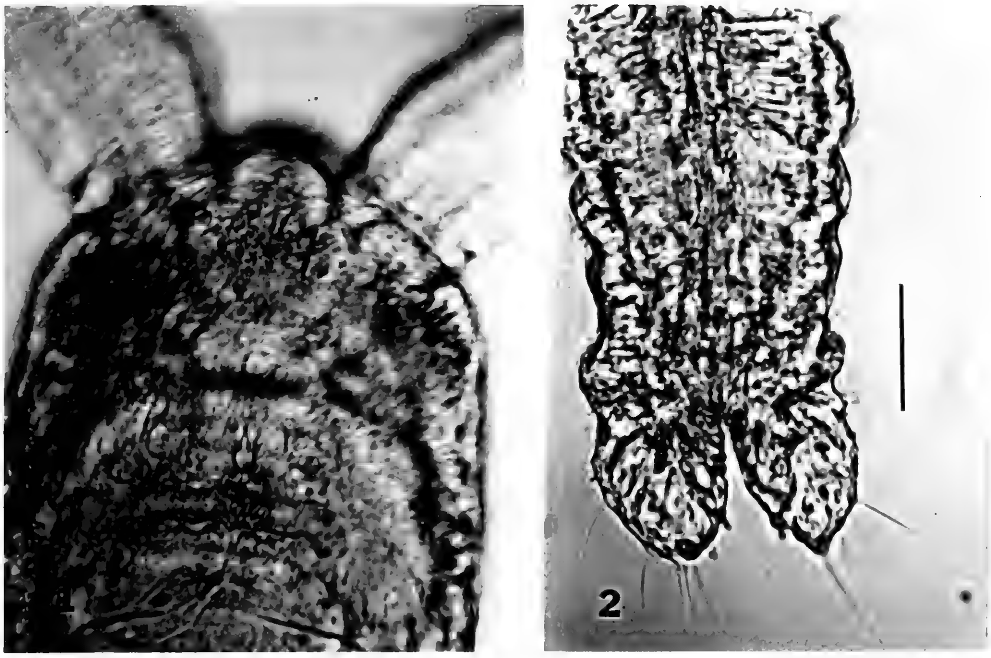
Abstract.—A new species of the interstitial meiofaunal polychaete genus *Protodrilus* (*P. gelderi*) is described from relatively stable, subtidal, shelly substrate that occurs in patches along the north shore of Massachusetts Bay, U.S.A. Males and females differ in total body length as well as in the distribution of salivary glands and gamete producing regions of the body. With the exception of the absence of segmentally arranged ciliated bands, males of the new species are morphologically quite similar to *P. ciliatus*. However, the females differ markedly from all previously described species in that the ovaries are present from the first segment to the posterior end of the body.

Interstitial meiofaunal polychaetes have commonly been encountered in coarse shelly substrate collected by divers at shallow depths in Massachusetts Bay. *Polygordius appendiculatus* Fraipont, 1887, *P. lacteus* (Schneider, 1868), and *P. triestinus* Hempelmann, 1906 are routinely present in large numbers in such substrate at depths of 3–30 m. In some of these samples from Nahant Bay and Broad Sound at depths of 6–20 m, a previously undescribed species belonging to the genus *Protodrilus*, usually numbering in excess of 50 per 8 ounce (volume) plastic bag of substrate, has also been present. Other species of *Protodrilus* have been encountered during intertidal meiofaunal studies along the shores of the Gulf of Maine, but this species appears to be strictly subtidal. Ruebush (1939) reported *Protodrilus leuckarti* Hatschek, 1880 from specimens collected intertidally by Dr. Donald Zinn at Branford, Connecticut, USA. No further details were presented in the paper; however, Jouin (1970) stated that it was more likely that the specimens were *P. ciliatus* Jägersten, 1952 and this unconfirmed report remains the only record of a species of the genus in New England. The following description of the new species from the subtidal is derived primarily from living specimens.

Materials and Methods

Substrate was collected by Scuba divers using garden trowels or large *Modiolus* shells for scooping into plastic bags. The bagged samples were maintained in the laboratory on a running seawater table to prevent temperature shock prior to sorting. The sediment was extracted with 7.5% $MgCl_2$, and decanted onto 153 μm screens from which the animals were washed into shallow dishes containing fresh sea water. More than 200 living individuals have been examined since the species was first encountered in 1976 in an effort to determine distribution of nephridia and location of sperm ducts. Weather conditions have prevented collecting between February and April. Stabilization of substrate following winter storms has necessitated an annual search to relocate areas occupied by animals of interest. The new species has only been obtained between June and January during which time, small and sexually immature specimens have been uncommon.

Anesthetized specimens were fixed in Hollande's cupri-picri-formal-acetic and



Figs. 1, 2. *Protodrilus gelderi*, living specimens. 1. Dorsal view of anterior prostomial region. 2. Caudal lobes, scale =0.08 mm.

whole mounts were stained with Mayer's alcoholic HCl carmine, in some instances counterstained with indigo-carmine. Suitable fixed individuals were selected for sectioning following embedding in Steedman's polyester wax. Mounted sections were treated and subsequently stained with Heidenhain's Azan or Alcian blue buffered to pH 2.5 (Humason 1967).

Family Protodrilidae Czerniavsky, 1881
Protodrilus gelderi, new species
Figs. 1–8

Type specimens.—Zoologisches Museum der Universität Hamburg: holotype female P-23532 and allotype male P-23533, whole mounts on one slide. Muséum National d'Histoire Naturelle de Paris: paratype male UE 622, female UE 623. American Museum of Natural History: paratype male AMNH 4194, female AMNH 4193. U. S. National Museum of Natural History: paratype male USNM 175429, Female USNM 175428.

Type locality.—Coarse shelly sand, off north side of Egg Rock, 20 m depth. Nahant Bay, MA., 42°26′N; 70°54′W.

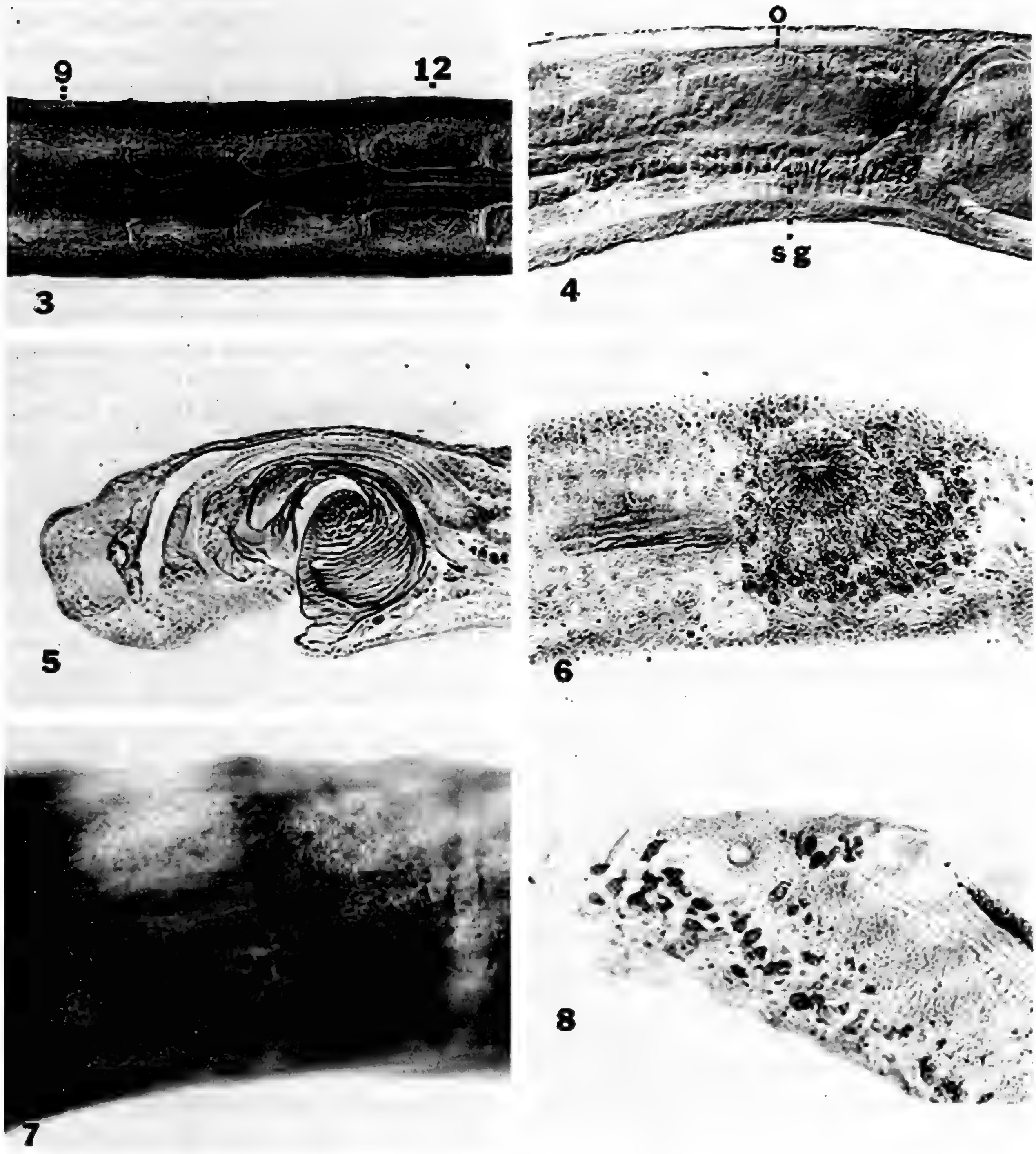
Description.—Body slightly transparent; red coloration associated with buccal mass; gut green to brown. Up to 44 segments in mature individuals, females to 9 mm in length and males to 7 mm. Head broader than following region of body; midbody slightly broader than head, tapering to posterior end. Caudal lobes broad, fan-shaped, with four or more large stereocilia (Fig. 2) projecting from posterior margin. Prostomium bluntly rounded with four stereocilia around apex. Tentacles up to 1.2 mm long, extending back to segment 6. Ocelli absent. Pair of anterior sensory organs ("statocysts") ~16 μm diameter to either side of prostomial apex. Nuchal organs large, slit-like, and lateral, at bases of tentacles. A single very long stereocilium about half head diameter, on dorsal surface immediately behind top of each nuchal organ. Small, ciliary patches present on head and body, ciliary annulations absent. A stereocilium is present laterally near the anterior and posterior end of each segment, and one is sometimes present in the middle of the lateral margin. Curved (gourd shaped) bacillary gland cells ~30 μm long and 7 μm maximum diameter, in thick double row across head behind nuchal organs, scattered in epidermis of anterior body segments becoming more abundant posteriorly, concentrated along sides of ventral ciliated furrow. Pygidial stylus not evident. Salivary glands extend into segment 12 in most males, to 19 maximum; at least into segment 15 and up to 30 in females. Ovaries occur from segment 1 or 2 into penultimate or antepenultimate segment. Oviducts and dorsal organs absent. Testes from segment 11 to antepenultimate segment. Male lateral organ in segment 7, large, round, surrounded by gland cells, followed by a continuous ciliated furrow from segment 8 to 17–18; spermducts in 12 through 15.

Etymology.—The species is dedicated to Dr. Stuart R. Gelder who as a predoctoral student carried out part of his dissertation investigations at our laboratory and introduced me to histochemical procedures which could be applied to the study of interstitial polychaetes.

Observations.—Total length and number of segments of mature animals are variable features frequently attributable to posterior regeneration. The anterior sensory organs contain an amorphous body and are not readily visible. In sections, these bodies appear as a gel, but in whole mounts are divided into two or three parts. The large, lateral, slit-like nuchal organs are the only obvious area on the head bearing motile cilia, as the cilia tufts on the head are insignificant. SEM indicates that the stereocilia on each body segment are arranged in three interrupted rings. A row of pigment cells extends across the prostomium (Fig. 1) immediately behind the nuchal organs. The bacilliary gland cells stain strongly with Alcian blue pH 2.5, and are cyanophilous with Azan. In sections, it can be seen that the cell bodies displace the other epidermal cells and bulge beneath them, so that the epidermis could be described as pseudostratified. They can be distinguished by their rods from other mucous cells which also expand beneath the surficial epidermal cells. Mucous cells are abundant in and along the sulcus between segments, and are dominant (Figs. 6, 8) outside the layer of serous cells which discharge into the lateral organ in segment 7 of the males. These serous cells are also subepidermal with long necks which pass between the ciliated support cells of the organ (Fig. 6). Parenchyme cells fill the area, laterally, between the epidermis and longitudinal muscles. However, the cells are absent near the middorsal and midventral lines of the body. There are usually nine diagonal muscle bundles on either side in each segment of mature individuals. Salensky (1907) stated "ungefähr 6–7" in the *Protodrilus* species which he investigated, noting that the number was much smaller than in the genus *Polygordius*. The arrangement of these muscles in sectioned material is similar to the diagram by Pierantoni (1908: pl. 2, fig. 2). Relaxation of these muscles allows a flattening of the body, and expansion of the ventral ciliated creeping groove.

The strong retractor muscles of the buccal mass usually contract following fixation, so that the esophagus is arched as it passes over the mass (Fig. 5) to open at the anterior margin of the mouth. As a result, the initial group of salivary glands are drawn forward along the sides of the arch. In living individuals, the base of the esophagus is a straight tube extending back from the arched portion. The epithelium of the esophagus is initially composed of tall, thin, simple columnar cells with long cilia (Fig. 5). The longest region is formed by cuboidal cells with relatively large roundish nuclei, and the cilia are spread apart. This is possibly an artifact resulting from the stretching of this region, although there is no intergradation (Fig. 5) with the cells of the anterior or posterior regions. The posterior straight part of the esophagus is lined with very tall ciliated columnar cells which are closely packed together.

Variation in the number of segments containing salivary glands may be the result of posterior regeneration and is most noticeable in females. The number of salivary gland cells is reduced, often to one or two,



Figs. 3–8. *Protodrilus gelderi*, segments 9–13 of male; dorsal view, whole mount, Mayer's carmine with indigo carmine counterstain. 4. Anterior segments behind buccal mass of holotype female; ovaries (o) of right side in focus, sg = salivary glands, Mayer's carmine. 5. Longitudinal section through esophageal region; Azan stain. 6. Slightly oblique section through aperture of male organ in segment 7; Azan stain. 7. Male organ in segment 7 with longitudinal trough extending posteriorly from it; whole mount, Mayer's carmine with indigo carmine counterstain. 8. Oblique section through aperture of male organ. Alcian blue pH 2.5 stain.

along each side of the midgut of the last few segments in which they occur.

The pair of testes in segment 11 (Fig. 3) have rarely contained spermiogenetic stages. The male lateral organ in segment 7 is large and obvious as is the ciliated furrow which begins immediately behind it (Fig. 7). The sulcus between segments 7 and 8 is densely ciliated with closely packed mucous cells. Only euspermatozoa have been observed.

The first pair of ovaries in preserved

specimens, frequently project forward against the buccal cavity as the result of the retraction of the buccal mass drawing the esophagus and initial salivary glands up over it. The first two pairs of ovaries are smaller than subsequent ones and contain fewer oocytes. They are often difficult to observe in cleared, preserved specimens and whole mounts (Fig. 4). Oocytes are small, attaining a diameter of ~25 μm with large germinal vesicles. There are slightly over 50 oocytes in each mature pair of ovaries. Maturation of ovaries is sequential with the smaller, less mature ovaries anterior and posterior to the mid-body region.

The only ciliary action observed in the body cavity has come from a large pair of metanephridia in segment 8 of both sexes. The metanephridia are located on each side in this segment, and they appear to be the only excretory organs in the body.

Protodrilus gelderi either attaches to the substrate with its caudal lobes or swims upward with a violent wriggling motion when disturbed, an escape strategy that was reported in the description of *Protodrilus albicans* Jouin, 1970. Specimens maintained in the laboratory are most frequently encountered on the sides of the bowls or gliding on the surface film. Individuals live for several weeks in finger bowls of clean sea water at approximately ambient sea temperature, but a satisfactory food source has not been discovered to maintain them. Loss of the red pigment around the buccal mass occurs in a few days after isolation.

Discussion

The histology and organology of the genus *Protodrilus* were extensively described by Pierantoni (1906) and Salensky (1907). Differences between species are not apparent at those levels except for the distribution of cell types in the epidermis. However, such variations may be attributable to different environmental conditions or a technic artifact. Gross anatomy of sexually mature individuals shows variation which allows for the identification of living worms, and often from stained whole mounts of well anesthetized individuals. The secondary sexual characters of males have been the most frequently used features to distinguish species. Females tend to be conservative in the degree of variation except for oocyte number and size, and the occurrence of cocoon glands.

The four stereocilia around the apex of the prostomium appear to be a basic character of the genus, and thus, plesiomorphic. Purschke (1990a, 1990b) examined the so called "statocysts" located near the apex of the prostomium of a number of species of *Protodrilus*. He concluded that they were not statocysts and based upon TEM observations were more likely involved in photoreception. Purschke (1990b) referred to them as anterior sensory organs to distinguish them from the phaosome-like posterior receptors of *Protodrilus adherens* Jägersten, 1952. They differ from pigmented ocelli, and he postulated that they constituted an autapomorphy for the genus. The opacity of the preoral region of the prostomium of living *P. gelderi* makes it very difficult to observe them with transmitted light, in spite of their size. The contents of the organelle, which appear as a partitioned gel in histological preparations, apparently are the paracrystalline bodies described from TEM observations by Purschke (1990b).

Protodrilus gelderi differs from other members of the genus in the presence of ovaries along almost the entire length of the female mid-gut. No species has been described previously in which ovaries are present anterior to the segment 7, or with salivary glands in females posterior to segment 20. Pierantoni (1906, 1908) noted that Uljanin (1877) and Hatschek (1880) had identified the salivary glands as ovaries, and they had concluded that the species of *Protodrilus* which they had described were hermaphroditic based upon the subsequent posterior occurrence of testes in the same specimens.

Males are morphologically similar to those of *P. ciliatus*, differing primarily in the absence of ciliary annulations. Among species lacking such annulations, they are similar to *Protodrilus submersus* von Nordheim, 1989 and *P. albicans*, in both of which, however, salivary glands are absent from the fertile region. Bacillary glands are densely packed in the dorsal epidermis, and nephridia are readily apparent in all segments of living *P. submersus* (pers. obs.) in contrast to the situation in *P. gelderi*. *Protodrilus albicans* is described as much larger than *P. gelderi* and is figured with oval, dorsal nuchal organs. Jouin (1970) did not mention pigmentation of the buccal mass for *P. albicans*, although she recorded it's presence for other species described in the same paper. The implication was that the mass was not pigmented.

Acknowledgments

Intertidal interstitial faunal investigations over the past thirty-five years have been extended into the subtidal by the cooperation of many students who, while diving to do their thesis research, carried plastic bags to obtain "any coarse sand" they might encounter. Their willingness to help is sincerely appreciated. This paper represents Contribution No. 224 from the Marine Science Center of Northeastern University.

Literature Cited

Hatschek, B. 1880. *Protodrilus leuckarti*, eine neue Gattung der Archianneliden.—Arbeiten aus den Zoologischen Instituten der Universität Wien 3: 79–92.

Humason, G. L. 1967. Animal tissue techniques. 2nd ed. Freeman, San Francisco, 569 pp.

Jouin, C. 1970. Recherches sur les Protodrilidae (Archiannélides). l.–Etude morphologique et systématique du genre *Protodrilus*.—Cahiers de Biologie Marine 11:367–434.

Nordheim, H. von 1989. Six new species of *Protodrilus* (Annelida, Polychaeta) from Europe and New Zealand, with a concise presentation of the genus.—Zoologica Scripta 18:245–268.

Pierantoni, U. 1906. Organi genitali e glandole salivari nei Protodrili.—Bollettino della Societá dei Naturalisti in Napoli 20:154–157.

———. 1908. *Protodrilus*.—Fauna und Flora des Golfes von Neapel 31:1–226.

Purschke, G. 1990a. Fine structure of the so-called statocysts in *Protodrilus adhaerens* (Protodrilidae, Polychaeta).—Zoologischer Anzeiger 224: 286–296.

———. 1990b. Ultrastructure of the "statocysts" in *Protodrilus* species (Polychaeta): Reconstruction of the cellular arganization with morphometric data from receptor cells.—Zoomorphology 110:91–104.

Ruebush, T. K. 1939. The occurrence of two rare genera *Protohydra* and *Protodrilus*, on the east coast of North America.—Science 90:617–618.

Salensky, W. 1907. Morphogenetische Studien an Würmern. II. Über die Anatomie der Archianneliden nebst Bemerkungen über den Bau einiger Organe des *Saccocirrus papillocercus*.—Mémoires de l'Académie Impériale des Sciences de Saint-Pétersbourg. s.8. Classe Physico-Mathématique 19:103–451.

Uljanin, W. N. 1877. Observations on the genus *Polygordius* of the Bay of Sebastopol.—Bulletin de la Société des Naturalistes de Moscou 52: 53–96. (in Russian)

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Synonymy of *Platicrista cheleusis* (Tardigrada: Eutardigrada: Hypsibiidae)

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Abstract.—The eutardigrades *Platicrista cheleusis* Kathman 1990 and *Diphascon craigi* Beasley 1990 are declared to be synonymous based on examination of the specimens from both authors.

Pilato (1987) revised the genus *Diphascon* Plate, 1889 and subdivided it into four genera: *Hebesuncus*, *Diphascon*, *Mesocrista*, and *Platicrista*. Characteristics of the bucco-pharyngeal apparatus were used to establish these new genera, as there tends to be little variability in these apparati within genera. *Diphascon* is separated from *Platicrista* by the following characters: in *Diphascon* the apophyses for the insertion of the stylet muscles are shaped like semilunar hooks, the furcae have thickened processes at the apices, the pharyngeal tube is longer than the buccal tube, and the stylet supports are inserted between half and three-quarters of the buccal tube length; in *Platicrista* the apophyses are in the shape of wide and flat ridges, the furcae are arch-shaped and taper at their apices, the pharyngeal tube is as long as or slightly shorter than the buccal tube, and the stylet supports are inserted at the end of the buccal tube.

Although the four genera established by Pilato (1987) are accepted today, confusion surrounding the descriptions and placement of species within these genera led some authors to continue to use only the name *Diphascon* of Plate, 1889, for several years. In 1990, Beasley described a new species of tardigrade from Colorado, USA, as *Diphascon craigi*. In that same year, Kathman described *Platicrista cheleusis* from British Columbia Canada.

The two descriptions of the holotypes, both deposited in the U.S. National Museum (USNM 234018 and USNM 234019), are very close, although there are some differences. The specimens from British Columbia did not have eyes, whereas those from Colorado did, although they are no longer apparent in the preserved material. The presence of eyes appears to be a variable trait, with eyes apparent during certain times of the year in the same species from the same location (pers. obs., senior author; pers. comm., D. R. Nelson, East Tennessee State University, Johnson City, Tennessee). The reason for such variability has not been investigated. Kathman (1990) states that there are "two cuticular bars on first three pairs of legs, one beside the external claw and the other at the base between the internal and external claws". Her drawing, however, indicates that the first of these bars is beside the internal claw, which is the correct position. In describing the two macroplacoids, Beasley (1990) states "first (4.8 μ) shorter than the second (22.3 μ)". His drawing suggests that the first length is probably erroneous; rather, the first is slightly more than twice as long as the second, based on the description of the paratypes, as well as new measurements of specimens from both collections. The other differences in measurements of various characters of the holotypes are most likely a result of the differences in size of the two animals (688 μm versus 530 μm length). Although Beasley found all six specimens from Colorado above 2900 m, Kathman found her 14 specimens from 150–1540 m.

Examination of specimens from both collections reveals the same cuticular patterning, although the decrease in size of the polygons in the cuticle from the anterior to posterior end is more noticeable in the specimens from British Columbia. In some specimens it is difficult to detect any change in size posteriorad. The sclerotized bar under the claws of the fourth pair of legs is variable among specimens, sometimes small and occurring between the two claws (as described by Kathman) and sometimes extending under the internal claw and reaching the middle of the bottom of the external claw. Perhaps this variability is a result of the stage of development of the tardigrade.

Beasley and Kathman have determined that the two species are synonymous. According to the rules of priority of the International Code of Zoological Nomenclature, the correct name is that of Kathman (1990), which appeared in publication several weeks prior to that of Beasley (1990).

It is interesting to note differences that appear to be due to the preservation techniques. The two sets of specimens were prepared and mounted in two different media—the ones from British Columbia were removed directly from water and placed in Hoyer's medium, while those from Colorado were fixed in Cuénot's fixative, dehydrated in glycerin and mounted in Faure's liquid. Several years later, the reticulated cuticle is barely visible in Hoyer's, while it is fairly distinct in Faure's. However, the eyes are no longer visible in the Colorado specimens. The sclerotized parts, such as the furcae, stylets and other mouthparts have been better preserved in Hoyer's.

Literature Cited

Beasley, C. W. 1990. Tardigrada from Gunnison Co., Colorado, with the description of a new species of *Diphascon*.—The Southwestern Naturalist 35:302–304.

Kathman, R. D. 1990. Eutardigrada from Vancouver Island, British Columbia, Canada, including a description of *Platicrista cheleusis* n. sp.—Canadian Journal of Zoology 68:1880–1895.

Pilato, G. 1987. Revision of the genus *Diphascon* Plate, 1889, with remarks on the subfamily Itaquasconinae (Eutardigrada, Hypsibiidae). Pp. 337–357 *in* R. Bertolani, ed., Biology of tardigrades.—Selected Symposia and Monographs 1:1–380. Unione Zoologica Italiana, Mucchi Editore, Modena.

Plate, L. 1889. Beitrage zur Naturgeschichte der Tardigraden.—Zoologische Jahrbücher Abteilung für Anatomie der Tiere 3:487–550.

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The cladoceran collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

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Abstract.—The cladoceran collection at the Smithsonian Institution National Museum of Natural History is both extensive and diverse. Wet materials (alcohol- and formalin-preserved) comprise over 18,000 littoral and limnetic zooplankton samples and approximately 300 lots of sorted, identified specimens. There are over 20,000 slides, the majority with specimens identified to species and in excellent, useable condition; about three quarters are grouped by taxon, the remainder according to country or specific location. Anomopod taxa (Chydoridae, *Daphnia*, and *Bosmina*) predominate in materials donated by D. G. Frey, R. W. Kiser, and E. S. and G. B. Deevey, respectively, but the collection includes representatives of the Onychopoda, Haplopoda, and Ctenopoda as well. The collection is world-wide in scope. Geographically, coastal regions of North America are particularly well represented; there is considerable material from Central and South America, Denmark, South Africa, and Australia. There are presently types of 52 species comprising about one hundred specimens, half on slides and half in alcohol. The comprehensive library given by D. G. Frey facilitates study of cladocerans at the museum.

Following receipt of gifts of sizeable collections of cladoceran specimens and samples to the National Museum of Natural History (NMNH) by R. W. Kiser and D. G. Frey, the cladoceran collection at the Natural History Building in Washington, District of Columbia, was moved to the Museum Support Center (MSC) in Suitland, Maryland. At the MSC, fluid-preserved ("wet") specimens and samples are housed in a controlled-environment storage pod, and slides, books, and papers are housed in a nearby room, the David G. Frey Cladoceran Library.

The NMNH cladoceran collection comprises one of the finest assemblages of cladoceran materials in the world. The British Museum (Natural History) holds more types and perhaps greater diversity in species and sorted specimens. The Canadian Museum of Nature (Ottawa) has a large collection of littoral samples, primarily from Canadian waters. However, the USNM cladoceran-containing, unsorted zooplankton collection is unparalleled, both in number and geographic range of samples. The cladoceran holdings of other North American museums are meager in comparison.

Categories of Material Comprising the Cladoceran Collection

The cladoceran materials held by the NMNH are curated by the Department of Invertebrate Zoology. They can be accessed in several ways. A six digit NMNH accession number is assigned all items donated by an individual or otherwise acquired at one time; items given at different times by the same individual will bear different NMNH accession numbers. NMNH catalogue numbers are given to individual lots of materials such as slides, bottles, etc. when they are catalogued by the Department of Invertebrate Zoology. Lastly, some items may be accessed by a number designated by a previous owner of the materials. A few older items in the collection lack accession and catalogue numbers (Berner 1995) and are not detailed below. All NMNH numbers reported here are accession numbers.

To facilitate description of the cladoceran collection, I group its diverse materials into two categories: sorted specimens identifiable by NMNH accession and catalogue numbers, and larger gifts of multiple items commonly recognized by the donor's name.

Specimens with NMNH Accession and Catalogue Numbers

Type material.—Approximately 100 type specimens, about half on slides and half in alcohol, representing 52 taxa. Many are species described by D. G. Frey from the Americas and elsewhere. Some of his paratypes, retained in his personal collection and included in his major gift (see below), have not yet been catalogued.

Wet material.—(In alcohol.) Approximately 90 vials of identified specimens, representing 40 genera, shelved by genus and species. Most are identified to species, some to genus only. There are catalogue cards for about 70 of them.

One hundred and five catalogued bottles of unidentified cladocerans. There are also at least 12 vials of unidentified cladocerans in one of E. B. Reed's gifts (NMNH 383116), located in the "Copepod holding area" at the NMNH. Reed's material, primarily from Colorado, may complement that in the Shantz and Dodds gifts (see below).

Slide material.—Approximately 365 catalogued slides, representing 50 genera. Many of these slides are of specimens collected in Brazil by H. Kleerekoper, whose samples are among those donated by R. Kiser (see below). These specimens were mounted, identified, and donated individually by Kiser and have accession and catalogue numbers different from the Kiser gift.

Data.—One set of catalogue cards for (mostly) identified specimens, either handwritten or computer-printed. Cards are arranged by genus and species; those for slides and wet specimens are interspersed. Types are identified by orange cards. The set does not include cards for catalogued bottles of unidentified cladoceran specimens, but does include cards for the vials of unidentified E. B. Reed cladocerans.

David G. Frey Gift, NMNH 403774

Because of the size and complexity of this gift, its components are evaluated separately below. The gift also included three discrete collections that Frey had acquired: the J. Richard collection and the E. A. Birge collection, which Frey obtained from the University of Wisconsin, Madison, and the E. S. and G. B. Deevey freshwater collection. Frey incorporated the Richard and Birge collections into his own, and they are considered as a subset of his gift. The Deevey freshwater materials are considered as a separate acquisition (see below).

The materials donated by Frey reflect his early training (under C. Juday) and life-long interest in limnology, his research on the paleoecology of lakes as revealed by cladoceran remains, and his world-wide studies on the speciation and distribution of chydorid cladocerans in relation to glaciation and continental drift. Frey and his colleagues sampled zooplankton extensively in the areas he studied: eastern North America, northern Europe, southern South America, South Africa, and Australia. Frey also collected indefatigably on his international travels, so most parts of the world are represented to some extent in his collection. Because they are primarily from the littoral zone, his zooplankton samples have a much higher diversity of microcrustaceans and other invertebrates than do limnetic samples. In addition to containing cladocerans, they potentially are a rich source of material for studies of copepods, ostracods, and other littoral organisms, and of the littoral biocoenosis. Enhancing the sample collection is Frey's meticulous documentation, by notes and mounted specimens, of the material he studied.

Wet material.—(3–4% formaldehyde solution with a few ml of glycerol added to prevent total drying if evaporation occurs. Some sorted specimens may be in alcohol.) Approximately 9260 bottles of samples and specimens housed in 49 boxes. Per Frey's accession books, 9193 samples have Frey's own F– – – numbers on the bottle tops; inside labels bear the same number, sample collection date and number, locality, and name of county, province, or country. Bottles comprising Richard and Birge samples are detailed below.

Two boxes marked "Types" contain bottles with identified specimens; they are not numbered or listed in Frey's accession ledgers. Twenty of the bottles are marked "Paratypes" and 47 have sorted, identified specimens. All have inner labels giving species name and collection data. They have not yet been catalogued by the NMNH and therefore have no identifying numbers.

Field data for the samples are scattered in 92 small notebooks, many labeled with year and place visited. In these, Frey detailed aspects of his trips as well as collection data; often, he later recorded his accession number for each sample in red ink next to its collection data and number.

Frey's samples are recorded (usually by batches in correspondence with dates of collection) in two "Collection Accession" ledgers that list Frey's sample number, locality, date, and collector's name. Samples, specimens, and some slides received from other collectors are similarly recorded. There is no index for finding samples from a particular locality.

Several thousand inventory cards, filed by Frey number, detail contents of samples Frey studied. Chydorid species are listed, other cladocerans are noted by genus, and there are notes on other Branchiopoda, algae, etc. Frey requested that anyone removing specimens from a sample note the species and number of specimens taken on the back of the corresponding card. If a visitor examined a sample Frey had not yet studied, he requested that the researcher make up an appropriate inventory card. These practices are being continued at the NMNH.

Slide material.—Several hundred slides of identified specimens (mostly chydorids), the large majority mounted in glycerine-jelly or polyvinyl-lactophenol with ringed coverslips, are arranged alphabetically by genus and species in a metal tray cabinet. They are in excellent condition, well-labeled, usually bearing the Frey number of the original sample.

Fourteen large and two small boxes contain Frey's working slides, also in excellent condition, of identified specimens and paratypes of particular taxa on which he published.

Twenty-four boxes house specimens, mostly identified, from diverse locales: Southhampton Islands; the Soviet Union (F 1421, a gift from N. N. Smirnov that includes three paratypes); Denmark; Holland; Africa; South America; U.S.A.; Canada; Maine-New Hampshire; Florida & southeastern U.S.A.; and Monroe County, Indiana, ponds. In addition, there are miscellaneous sets of slides in wooden boxes: two boxes of cladocerans from the S. Wright collection (35 slides of poor quality), five boxes from Nova Scotia by G. Doran, and six boxes of various origin and content.

Eleven large and 19 small boxes have slides of lake sediments and cores, representing paleolimnological and taxonomical studies by Frey and his students.

There is no inventory of Frey's slides.

Library.—The library reflects Frey's emphasis on chydorid cladocerans. While strong in all the early cladoceran literature, it lacks many recent papers on non-chydorid cladoceran taxonomy as well as some important contemporary guides with keys. It is usefully organized:

Eleven shelves of bound books, offprints, and photocopies (about 2500 items) of publications relevant to cladoceran taxonomy, evolution, and ecology. These are numbered and entered into Frey's "Accession Book for Literature" and are arranged on the shelves alphabetically by author.

Two shelves of theses and dissertations relevant to limnology and cladoceran taxonomy.

Three shelves of books on limnology, paleontology, and taxonomy, most of which have relevance to cladoceran systematics. These do not have Frey accession numbers and are loosely arranged by topic and author.

Numerous unbound offprints of papers not directly related to chydorid systematics; these are housed by author in a small, multidrawer file cabinet.

There are both a literature accession ledger and an index card file of literature.

Papers.—Papers filling several file cabinets were received with the Frey gift, products of his lifetime of research, teaching, and professional activities. Materials pertaining to cladoceran systematics presently kept in the Frey Cladoceran Library are:

Research data for specific ecological, paleolimnological, paleotaxonomic, and taxonomic studies. Generally, a single folder contains all the material related to a single publication: data (counts, measurements, species lists, etc.) from samples that Frey studied, manuscript drafts, and sometimes related correspondence.

Research and correspondence on historic, systematic publications, e.g., publication of the fascimile of Lilljeborg's Cladocera Sueciae and of Sars' unpublished 1861 manuscript.

Negatives and prints of scanning electron micrographs associated with the above research and publications.

Plates, maps, and miscellaneous drawings associated with research publications.

A set of computer punch cards with data on Frey's collections. The key to these cards (which are on a shelf of the library) appears to be a large posterboard diagram lying in a map drawer.

Frey's correspondence with other professionals. Many of these are cladocerologists and some letters contain taxonomic information.

The J. Richard and E. A. Birge Materials (Gift of D. G. Frey)

The impact of E. A. Birge's early taxonomic studies of North American cladocerans, and the roles he and his associate, C. Juday, played in the development of American limnology are well-documented (Frey 1963, Beckel 1987). Birge was in communication with the French taxonomist, J. Richard, who had studied material collected from foreign countries in the late 1800's by numerous persons. When Richard retired, Birge purchased his collection of samples and slides. D. G. Frey acquired that collection as well as samples, slides, and miscellaneous papers and notebooks belonging to Birge and Juday from the Museum of Zoology (formerly, the Wisconsin Geological and Natural History Survey) at Madison, Wisconsin. Some of the samples in the Birge collection apparently were collected in South America by Harriet B. Merrill, an assistant to Birge (Hartridge 1995), and had been thought lost (Reid 1991). Frey incorporated the Richard and Birge samples into his wet collection, but kept the slides separate. During this survey, papers and notebooks relevant to these materials were found scattered among Frey's papers and were assembled together in marked file cabinet drawers.

Richard and Birge described numerous new cladoceran species. The former did not designate or set aside types and although the latter indicated that types would be deposited for some of the species he described (Birge 1910), they are not to be found in the museum at Madison, Wisconsin (F. Iwen, pers. comm.). Therefore, these materials are of great importance. For instance, during this review the slides from which Birge made the drawings for his description of *Wlassicsia kinistiensis* were found, but none was designated as a type. Also located was a slide of *Ceriodaphnia acanthina*

Ross, 1896 from the type locality and date; as no type exists for this species, Birge's slide might be significant. Furthermore, it is possible that specimens from type localities are in certain of the Richard and Birge samples.

Because of the significance of the Richard and Birge materials to cladoceran taxonomy, they warrant further careful study and documentation.

Wet material.—(In formalin.) According to Frey's accession book, samples from the Richard collection are: F 701–1041 (from Africa, Sumatra, South America & Haiti, the Soviet Union, China, and France).

Samples belonging to the Birge collection are: F 607–676 (from Wisconsin, South and Central America); 1042–1232 (1902–1903, from South America); 1095–1232, 1277–1282, and 1284 (1900–1929, from Wisconsin).

Slides.—Six metal, tabletop file cabinets, with 25 trays per cabinet, not all full of slides. Four cabinets are labeled A–D (perhaps by Frey) and have labeled trays; the remaining two were labeled E and F for this review. No inventory of the slides was found.

Twenty trays, mostly in cabinets A and F, appear to be Richard's slides (as determined by the handwriting and French labels). The remaining slides apparently are Birge's. Their condition ranges from excellent (specimens remounted in polyvinyl lactophenol and relabeled in 1966–1967 by "J.V.B.") to useless: some slides lack coverslips and specimens or have uninformative labels.

Data.—A drawer of index cards, apparently made by Birge, with various data. A subset of the cards relates to the Richard samples.

Field notebooks from South American collections, apparently made by H. B. Merrill.

A bound volume of Birge's correspondence, assembled by the Museum at Madison. His purchase of the Richard collection is documented here.

Frey's analysis of H. B. Merrill's work, the cladocerans found in each of her samples, and correspondence related to a paper he wrote about it. That paper was not found; Frey apparently sent it to M. L. Hartridge, Merrill's niece (cf. Hartridge 1995).

A folder of photocopies, made by Frey, from Birge's (H. Merrill's?) notebooks and Merrill's letters to Birge. The originals apparently were deposited by Frey at the State Historical Society of Wisconsin, in accord with a request by M. L. Hartridge, Merrill's niece (M. L. H. pers. comm.).

These materials have been put together in drawers marked "Birge Collection".

Edward S. and Georgiana B. Deevey Gift

The Deeveys gave their marine collections directly to the NMNH but their freshwater materials to D. G. Frey, who kept them apart from his collection. Although received by the NMNH as part of the Frey gift, the Deevey freshwater materials are being treated as a separate acquisition.

A large amount of this material derives from limnetic plankton tows, and is related to the Deevey studies on *Bosmina* and *Eubosmina*. Florida, Central America, Australia, and New Zealand are particularly well represented. Deevey & Deevey (1971), available in the Frey library, is a valuable reference for locating many of the habitats represented in this material.

Wet material.—(In formalin.) Sixteen boxes, all marked "Deevey", containing glass and plastic vials and bottles of unsorted zooplankton that are mostly labeled only with a date and lake name. A few bottles contain sorted, identified specimens. Locales marked on the boxes are: Wisconsin & Michigan; Costa Rica, etc.; Spain; Denmark, Hungary, Poland, Ireland; Vietnam; Australia & Tasmania; Australia & New Caledonia; New Zealand; Venezuela & Brazil; Nova Scotia, Newfoundland, U.S.A./Canada; Florida (two boxes); Texas, Virginia, Kansas, Vermont, Maine, U.S.A; Unknown Countries.

Reference to samples containing marine and brackish water cladocerans is in the Deevey notebooks labeled Long Island Sound, Long Island 1950, and Tisbury Great Pond located in the Department of Invertebrate Zoology at the Natural History Building in Washington, District of Columbia.

Slides.—Eight boxes of slides, marked: Rodgers Lake & Queechy Lake, Connecticut (two boxes); Mexico-Guatemala; Mexico, Guatemala, Texas (contains some slides from New York, Ireland, Denmark); Guatemala; Linsley Pond (Connecticut), Mexico, Guatemala, Texas, (includes some slides from the Killarney Lakes, Ireland); New Zealand; Australia (also contains slides from Tasmania, Poland, and Brazil). Many of the slides are of *Bosmina*; some have mixed zooplankton. Their general condition was not assessed.

Data.—Five large, looseleaf notebooks, marked "Deevey" and: Florida Lakes; Rodgers & Queechy Lakes; New Zealand Lakes; New Zealand, Tasmania, Australia; Guatemala Lakes. They contain research data on measurements of *Bosmina* from diverse habitats, drawings, some information on copepods, and other miscellaneous information. No field notebooks with collection data were found.

Alfred A. Doolittle Gift, NMNH 157575

A. A. Doolittle, a teacher at Central High School in Washington, District of Columbia, studied cladocerans as an avocation, collecting them in the eastern United States and especially in and near Sebago Lake, Maine, where he summered. *Chydorus bicornutus*, a North American endemic that he described, later triggered D. G. Frey's studies on the "honeycombed" species of *Chydorus*. Doolittle's material is primarily from Sebago Lake, Maine, and Lake Cooper, Iowa. There are samples from other lakes in those areas, from various northeastern U.S.A. states, and a few from Mexico.

Wet material.—(In alcohol.) Twenty-four jars, labeled by state, containing vials of unsorted zooplankton samples. (One District of Columbia bottle has two vials of sorted specimens). Vials contain labels with sample dates only; jars contain labels with Doolittle's name and NMNH accession number.

Slides.—One box, mostly of identified cladocerans from lakes in Maine, mainly Sebago Lake. About two thirds appear to be in useable condition. The box is temporarily labeled "Doolittle Collection". There is no inventory of the slides, and they have not been catalogued.

Data.—Two boxes, one with notebooks and one with index cards. The notebooks contain data on collection sites and meteorological data on Lake Sebago. They are labeled: 1904 Memoranda, 1904 Connecticut Lakes, 1905 Umbagog Lake, 1906 Sebago Lake, 1907 Sebago Lake, 1908 Sebago Lake, 1911 Sebago Lake, 1914 Lake Cooper, 1916 Miscellaneous (this contains collection data through 1921), and Miscellaneous Notes on Freshwater Cladocera.

There are four categories of index cards, only the first two of which can be correlated to data in the collection books:

Locations of collections (presently grouped by state), some having lists of species found and a few with quantitative counts.

Species names, listing locations where they were found.

A small set of references on fish diet.

A miscellaneous set of cards with data concerning material from other collectors and localities.

Rufus W. Kiser Gift, NMNH 356548

R. F. Kiser was a professor at Centralia Junior College, Washington, whose particular interest was the taxonomy of *Daphnia*. He collected extensively throughout the Pacific Northwest, especially Washington and Oregon. His collection includes samples from Alaska to southern California made by Trevor Kincaid, a copepodologist at the

University of Washington. He also received South American material from Herman Kleerekoper, a Dutch limnologist who worked in Brazil for a number of years before moving to Canada (J. Reid, pers. comm.). D. G. Frey became interested in Kiser's collection and persuaded him to donate it to the NMNH (cf. the "Kiser" file among Frey's papers at the NMNH.)

Wet material.—(In alcohol.) Over 8000 vials of unsorted zooplankton samples, stored in about 135 1–2 liter bottles filled with alcohol. All vials contain Kiser's sample number. Most bottles have an interior list of the vials they contain; outside they are identified by Kiser's original bottle number.

Most of the samples arrived at the NMNH stained by Kiser with Fast Green or Acid Fuchsin, dehydrated and in xylene in preparation for mounting specimens on slides. Others, that had been loaned to D. G. Frey, were in formalin. The formalin and xylene were replaced with alcohol at the NMNH.

The bulk of the samples is from west coast states. There are a few samples from New Zealand, Mexico, Brazil (Kleerekoper's samples), British Columbia, and the north-central U.S.A. states. The majority of the samples above 2500 are from synoptic sampling of Oregon lakes, especially Fern Lake.

Slides.—One hundred, seventy-nine boxes of stained, balsam-mounted specimens. Most boxes are organized by genera; *Daphnia* predominate. Six boxes have specimens from specific areas (China, Brazil, South America, New Zealand, and Scotland), one box has slides with University of Michigan Zoological Laboratory labels, one has mixed zooplankton from Oregon, and one has copepods.

Most of the slides are well-labeled and nearly all bear the sample number from which the specimens came. They appear to be in excellent condition. Within the boxes, slides are not ordered by sample number or by species.

Data.—Kiser's typed index labeled "Plankton Collection of Rufus W. Kiser" giving sample number, location (including county and state or country), other pertinent data, and date.

Kiser's typed inventory of the vials contained in each bottle, stating if they were in xylene or formalin.

A typed NMNH list of the location of each sample by sample number and bottle number. This list was made by reference to Kiser's bottle inventory, and may be partially incorrect since some vials were misplaced.

Kiser's sample numbering system started with 100 (cf. his letter of reply to a query from Frey, in the Frey "Kiser" correspondence file). Some slides have numbers less than 100, or are marked ***A (with data not corresponding to Kiser's sample data). These specimens are from collectors other than Kiser, and there appear to be no supporting data for them.

Kiser apparently had 46 bound notebooks recording information on his samples, and an accession file of 3 × 5 in. cards. (See letter of D. G. Frey to R. B. Manning, 28 May, 1983, in Frey's correspondence.) These are not among the materials at the MSC and Kiser may have kept them.

There is no inventory of the slides in the Kiser collection.

S. F. Light Gift, NMNH 177850

S. F. Light was a copepodologist at the University of California, Berkeley, where Mildred S. Wilson was his assistant for a time (Damkaer 1988). This cladoceran material has been separated from his larger zooplankton collection. It has specimens primarily from the western states as well as some from other localities and collectors (e.g., Wisconsin, from C. Juday).

Wet material.—(In alcohol.) Five mason jars and one small bottle, filled with vials of cladoceran specimens sorted by genus and species. In 1983, these sorted cladoceran specimens were found on the shelves of the cladoceran collection but there was no record of them in the files. At that time some of the vials had dried out; they have since been rehydrated. They are not catalogued.

Data.—A list of collection stations and dates and one small box of file cards with SFL on the top; the cards bear sample numbers and a list of cladoceran species in each.

H. L. Shantz Gift

In 1903, H. B. Ward, of the University of Nebraska, investigated lakes in the Pikes Peak, Colorado, and Lake Tahoe, California, regions; E. A. Birge and C. D. Marsh contributed analyses of the cladocerans and copepods, respectively, in his collections (Ward 1904). H. L. Shantz, also of the University of Nebraska, did a limnological study of some of the same lakes in the Pikes Peak area under Ward's direction (Shantz 1907), but he did not analyze the cladocerans in his collections. G. S. Dodds (1924) later published a list of the cladocerans in Shantz's samples. Shantz's specimens were found in 1995 among Dodds' material at the NMNH. These materials are of historic interest because in 1906 several of the Pikes Peak lakes were converted into reservoirs (Shantz 1907) and in 1995 I found that another, the type locale for the rare cladoceran *Macrothrix montana* Birge, has recently been drained.

Wet material.—(In alcohol.) One large, unidentified jar with vials of unsorted zooplankton samples; labels inside vials give lake names and collection dates. Jar is now temporarily labeled.

Data.—None found. Shantz (1907) gives the lake locales and Dodds (1924) lists the cladocerans in the samples.

Gideon S. Dodds Gift, NMNH 061153

G. S. Dodds worked at the University of Colorado. This collection represents an altitudinal study of Branchiopoda in Colorado lakes (Dodds 1917). Comparable material may be in the Shantz Gift (see above) and in E. B. Reed's material (see below).

Wet material.—(In alcohol.) Three hundred and one small vials of sorted zooplankton specimens (cladocerans and copepods), each containing a sample number. From two to four vials, all from one locality, are stored together in small bottles, each bearing a catalogue number. Interior labels in the bottles list catalogue and sample numbers, approximate number of specimens, locality and county, date, and other pertinent data. Species names are listed on the reverse side of the interior labels.

This material is housed in one large jar full of vials and in six boxes holding about 30 bottles each, not in strict order according to catalogue number.

Data.—Dodds' list of sample number, location (lake name), date, and county and terrain (mountain or plains).

Other Sources of Cladoceran Materials

The following, while not included in the cladoceran collection, might contain material useful to cladoceran researchers:

The Albatross Expedition collection.—No NMNH accession number. This collection includes freshwater samples made across the United States. The computerized database can be consulted to locate appropriate material.

The M. S. Wilson gifts.—Several NMNH numbers. The catalogue list and materials on the "Copepod holding area" shelves at the Natural History Building in Washington, District of Columbia, should be consulted. Lots under NMNH 319629 might be most useful.

The E. B. Reed gifts.—Several NMNH numbers. The catalogue list and materials on the "Copepod holding area" shelves should be consulted. About 16 lots of unidentified cladocerans under NMNH 383116 have been catalogued. Reed's collections are primarily from Alaska, the Rocky Mountains, and plains lakes near Fort Collins, Colorado.

The C. D. Marsh gift.—NMNH 120079. There are containers marked "Entomostraca" on the "Copepod holding area" shelves that may contain cladocerans.

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Literature Cited

Berner, D. B. 1995. The cladoceran collection of the United States National Museum of Natural History (The Smithsonian Institution).—Unpublished report, 19 pp.

Beckel, A. L. 1987. Breaking new waters. A century of limnology at the University of Wisconsin.—Transactions of the Wisconsin Academy of Sciences, Arts, & Letters. Special issue, 122 pp.

Birge, E. A. 1910. Notes on Cladocera IV.—Transactions of the Wisconsin Academy of Sciences, Arts, & Letters 16:1017–1066.

Damkaer, D. M. 1988. Mildred Stratton Wilson, copepodologist (1909–1973).—Journal of Crustacean Biology 8:131–146.

Deevey, E. S., Jr., & G. B. Deevey. 1971. The American species of *Eubosmina* Seligo (Crustacea, Cladocera).—Limnology and Oceanography 16:201–218.

Dodds, G. S. 1917. Altitudinal distribution of Entomostraca in Colorado.—Proceedings of the United States National Museum 54:59–87.

———. 1924. Notes on Entomostraca from Colorado. The Shantz collections from the Pikes Peak region.—Proceedings of the United States National Museum 65:1–7.

Frey, D. G. 1963. Wisconsin: The Birge-Juday era. Pp. 3–54 *in* D. G. Frey, ed., Limnology in North America. The University of Wisconsin Press, Madison, 734 pp.

Hartridge, M. L. 1995. H. B. Merrill: early Wisconsin scientist and adventurer.—Wisconsin Academy Review 41:16–22.

Reid, J. W. 1991. The Stillman Wright collection of Copepoda (Crustacea) from South America in the National Museum of Natural History, Smithsonian Institution.—Proceedings of the Biological Society of Washington 104:736–741.

Shantz, H. L. 1907. A biological study of the lakes of the Pikes Peak region-preliminary report.—Transactions of the American Microscopical Society 27:75–98.

Ward, H. B. 1904. A biological reconnaissance of some elevated lakes in the Sierras and the Rockies.—Transactions of the American Microscopical Society 25:127–154.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(4):569–580. 1997.

Aglaodiaptomus atomicus, a new species (Crustacea: Copepoda: Calanoida: Diaptomidae) from freshwater wetland ponds in South Carolina, U.S.A., and a redescription of *A. saskatchewanensis* (Wilson 1958)

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Abstract.—A new calanoid copepod, *Aglaodiaptomus atomicus*, is described from freshwater wetland ponds in Aiken County, South Carolina, U.S.A. It is common in Aiken and Barnwell Counties. It has been collected from shallow, acidic wetland ponds, most of which dry periodically. *Aglaodiaptomus atomicus* resembles *A. saskatchewanensis*, which is redescribed from Saskatchewan, Canada, and Louisiana, U. S. A. The male of *A. atomicus* differs from all of its congeners by possessing a distinctively large distolateral process on the right leg 5, exopod 1. The female differs from its closest congener, *A. saskatchewanensis*, in possessing nearly symmetrical thoracic wings. In *A. saskatchewanensis*, the wings are distinctly asymmetrical.

A survey of freshwater wetland ponds on the upper coastal plain of western South Carolina revealed an apparently undescribed calanoid copepod species. This species, which was incorrectly reported as *Diaptomus conipedatus* Marsh, 1907 by Mahoney et al. (1990), is one of the most common calanoid copepod species occurring in Carolina bays and other isolated, shallow, wetland ponds in Aiken and Barnwell Counties, South Carolina. It most closely resembles *Aglaodiaptomus saskatchewanensis* Wilson, 1958. However, detailed comparisons with specimens of *A. saskatchewanensis* proved it to be a separate, undescribed species.

In her original description of *Aglaodiaptomus saskatchewanensis*, Wilson (1958) provided an illustration of only the male fifth leg and a partial description of the species. Few additional details were added to her 1959 key (Wilson 1959). A more detailed description of *A. saskatchewanensis* is presented here, as well as a description of the new species, *A. atomicus*.

Diaptomid copepods vary in the following morphological characteristics: body length, features of the thoracic somites (especially the 6th somite), length, number of and armature of the antennules in both sexes, number of somites of the female urosome, and segmentation, shape and ornamentation of the fifth leg of both sexes (Wilson 1959). The mouth parts and legs 1–4 of the species presented in this paper correspond to those of *Leptodiaptomus siciloides* (Comita & Tommerdahl 1960).

Descriptions and measurements of whole copepods were made in glycerine. Dissected specimens were mounted either in lactophenol or in CMC-9. Most were stained with Chlorazol Black E before being mounted.

Family Diaptomidae Baird 1850
Genus *Aglaodiaptomus* Light, 1939
Aglaodiaptomus saskatchewanensis (Wilson 1958)
Figs. 1–3

Diaptomus saskatchewanensis Wilson, 1958:490–491, 493–495, fig. 3.—*Diaptomus* (*Aglaodiaptomus*) *saskatchewanensis* Robertson, 1972:202.—*Aglaodiaptomus saskatchewanensis*, Chengalath & Shih, 1994:2422.

Material.—Saskatchewan: 8 ♂♂, 6 ♀♀; farm reservoir near Lucky Lake, Saskatchewan, Canada, 107°20'N, 50°10'W, 16 Jun 1948; USNM 210784; coll. J. R. Nursall. Louisiana: 33 ♂♂, 28 ♀♀; shallow roadside pond 19.4 km south of Natchitoches, Natchitoches Parish, Louisiana, U.S.A., 31°60'N, 93°05'W, 10 Apr 1953; USNM 278233; coll. W. G. Moore.

Female.—Length, excluding caudal setae, of specimens from Saskatchewan, range: 1.24–1.64 mm (*n* = 6), from Louisiana, range: 1.34–1.64 mm (*n* = 28). Body broadest at pedigers 1 and 2 in dorsal view (Fig. 1A). Pedigers 4 and 5 incompletely separated with faint sutures visible laterally. Pediger 5 small with posteriorly-directed wings (Fig. 1B). Left wing with large dorsomedial lobe (Fig. 1C) reaching beyond posterior margin of wing in dorsal view (Fig. 1B). Right wing has 2 poorly-developed lobes (Fig. 1D). Each lobe on both wings tipped with short sensillum. Urosome of 3 segments (Fig. 1B). Genital segment with slight asymmetrical lateral protrusions; left protrusion more rounded than right. Both protrusions tipped with sensillum. Caudal rami (Fig. 1B) nearly twice as long as broad; inner margins hairy.

Antennules 25-segmented, extending to middle of caudal setae (Fig. 1A). Appendages per segment as follows (Roman numeral = segment, Arabic numeral = number of setae, sp = spine, a = aesthetasc): I(1+a), II(3+a), III(1+a), IV(1), V(1+a), VI(1), VII(1+a), VIII(1+sp), IX(2+a), X(1), XI(2), XII(1+sp+a), XIII(1), XIV(1+a), XV(1), XVI(1+a), XVII(1), XVIII(1), XIX(1+a), XX(1), XXI(1), XXII(2), XXIII(2), XXIV(2), XXV(5+a). Setae on segments 17, 19, 20, 22 with hooked ends (Fig. 1E); length of seta approximately ¾ that of respective segment.

Leg 2 endopod 2 with Schmeil's organ (not figured).

Leg 5 (Fig. 1F): Coxa with posterior lateral protrusion ending in sensillum. Basis with short lateral seta. Exopod segments 1 and 2 approximately equal in length. Claw of exopod 2 slightly curved with denticles on inner and outer margins. Exopod 3 not articulated. Lateral spine of exopod 2 about ¾ the length of outer seta of exopod 3. Exopod 3 inner seta plumose, twice the length of outer seta. Endopod single-segmented, equal in length to exopod 1, two plumose setae and pointed protrusion at tip (Fig. 1G).

Male.—Length, excluding caudal setae, of specimens from Saskatchewan, range: 1.24-1.44 mm (*n* = 8), of specimens from Louisiana, range: 1.28-1.64 mm (*n* = 33). Body (Fig. 2A) as in female, with 5-segmented urosome. Thoracic wings (Fig. 2B) asymmetrical, right wing developed into elongated lobe, left wing small. Each wing with 2 sensilla; sensilla of right wing twice as large as left. Urosome (Fig. 2B): segment 1 asymmetrical in dorsal view, left margin shorter than right; left posterior corner bifid with obliquely directed lobe tipped with sensillum, right posterior corner simple, also tipped with sensillum. Segments 2–4 approximately equal in size; ventral sensilla on segments 2 and 3 visible under high magnification (not figured). Segment 4 asymmetrical, left margin shorter than right. Caudal rami with hairs on inner margins.

Antennules (Fig. 2A, C–E) extend to proximal margin of caudal rami. Right antennule geniculate between segments 18–19 and 20–21. Segments 18–19 (Fig. 2D), 20–21 (not figured) and 22–23 (Fig. 2E) fused. Large parallel spiniform processes on segments 10, 11; additional large spine on segment 13 (Fig. 2C). Spines on segments 10

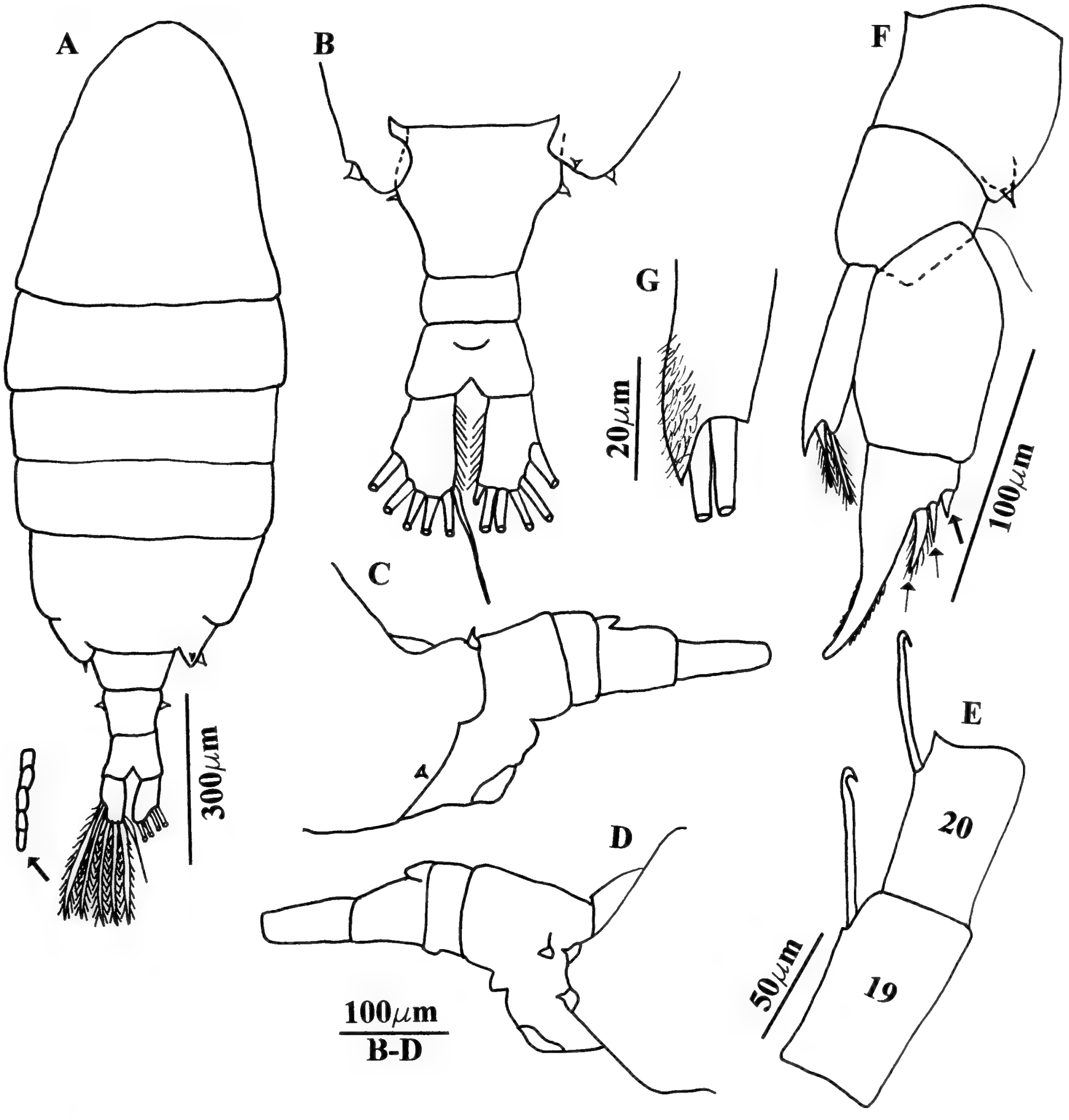

Fig. 1. *Aglaodiaptomus saskatchewanensis* Wilson, 1958. Paratype female (USNM 278233): A, Habitus, dorsal, distal segments of antennule indicated by arrow; B, Urosome, dorsal; C, Left thoracic wing and urosome, lateral; D, Right thoracic wing and urosome, lateral; E, Antennule, segments 19, 20; F, Leg 5, anterior, setae of exopod 3 (thin arrows), lateral seta of exopod 2 (thick arrow); G, Leg 5 endopod, distal end.

and 11 equal in length, shorter than spine on segment 13. Spines on segments 15–17 with bifurcated tip (Figs. 2C, D). Segment 17 (Fig. 2D) with flat, digitiform seta extending to center of segment 18–19. Additional modified seta arising from proximal ¼ of segment 18–19, running length of segment. Segment 22–23 (Fig. 2E) with curved distal process; process about as long as segment 24.

Left leg 5 (Figs. 3A–E): Leg (excluding spines) extending slightly beyond right basis. Coxa, small process tipped with sensillum near outer posterodistal margin. Basis with short lateral seta. Exopod segment 1 longer than segment 2; inner margin with pad; distal corner of pad hairy (Fig. 3B). Exopod 2 articulating at distolateral margin of exopod 1. Inner margin of exopod 2 with hairs extending the length of the segment

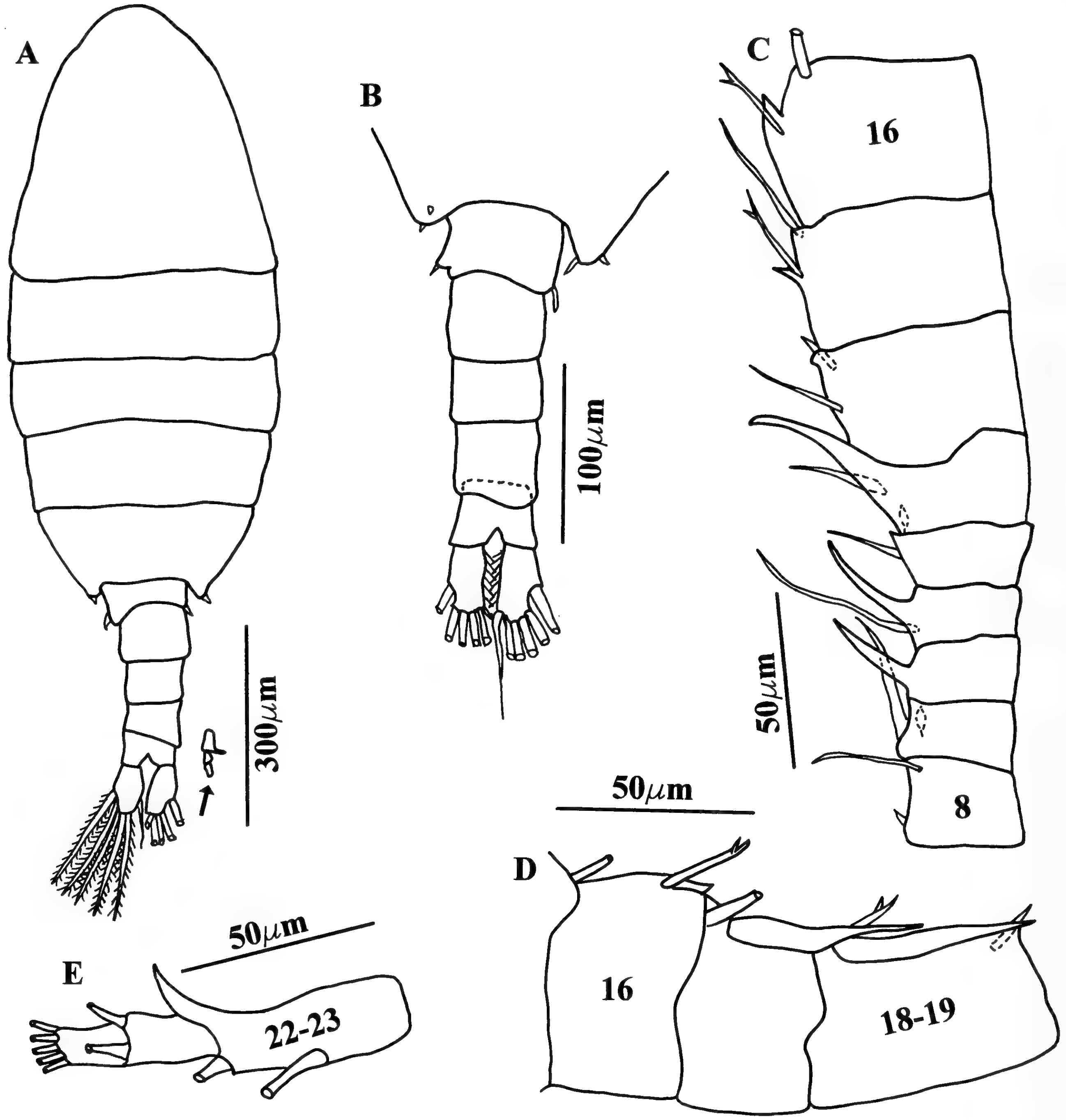

Fig. 2. *Aglaodiaptomus saskatchewanensis* Wilson, 1958. Paratype male (USNM 278233): A, Habitus, dorsal, distal segments of antennule indicated by arrow; B, Urosome, dorsal; C, Right antennule, segments 8–16; D, Right antennule, segments 16–19; E, Right antennule, segments 23–25.

(Fig. 3B); hairs extend to cover ⅓ of anterior surface (Fig. 3C). Outer distal quadrant of exopod 2 covered with minute protuberances in both anterior and posterior views. Terminal seta about as long as segment and plumose, terminally placed on inner margin; short, rounded digitiform process placed on outer distal margin, covered with short hairs. Endopod as long as exopod; outer margin of posterior face (Fig. 3D) with crenate longitudinal groove; remaining surface of endopod with small rows or clusters of short spinules. Outer ⅔ of anterior face of endopod (Fig. 3E) crenulate; small pad on inner distal edge covered with tiny spinules.

Right leg 5 (Fig. 3A): Coxa with distomedial lobe on posterior surface tipped with sensillum. Basis with narrow, inwardly rounded longitudinal hyaline membrane on

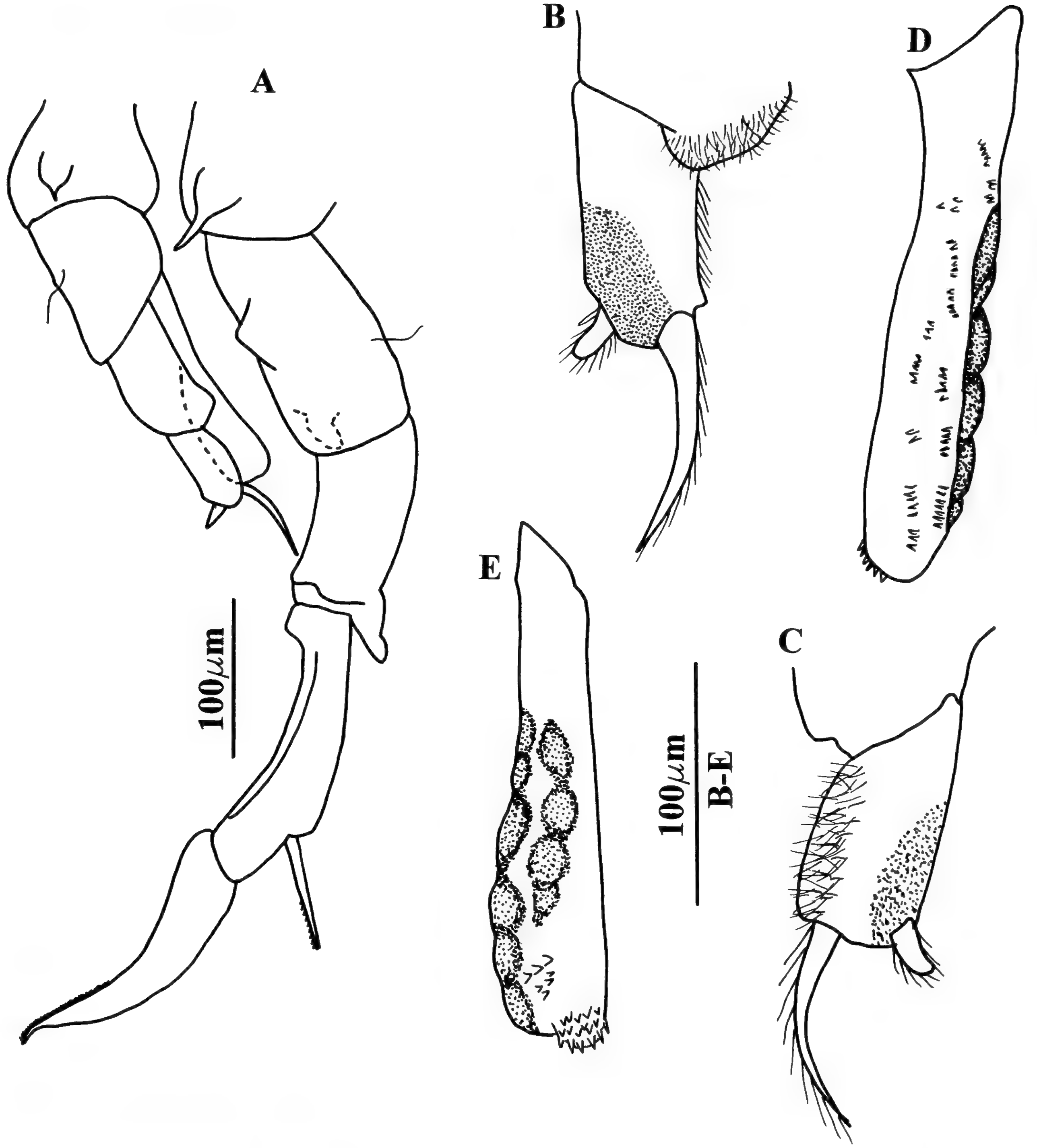

Fig. 3. *Aglaodiaptomus saskatchewanensis* Wilson, 1958. Paratype male (USNM 278233): A, Leg 5, posterior; B, Left leg 5 exopod 2, posterior; C, Left leg 5 exopod 2, anterior; D, Left leg 5 endopod, posterior; E, Left leg 5 endopod, anterior.

posteromedial face; fine setule on lateral margin slightly distal to mid-length of segment margin. Endopod greatly reduced, with fine setae on distomedial surface. Exopod 1 with distally directed process on distolateral corner, less than ¼ length of segment. Exopod 2, slightly longer than exopod 1. Lateral spine inserted at ¾ the length of the segment, spine about ½ as long as exopod 2, distal ½ of inner surface with fine teeth. Terminal claw as long as exopod 1; distal ¾ of inner surface lined with fine denticles.

Distribution and ecology.—Only three records exist beyond the Louisiana and southern Saskatchewan collections used for Wilson's (1958) description. Reed (1959) collected specimens from Frobisher Lake on the upper Churchill River in Saskatchewan, extending the range of *A. saskatchewanensis* northward. Patalas & Salki (1984) recorded it in Southern Indian Lake, Manitoba, another lake along the Churchill River. Robertson (1972) reported *A. saskatchewanensis* from southeastern Oklahoma in oxbow lakes, farm reservoirs, ditches and swampy areas.

Family Diaptomidae Baird 1850
Genus *Aglaodiaptomus* Light, 1939
Aglaodiaptomus atomicus, new species
Figs. 4–6

Diaptomus conipedatus Mahoney et al., 1990: 247, 252, Fig. 2.

Diaptomus sp. DeBiase & Taylor, 1993: 388; Boileau & Taylor, 1994:193, 195–196, 197–199, Figs. 1–3.

Type material.—Holotype, ♂, USNM 259989; allotype ♀, USNM 259990, each dissected on slide in lactophenol; paratypes: 5 ♂♂ 5♀♀, each dissected on slide in lactophenol, and 20 ♂♂ 20 ♀♀, USNM 267334; all from South Carolina, Aiken County, Flamingo Bay (Bay 3), 33°20′N, 81°41′W, Savannah River Site, 300 m west side of Road F at about 0.8 km south of intersection of Roads 2 and F. All collected 7 Feb 1994 with 102 μm dip net by A. E. DeBiase. All undissected paratypes preserved in ethanol.

Additional, non-type material.—20 ♂♂ 20 ♀♀, USNM 267333, South Carolina, Barnwell County, Bay 40, 33°16′N, 81°46′W, Savannah River Site, 25 m north of Road F-6 and 500 m east of Road F; 20 ♂♂ 20 ♀♀, USNM 267332, South Carolina, Aiken County, Bay 11, 33°1′N, 81°36′W, Savannah River Site, 400 m west of SC 125, about 500 m south of Gate 6. All paratypes undissected and preserved in ethanol. Also 500+ ♂♂ ♀♀, dissected on slides in glycerin, and 2000+ ♂♂ ♀♀ + copepodids, undissected in formalin, from 25 additional ponds in South Carolina, Aiken and Barnwell Counties (all located on Savannah River Site, 33°05′–33°24′N, 81°27′–81°47′W). All collected February and December 1990 with 102 μm mesh dip net by A. E. DeBiase.

Co-occurring Diaptomidae.—Flamingo Bay: *Aglaodiaptomus clavipoides* Wilson, 1955, *A. stagnalis* Forbes, 1882, *Leptodiaptomus moorei* Wilson, 1954, *Onychodiaptomus sanguineus* Forbes, 1876; Bay 11: *Hesperodiaptomus augustaensis* Turner, 1910, *O. sanguineus*; Bay 40: no other diaptomids; other SRS ponds: *A. clavipoides*, *A. stagnalis*, *H. augustaensis*, *L. moorei*, *Onychodiaptomus birgei* Marsh, 1894, *O. sanguineus*, *Skistodiaptomus pallidus* Herrick, 1879, up to five of these species per pond.

Female.—Length, excluding caudal setae: 1.65–2.00 mm ($n = 25$). Body broadest at pedigers 1 and 2 in dorsal view (Fig. 4A). Pedigers 4 and 5 incompletely fused. Weakly asymmetrical thoracic wings; left dorsomedial lobe (Fig. 4C) slightly more developed than ventrolateral lobe; each lobe tipped with small sensillum. Lobes of right wing (Fig. 4B) of equal size, each tipped with small sensillum. Urosome of 3 segments (Fig. 4D). Genital segment twice as long as broad, with very slight, rounded lateral expansions at mid-length, each with short, laterally-directed spine. Left expansion slightly more distally placed than right. Caudal rami about 1½ times longer than broad; inner margins hairy.

Antennules 25-segmented, reaching slightly beyond distal end of caudal rami (Fig. 4A). Appendages per segment as follows (Roman numeral = segment, Arabic numeral = number of setae, a = aesthetasc, sp = spine): I(1+a), II(3+a), III(1+a), IV(1), V(1+a), VI(1), VII(1+a), VIII(1+sp), IX(2+a), X(1), XI(2), XII(1+sp+a), XIII (1), XIV(1+a), XV(1), XVI(1+a), XVII(1), XVIII(1), XIX(1+a), XX(1), XXI(1), XXII (2), XXIII(2), XXIV(2), XXV(5+a). As in *A. saskatchewanensis*, setae (see Fig. 1E) on segments 17, 19, 20, 22 with hooked ends; length of setae approximately ¾ that of respective segments.

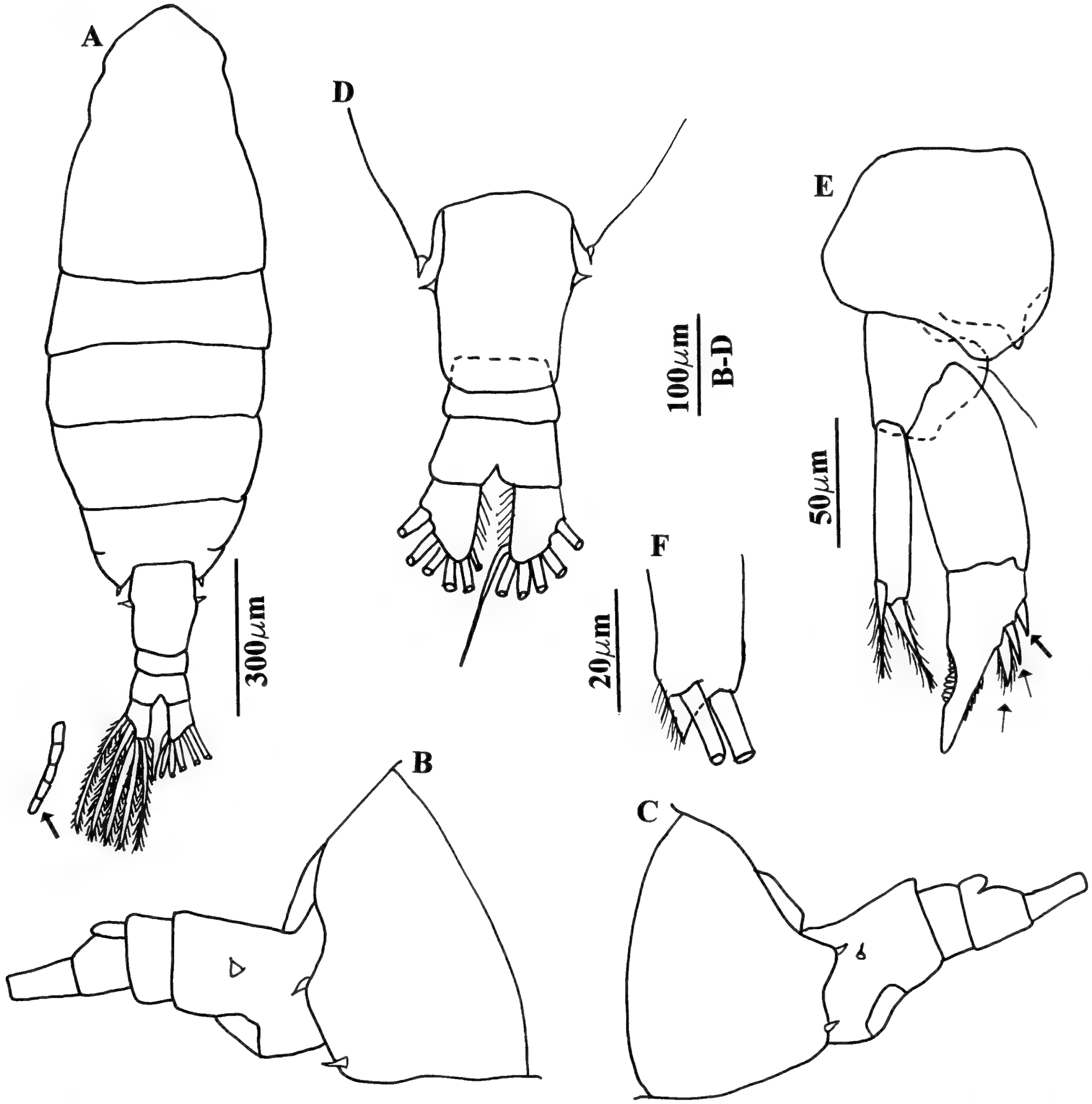

Fig. 4. *Aglaodiaptomus atomicus*, new species. Paratype female (USNM 267334): A, Habitus, dorsal, distal segments of antennule indicated by arrow; B, Right thoracic wing and urosome, lateral; C, Left thoracic wing and urosome, lateral; D, Urosome, dorsal; E, Leg 5, anterior, setae of exopod 3 (thin arrows), lateral seta of exopod 2 (thick arrow); F, Leg 5 endopod, distal end.

Leg 2 endopod 2 with Schmeil's organ (not figured).

Leg 5 (Fig. 4E): Coxa with posterior lateral protrusion tipped with sensillum. Basis with lateral seta. Exopod 1 approximately equal in length to exopod 2. Exopod 2 claw slightly curved with denticles on inner and outer margins. Exopod 3 not articulated. Lateral spine of exopod 2 about ⅔ the length of outer seta of exopod 3. Exopod 3 inner seta plumose, twice the length of outer seta. Endopod reaching slightly beyond distal end of exopod 1; tipped with two plumose setae and pointed protrusion (Fig. 4F).

Male.—Length, excluding caudal setae: 1.50–1.85 mm (n = 25). Prosome segmentation as in female (Fig. 5A). Thoracic wings reduced, with small dorsolateral and ventromedial sensilla; sensilla of right wing twice as long as left. Left posterior corner of urosome segment 1 bifid, tipped with

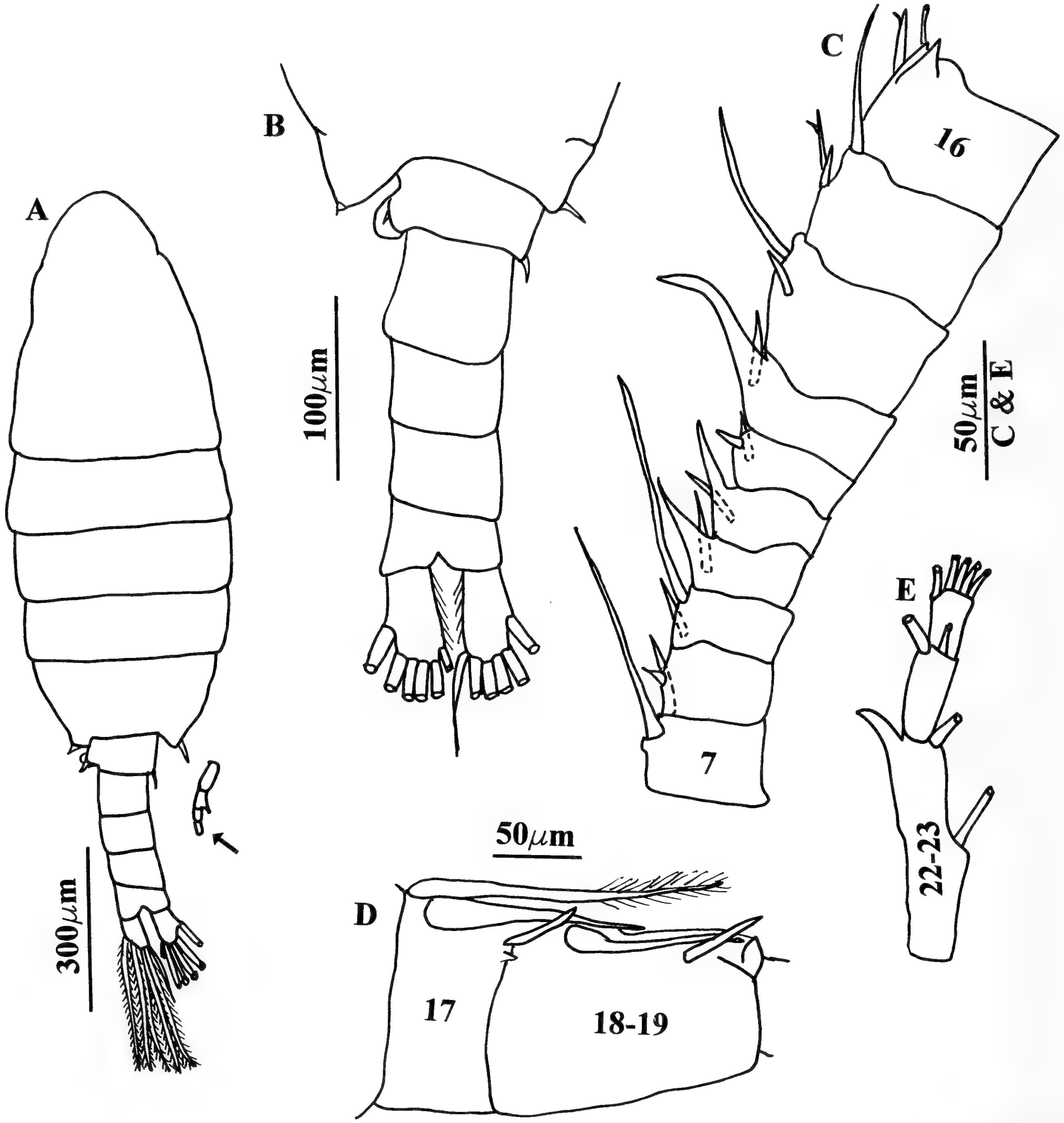

Fig. 5. *Aglaodiaptomus atomicus,* new species. Paratype male (USNM 267334): A, Habitus, dorsal, distal segments of antennule indicated by arrow; B, Urosome, dorsal; C, Right antennule, segments 7–16; D, Right antennule, segments 17–19; E, Right antennule, segments 23–25.

sensillum; right posterior corner simple, with sensillum that is slightly larger than left. Urosome 5-segmented (Fig. 5B). Segments 2–3, ventral margin lined with fine hair-like setae visible in lateral view under high magnification (not figured). Fourth segment asymmetrical, right margin longer than left. Caudal rami with fine setules lining inner margins.

Antennules extend to mid-length of urosome (Fig. 5A). Right antennule geniculate between segments 18–19 and 20–21. Segments 18–19 (Fig. 5D), 20–21 (not figured) and 22–23 (Fig. 5E) fused. Long, parallel spines (Fig. 5C) on segments 10, 11, and 13. Spines on segments 15 and 16 bifurcated (Fig. 5C). Modified digitiform seta (Fig. 5D) emerging from proximal ¼ of segment 17 and extending to mid-length of segment 18–19. Additional modified seta emerging from proximal ¼ of segment 18–19, extending length of segment. Curved distal process (Fig. 5E) on segment 22–23 about ½ as long as segment 24.

Left leg 5 (Figs. 6A–E): Leg (excluding spines) extending approximately to distal edge of basis. Lateral lobe of coxa minute, tipped with sensillum. Basis with fine lateral seta. Exopod 1 longer than exopod 2, with hairy pad on distomedial corner. Exopod 2 (Figs. 6B,C) articulating at distolateral margin of exopod 1; processes placed subterminally. Inner process is about as long as exopod 2, outer margin covered with setules. Outer process about ⅓ length of inner process, covered with setules. Outer distal quadrant of exopod 2 with minute protuberances on posterior surface (Fig. 6B). Endopod about as long as exopod with long patch of small teeth on distal ⅓ paralleling inner margin of posterior face (Fig. 6D). Outer margin crenulated (Figs. 6D, E); crenation more developed on anterior surface.

Right leg 5 (Figs. 6A): Coxa with distomedial lobe tipped with sensillum. Basis ornamented only with bilobed protrusion on median-posterior face, proximal lobe slightly larger; outer seta on lateral margin of segment. Endopod reduced, represented by laterally bent lobe, covered with fine setae. Process on distolateral corner of exopod 1, about ¼ length of exopod 1. Exopod 1 shorter than exopod 2, claw equal in length to exopod 2. Lateral spine inserted at ⅘ length of segment, about ⅔ the length of the claw, inner surface with fine denticles. Terminal claw as long as exopod 2; distal ¾ of inner surface lined with fine denticles.

Color.—Body pale blue; legs, distal ⅓ of antennule, and setae of caudal rami bright red-orange. The blue pigment is lost during preservation. If the specimens are preserved in formalin, the red pigment remains but becomes purple-red.

Type locality.—Flamingo Bay (Bay 3), 33°20′N, 81°41′W, Savannah River Site, Aiken County, South Carolina.

Etymology.—The species name is given after the Savannah River Site (SRS), where this species was first recognized. The SRS is a production facility for nuclear materials and was originally operated by the United States Atomic Energy commission.

Distribution and ecology.—*Aglaodiaptomus atomicus* is known only from Carolina bays and other shallow (usually <1 m deep) isolated wetland ponds in Aiken and Barnwell Counties, South Carolina. The ponds range in size from 0.1–50 ha. Most of these are temporary ponds. Hydrology is controlled mainly by precipitation and evapotranspiration (Lide et al. 1995). Filling tends to occur during late autumn–early winter, and drying during late spring–early summer.

The ponds usually lack fish, and all are acidic (pH 4.4–6.6). *Aglaodiaptomus atomicus* most often occurs at pH 5.1–5.7, and has a broad temperature range (10–35°C).

Discussion and comparisons.—The male of *A. atomicus* differs from all other congeners by possessing a relatively large protuberance on the outer distal corner of exopod 1 of right leg 5. It is at least ¼ the length of exopod 1, while this projection, when present on males of other species, is much shorter. The exception is *A. dilobatus* Wilson, 1958, which has a fairly long protuberance. However, the left leg 5 of *A. dilobatus* is morphologically different from that of *A. atomicus*. It possesses an exopod 1 which widens distally and a globular exopod 2. Both of these segments are relatively rectangular in *A. atomicus*.

The female of *A. atomicus* most closely resembles *A. forbesi* Light, 1938, *A. lintoni* Forbes, 1893 and *A. saskatchewanensis*. These species are difficult to tell apart, except that the endopod of *A. lintoni* reaches well beyond exopod 1, while it is approximately as long as exopod 1 in the others. Also, exopod 3 is more developed in *A. lintoni* and *A. forbesi*. *Aglaodiaptomus atomicus* can be distinguished from *A. saskatchewanensis* by the thoracic wings. The wings of *A. saskatchewanensis* are asymmetrical, with the left dorsal lobe more developed

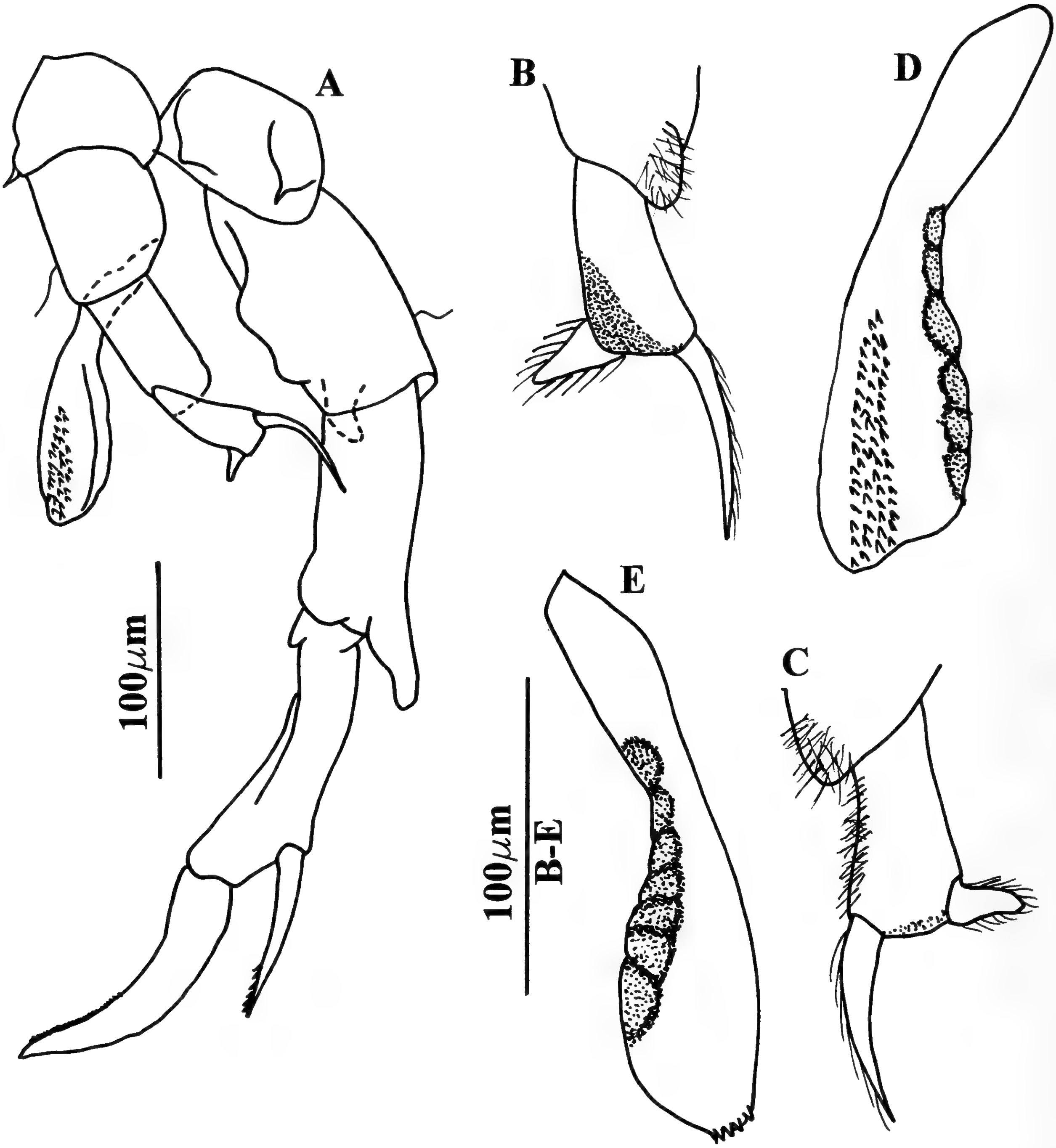

Fig. 6. *Aglaodiaptomus atomicus,* new species. Paratype male (USNM 267334): A, Leg 5, posterior; B, Left leg 5 exopod 2, posterior; C, Left leg 5 exopod 2, anterior; D, Left leg 5 endopod, posterior; E, Left leg 5 endopod, anterior.

than the right dorsal lobe, while the lobes of *A. atomicus* are almost equally developed on both sides.

Aglaodiaptomus atomicus keys out to *A. saskatchewanensis* in Wilson (1959). These species are easily separated by the ornamentation of the male antennules and leg 5 and the female thoracic wings. Also, *A. atomicus* is slightly larger.

Aglaodiaptomus atomicus and *A. saskatchewanensis* may also be separated geographically. As described in the "Distribution and ecology" section, *A. saskatchewanensis* has been reported from a few widely separated locations from the south–central and north–central regions of North America, while *A. atomicus* was discovered in southeastern North America. Most studies in central North America have concentrated on large reservoirs and lakes. Studies on wetlands and farm ponds, which appear to be the preferred habitat of *A. saskatchewanensis*, have dealt mainly with other microcrustacean groups, particularly cladocerans. A similar problem occurs with *A. atomicus*. Southeastern North America is also a relatively unstudied region, and few records of calanoid copepods exist for this area. There are no other reports of *A. atomicus*, *A. saskatchewanensis* or similar unidentified species from this area.

Acknowledgments

We greatly appreciated the encouragement and guidance of the late Dr. T. E. Bowman of the National Museum of Natural History, Smithsonian Institution (NMNH). Additional help was generously provided by Dr. J. W. Reid, NMNH. Advice from Dr. Frank Ferrari and Dr. J. Williams-Howze is also appreciated. Improvements on this manuscript came from comments by Dr. Bowman, Dr. Reid, D. A. Leeper, and three anonymous reviewers. We thank the NMNH for loan of their *Aglaodiaptomus saskatchewanensis* specimens. This research was supported by Financial Assistance Award Number DE-FC09-96SR18546 from the United States Department of Energy to the University of Georgia Research Foundation.

Literature Cited

Baird, W. 1850. The natural history of the British Entomostraca. The Ray Society, London. 364 pp. + 36 pls.

Boileau, M. G., & B. E. Taylor. 1994. Chance events, habitat age, and the genetic structure of pond populations.—Archiv für Hydrobiologie 132(2): 191–202.

Chengalath, R., & C. Shih. 1994. Littoral freshwater copepods of northwestern North America: Northern British Columbia.—Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 25(4):2421–2431.

Comita, G. W., & D. M. Tommerdahl. 1960. The postembryonic developmental instars of *Diaptomus siciloides* Lilljeborg.—Journal of Morphology 107:297–355.

DeBiase, A. E., & B. E. Taylor. 1993. New occurrences of *Eurytemora affinis* and *Epischura fluviatilis*, freshwater calanoid copepod species of the family Temoridae, in South Carolina.—American Midland Naturalist 130(2):386–392.

Forbes, S. A. 1876. List of Illinois Crustacea, with descriptions of new species.—Bulletin of the Illinois Museum of Natural History 1:3–76.

———. 1882. On some Entomostraca of Lake Michigan and adjacent waters.—American Naturalist 16:537–543, 640–650 + plt. VIII, IX.

———. 1893. A preliminary report on the aquatic invertebrate fauna of the Yellowstone National Park, Wyoming, and of the Flathead region of Montana.—Bulletin of the United States Fish Commission for 1891:207–258 + pls. XXXVII–XLII.

Herrick, C. L. 1879. Microscopic Entomostraca.—Annual Report to the Regents of the University of Minnesota for 1878:81–123.

Lide, R. L., V. G. Meentemeyer, J. E. Pinder, III, & L. M. Beatty. 1995. Hydrology of a Carolina bay located on the upper coastal plain of western South Carolina.—Wetlands 15(1):47–57.

Light, S. F. 1938. New subgenera and species of Diaptomid copepods from the inland waters of California and Nevada.—University of California Publications in Zoology 43(3):67–78.

———. 1939. New American subgenera of *Diaptomus* Westwood (Copepoda, Calanoida).—Transactions of the American Microscopical Society 58(4):473–484.

Mahoney, D. L., M. A. Mort, & B. E. Taylor. 1990. Species richness of calanoid copepods, cladocerans and other branchiopods in Carolina bay temporary ponds.—American Midland Naturalist 123(2):244–258.

Marsh, C. D. 1894. On two new species of *Diaptomus*.—Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 10:15–18.

———. 1907. A revision of the North American species of *Diaptomus*.—Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 15(2):381–516.

Patalas, K., & A. Salki. 1984. Effects of impoundment on the crustacean plankton of Southern Indian Lake.—Canadian Journal of Fisheries and Aquatic Sciences 41(4):613–637.

Reed, E. B. 1959. The distribution and ecology of fresh-water Entomostraca in arctic and subarctic North America. Unpublished Ph. D. thesis, University of Saskatchewan. Saskatoon, Saskatchewan, Canada, 160 pp.

Robertson, A. 1972. Calanoid copepods: New records from Oklahoma.—Southwestern Naturalist 17(2):201–203.

Turner, C. H. 1910. Ecological notes on the Cladocera and Copepoda of Augusta, Georgia, with descriptions of new or little known species.—Transactions of the Academy of Sciences of St. Louis 19(2):151–176.

Wilson, M. S. 1954. A new species of *Diaptomus* from Louisiana and Texas with notes on the subgenus *Leptodiaptomus*.—Tulane Studies in Zoology 2(3):49–60.

———. 1955. A new Louisiana copepod related to *Diaptomus* (*Aglaodiaptomus*) *clavipes* Schacht.—Tulane Studies in Zoology 3(1):35–47.

———. 1958. New records and species of calanoid copepods from Saskatchewan and Louisiana.—Canadian Journal of Zoology 36(3):489–497.

———. 1959. Free-living Copepoda: Calanoida. Pp. 738–794 *in* W. T. Edmondson, ed., Ward and Whipple's Freshwater Biology. Second edition. John Wiley and Sons, New York, 1248 pp.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(4):581–600. 1997.

Argyrodiaptomus nhumirim, a new species, and *Austrinodiaptomus kleerekoperi*, a new genus and species, with redescription of *Argyrodiaptomus macrochaetus* Brehm, new rank, from Brazil (Crustacea: Copepoda: Diaptomidae)

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Abstract.—Two species of diaptomid calanoid copepods are described, and one species is redescribed from Brazilian specimens. *Argyrodiaptomus nhumirim*, new species, inhabits small fishless freshwater ponds in the Pantanal, State of Mato Grosso do Sul. *Argyrodiaptomus furcatus* var. *macrochaetus* Brehm is redescribed from the State of Rio Grande do Sul and raised to species rank. A new genus and species *Austrinodiaptomus kleerekoperi* is described, also from Rio Grande do Sul. *Diaptomus* s.l. *inexspectatus* Brehm is transferred to *Austrinodiaptomus*. The first record from the State of Sergipe is given for *Argyrodiaptomus azevedoi* (Wright).

Samples from small ponds in the Pantanal, State of Mato Grosso do Sul, Brazil, contained a hitherto unknown species of the diaptomid calanoid copepod genus *Argyrodiaptomus*. The new species is described and compared with *A. azevedoi* (Wright 1935). The first record from the State of Sergipe, Brazil, is given for the latter.

Samples from temporary ponds in the State of Rio Grande do Sul, Brazil, collected in 1941 by H. Kleerekoper and now in the R. W. Kiser Collection in the National Museum of Natural History, Smithsonian Institution, proved to contain two interesting species of calanoids. *Argyrodiaptomus furcatus* var. *macrochaetus* Brehm, 1937, is redescribed and raised to species rank. A new genus and species of the subfamily Diaptominae is described, and the similar *Diaptomus* s.l. *inexspectatus* Brehm, 1958 is transferred to the new genus.

Drawings were made using a Wild M30 microscope fitted with a drawing tube, from specimens in lactic acid or, after dissection, in commercial polyvinyl lactophenol or CMC-10 with a little Chlorazol Black E added to the medium. Most drawings were made from supported mounts except those of antennules and of the male of *A. nhumirim*, which were made after dissection and permanent mounting. The specimens were deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the United States National Museum of Natural History, Smithsonian Institution (USNM).

Order Calanoida G. O. Sars, 1903
Family Diaptomidae Baird, 1850
Subfamily Diaptominae Kiefer, 1932
Genus *Argyrodiaptomus* Brehm, 1933
Argyrodiaptomus nhumirim, new species
Figs. 1–16

Argyrodiaptomus sp.—Reid & Moreno 1990:725–728, tab. 2.

Material examined.—Holotype ♂, fully dissected and mounted on slide in polyvinyl lactophenol (MZUSP 12286); allotype ♀, fully dissected and mounted on slide in CMC-10 (MZUSP 12287); and undissected paratype ♀ in 70% ethanol (USNM 284931); all from among aquatic macrophytes in Baía da Carandazal (Baía 29), Fazenda Nhumirim, State of Mato Grosso do Sul, Brazil, 4 Apr 1987, leg. J. W. Reid. Accompanying copepod species: *Notodiaptomus coniferoides* (Wright; USNM 284939, 284940), *Notodiaptomus* sp. (USNM 284949), *Mesocyclops longisetus* (Thiébaud) s.s. (USNM 284965), *Mesocyclops meridianus* (Kiefer; USNM 284972, 284973), *Microcyclops anceps* (Richard) s.s. (USNM 284981), *Neutrocyclops brevifurca* (Lowndes; USNM 284990), and *Ectocyclops* cf. *phaleratus* (Koch; USNM 284963). Additional paratype: 1 undissected copepodid in 70% ethanol (USNM 284932), from among *Nymphaea* spp., Baía 57, Fazenda Nhumirim, 5 Apr 1987, leg. J. W. Reid. Accompanying copepods: *Notodiaptomus* sp. (USNM 284950), *M. longisetus* (USNM 284964), *Microcyclops ceibaensis* (Marsh; USNM 284988). These records were previously reported by Reid & Moreno (1990). Geographical coordinates of Fazenda Nhumirim: 18°59′S, 56°39′W.

The only male specimen was dissected and mounted before it was recognized as a new species. No habitus drawing of the unmounted male was made.

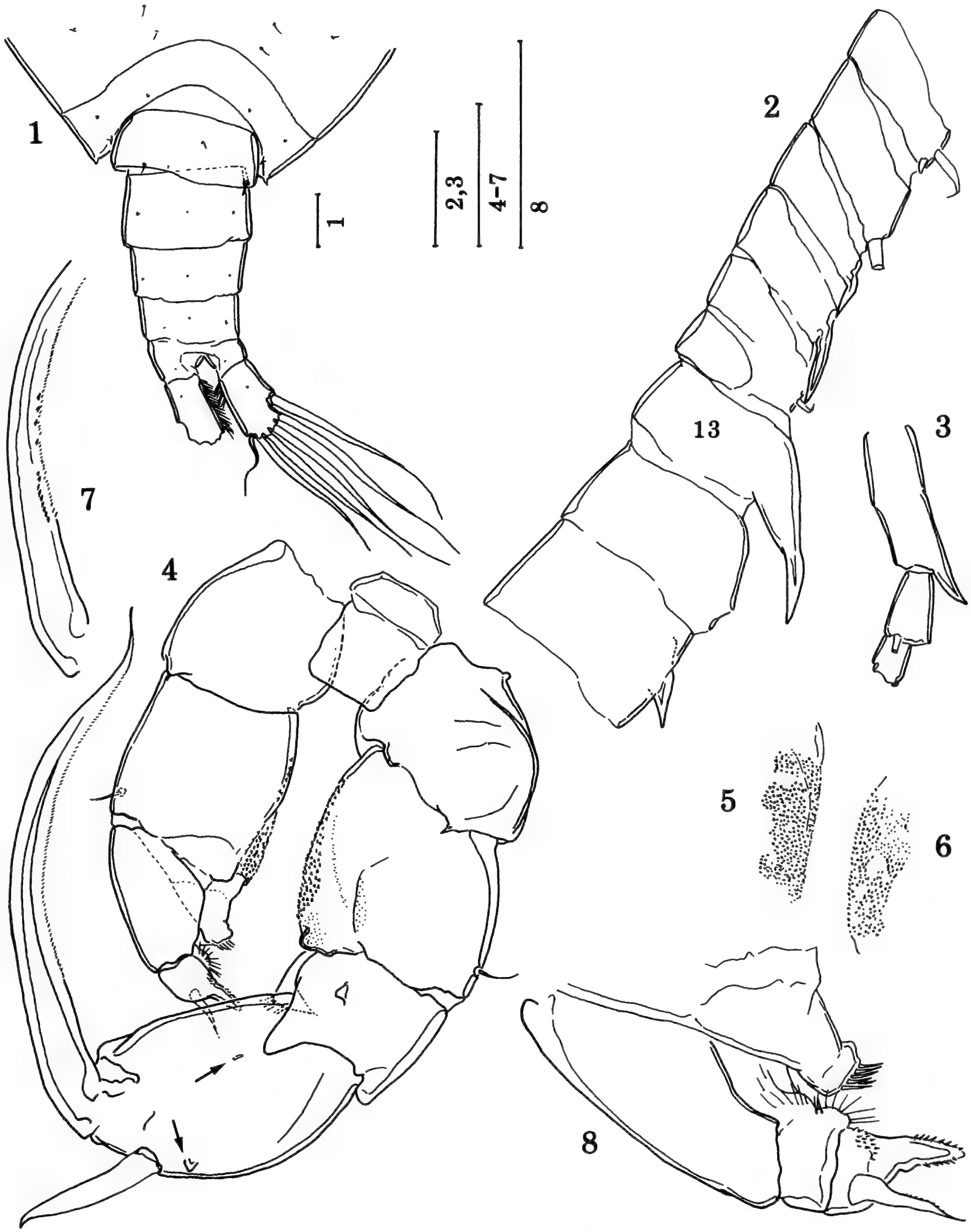
Male.—Length of holotype 2.0 mm. Pedigers 4 and 5 (Fig. 1) distinct. Lateral wings of pediger 5 nearly symmetrical, right wing slightly longer, each with dorsal hairlike sensillum and ventral spiniform sensillum on margin. Urosomite 1 slightly inflated, with short sensillum on right distolateral corner and short hair near left distolateral corner. Urosomites and caudal rami each with few dorsal pores. Caudal rami about 1.7 times longer than broad, haired on medial margins only. Terminal caudal setae uniformly and finely plumose; medialmost (dorsal) caudal seta slender, also uniformly plumose; setae of left and right rami identical.

Right antennule (Figs. 2, 3) with 22 segments, geniculate between segments 18 and 19. Segment 12 partly divided. Segments 8 and compound segment 12 each with small socketed spine; spiniform processes of segments 10 and 11 parallel to longitudinal axis of antennule, reaching base of process or spine of next distal segment; spiniform process of segment 13 large; segments 14 and 16 without, segment 15 with spiniform process. Antepenultimate segment with stout curved process extending to midlength of penultimate segment.

Left antennule with 25 segments. Number of setae (s), spines (sp), and aesthetascs (a) of each segment as follows: (1) s + a, (2) 3s + a, (3) s + a, (4) s, (5) s + a, (6) s, (7) s + a, (8) s + sp, (9) 2s + a, (10) s, (11) s, (12) s + sp + a, (13) s, (14) s + a, (15) s, (16) s + a, (17) s, (18) s, (19) s + a, (20) s, (21) s, (22) 2s, (23) 2s, (24) 2s, (25) 5s + a. Of terminal setae, 3 setae longer than segment 25, remaining 2 setae short. No seta longer than succeeding 2 segments.

Antenna, mouthparts, and legs 1–4 like corresponding structures of *Austrinodiaptomus kleerekoperi*, new genus, new species (see following section). Schmeil's organ as in female (compare Fig. 13).

Leg 5 (Figs. 4–8): each coxopodite with small spiniform sensillum on small, distally directed process. Right basipodite (Fig. 4) not lobate except for small lobe covered with fine granules at distomedial corner; medial surface (Figs. 4, 6) with coarse denticles, caudal surface with 3 areas of fine granules. Right exopodite 1 broader than long, with small blunt process on caudal surface, and stout, distally directed process near distomedial corner. Right exopodite 2 broad, smoothly ovate, with small blunt process and short ridge on caudal surface (indicated by arrows in Fig. 4); lateral spine subterminal, stout, smooth, with slightly recurved tip; terminal claw nearly as long as entire right leg, gently and regularly curved, with slender recurved tip, and several accessory spinules on frontal surface in addition to spinules along most of medial margin (Fig. 7). Right endopodite short, broadly triangular, with apical row of hairs. Left basipodite without notable structure except irregular field of coarse denticles on



Figs. 1–8. *Argyrodiaptomus nhumirim*, new species, holotype ♂ (MZUSP 12286): 1, Pedigers 4 and 5 and urosome, dorsal (in flattened mount); 2, Right antennule segments 8–15 (most setae omitted); 3, Right antennule terminal segments (most setae omitted); 4, Leg 5, caudal; 5, Pattern of tiny spinules on left leg 5 basipodite, frontal (drawn reversed); 6, Pattern of tiny spinules on right leg 5 basipodite, frontal (reversed); 7, Proximal section of terminal claw of right leg 5, frontal (reversed); 8, Left leg 5 exopodite and endopodite, frontal (reversed). Scales = 100 μm.

medial and frontal surfaces (Fig. 5). Left exopodite 1 with proximal haired pad little developed. Left exopodite 2 (Fig. 8) appearing divided on frontal surface, with haired pad on proximal part of medial margin, and ending in narrow, coarsely serrate digitiform process; frontal side with field of tiny denticles proximal to digitiform process; proximal spine minutely serrate, with hairlike tip, extending only slightly past tip of digitiform process. Left endopodite indistinctly 2-segmented, with terminal row of 6 stout spinules.

Female.—Length of allotype 1.8 mm, of paratype 2.0 mm. Body (Figs. 9–11) stout. Prosome without ornamentation except few pairs of pores, some with hairs. Rostral points (not illustrated) acute. Pedigers 4 and 5 fused, faint fusion line visible laterally only. Posterodorsal margins of pedigers 4 and 5 not elevated. Lateral wings of pediger 5 small, posteriorly directed, right wing slightly larger than left wing, each wing with small dorsal sensillum tipped with fine hair and larger ventral spiniform sensillum, wing widest posteriorly at level of ventral spiniform sensillum. Urosome of 3 segments plus caudal rami. Genital compound segment nearly symmetrical, except right margin slightly produced posteriorly, and right spiniform sensillum placed slightly more anteriorly than left spiniform sensillum; left sensillum (Fig. 10) with acute bifid tip, right sensillum (Fig. 11) with blunt tip. Urosomite 2 slightly broader than long, proximal half telescoped into genital compound segment. Genital operculum (Fig. 12) with narrow crescentic proximal plate and broad distal plate with prominent lateral arms set wide apart (terminology after Cicchino 1994). Urosomites and caudal rami with several pairs of pores. Caudal rami about 1.7 times longer than broad, haired on medial margins only. Lateral and lateralmost terminal caudal setae stouter than more medial setae; dorsal seta slender; all setae finely and uniformly plumed.

Antennules reaching just past anterior margin of genital compound segment. Number of segments and armature as in left antennule of male.

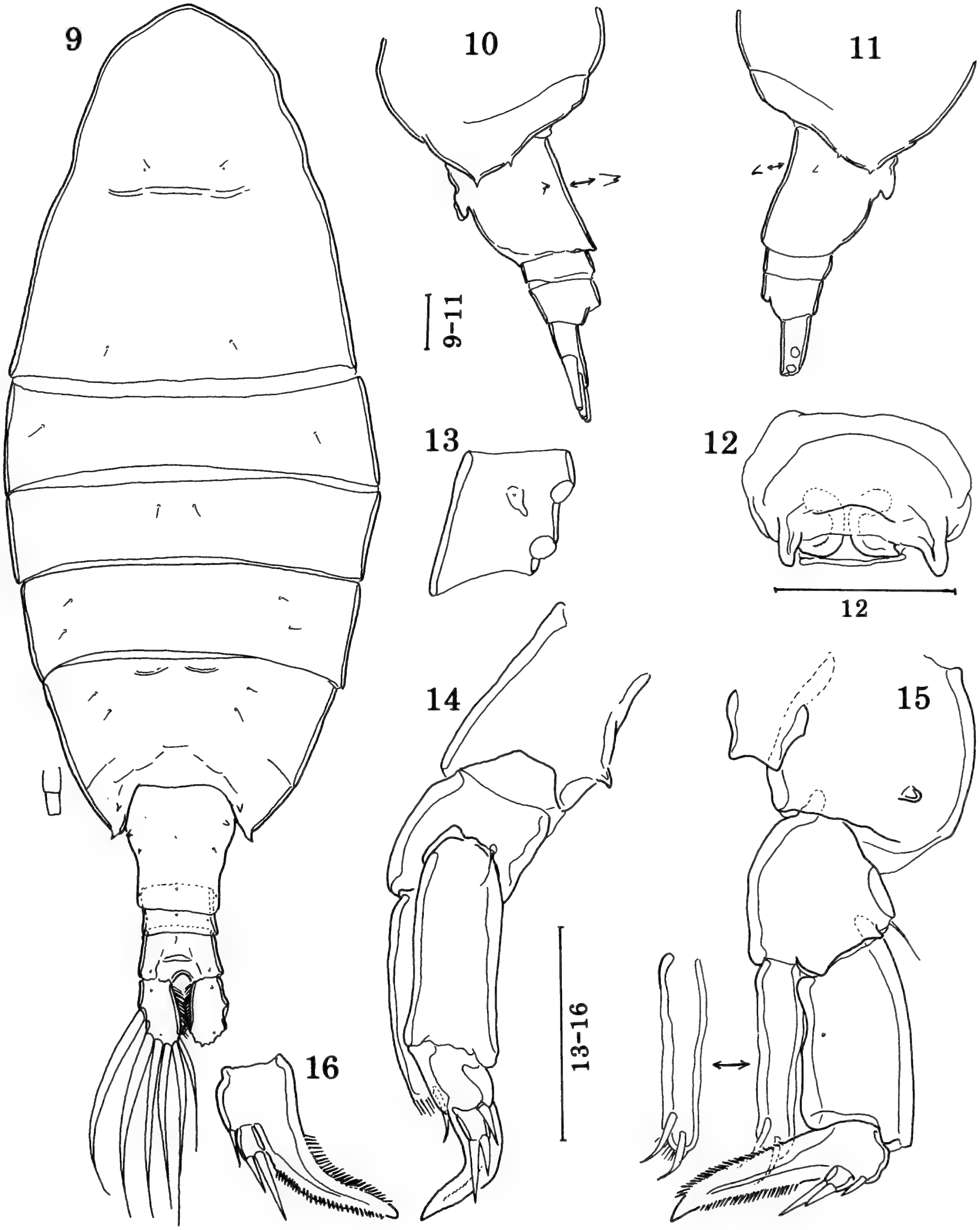
Antenna, mouthparts, and legs 1–4 as in male. Schmeil's organ (Fig. 13) mammiform, borne on caudal surface of leg 2 endopodite 2 (compare Fig. 55).

Leg 5 (Figs. 14–16): coxopodite stout, with blunt prominence on caudal surface. Basipodite with long convex medial margin, short lateral margin, and short seta at distolateral corner. Exopodite 1 about twice as long as broad, lateral margin slightly convex, medial margin uneven; with pore on caudal surface near midlength of medial margin. Exopodite 2 with small spine at base of exopodite 3, spine as long as exopodite 3; claw coarsely serrate along most of both margins; claw of each foot curved anteriorly and slightly distally, left claw more strongly curved than right claw (Fig. 14). Exopodite 3 distinct from exopodite 2, with 2 terminal spines of which lateral spine is slightly more than half length of medial spine. Endopodite slightly longer than exopodite 1, unsegmented, bearing terminal row of hairs and 2 long, curved subterminal spines.

Color of living specimens.—Light blue.

Etymology.—Named for the Fazenda Nhumirim where the species was collected; proposed as a noun in apposition.

Discussion and comparisons.—*Argyrodiaptomus nhumirim* falls morphologically and geographically among three congeners: *A. denticulatus* (Pesta, 1927), known from Argentina and Bolivia; *A. azevedoi* (Wright, 1935), from the Brazilian Northeast and Amazon Basin; and *A. robertsonae* Dussart, 1985a, from the Brazilian Amazon Basin. The male of *A. nhumirim* is easily distinguished from that of *A. denticulatus* by several characters of the 5th leg, the latter species having prominent lobes on the right basipodite medial margin, a long lateral spine on the right exopodite 2, and a long spiniform proximal process on the left exopodite 2. The spiniform process on the antennular antepenultimate segment is long in *A. denticulatus*, reaching the end of the pen-



Figs. 9–16. *Argyrodiaptomus nhumirim*, new species, allotype ♀ (MZUSP 12287): 9, Habitus, dorsal; 10, Pedigers 4 and 5 and urosome, left lateral, with enlarged illustration of bifid spiniform sensillum; 11, Pedigers 4 and 5 and urosome, right lateral, with enlarged illustration of acute spiniform sensillum; 12, Genital operculum; 13, Leg 2 endopodite 2, caudal, showing Schmeil's organ; 14, Left leg 5, lateral; 15, Right leg 5, caudal, with detail of endopodite; 16, Left leg 5 exopodites 2 and 3, caudal. Scales = 100 μm.

ultimate segment. Females of *A. denticulatus* usually have a row of spines along the lateral part of the line of fusion between pedigers 4 and 5, although these spines are lacking in some populations (J. C. Paggi, in litt. 1997). Females of *A. denticulatus* consistently have the dorsal sensillum of each wing set on an expansion; a longer, more slender genital compound segment with the left and right spiniform sensilla set at the same level; and the leg 5 with a short, two-segmented endopodite, and no spine lateral to the base of exopodite 3 (after the redescription by Dussart 1985a).

The male of *A. robertsonae* differs from that of *A. nhumirim* in having pedigers 4 and 5 fused, urosomite 1 (the genital somite) not inflated, the spiniform process on the right antennule segment 11 reaching the distal end of segment 12, and especially in having the right leg 5 basipodite with a large lobe on its caudal surface, and the distal process of the right exopodite 1 directed laterally. The female of *A. robertsonae* differs in having the lateral wings of pediger 5 most produced at the level of each dorsal spiniform sensillum, urosomite 2 much broader than long, and leg 5 exopodite 3 with a tiny lateroterminal spine, less than ⅕ the length of the medioterminal spine (from Dussart 1985a:Pl. 2 Fig. 10).

Argyrodiaptomus azevedoi is morphologically closest to *A. nhumirim*, but the male of the former differs in a few characters of the right leg 5: there is a large lobe on the caudal surface of the basipodite, the caudal surface of exopodites 1 and 2 lacks processes, and the terminal claw is doubly angled with the middle part straight. These features are consistent in the representations of Wright (1935, 1938), Kiefer (1936), and Brandorff (1972), and were confirmed by inspection of a male from Betume (near Neópolis), State of Sergipe, Brazil, 13 March 1983, leg. E. R. dos Santos, identified by C. E. F. da Rocha (USNM 227122). Wright (1935) stated that the left leg 5 endopodite of the male is one-segmented, but it is indistinctly divided in the specimen from Sergipe. In the female of *A. azevedoi* (confirmed by inspection of a female from USNM 227122), there is a lateral groove but not a suture line between the fused pedigers 4 and 5, both spiniform sensilla of the genital compound segment are acute, the antennules extend to the posterior end of the genital compound segment, and the lateroterminal spine of leg 5 exopodite 3 is less than ⅓ the length of the medioterminal spine. The armature of the antennules of the female and the left antennule of the male is identical in both species. *Argyrodiaptomus azevedoi* has been reported from the northeastern Brazilian States of Bahia, Ceará, and Paraíba, and the Brazilian Amazon Basin (States of Amazonas and Pará). This is the first published record from Sergipe.

Males of the remaining congeners, *Argyrodiaptomus bergi* (Richard 1897), *A. falcifer* (Daday 1905) (=*Diaptomus argentinus* Wright, 1938), *A. furcatus* (G. O. Sars 1901) (=*D. aculeatus* Van Douwe 1911, 1912), *A. furcatus* f. *exilis* Dussart, 1985b, *A. granulosus* Brehm, 1933, *A. macrochaetus* Brehm, 1937, and *A. neglectus* (Wright 1938) all lack denticles on the medial surface of the right leg 5 basipodite (although some have areas of minute granules on the caudal surface of this segment). In the females of all these, the leg 5 endopodite is distinctly two-segmented, and except in *A. macrochaetus* and some populations of *A. furcatus*, it is much shorter than exopodite 1.

All known species of *Argyrodiaptomus* are South American (Brandorff 1976). The Chinese *Argyrodiaptomus ferus* Shen & Tai, 1964 and *A. cavernicolax* Shen & Tai, 1965 were improperly assigned to this genus (Dussart & Defaye 1983, Dussart 1985a). Both are in need of redescription and re-evaluation as to their generic affiliation, which is beyond the scope of the present article.

The Fazenda Nhumirim is maintained for agricultural and ecological research by the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). It contains numerous permanent and ephemeral freshwater and saline ponds, locally termed "baías" and "salinas" respectively. Of 19 localities in the southern Pantanal investigated by Reid & Moreno (1990), *A. nhumirim* appeared in only two small, shallow, fishless baías.

Argyrodiaptomus macrochaetus Brehm, 1937, new rank
Figs. 17–31

Argyrodiaptomus furcatus var. *macrochaetus* Brehm, 1937:122–125, figs. 3, 4.—Dussart & Defaye 1983:131.

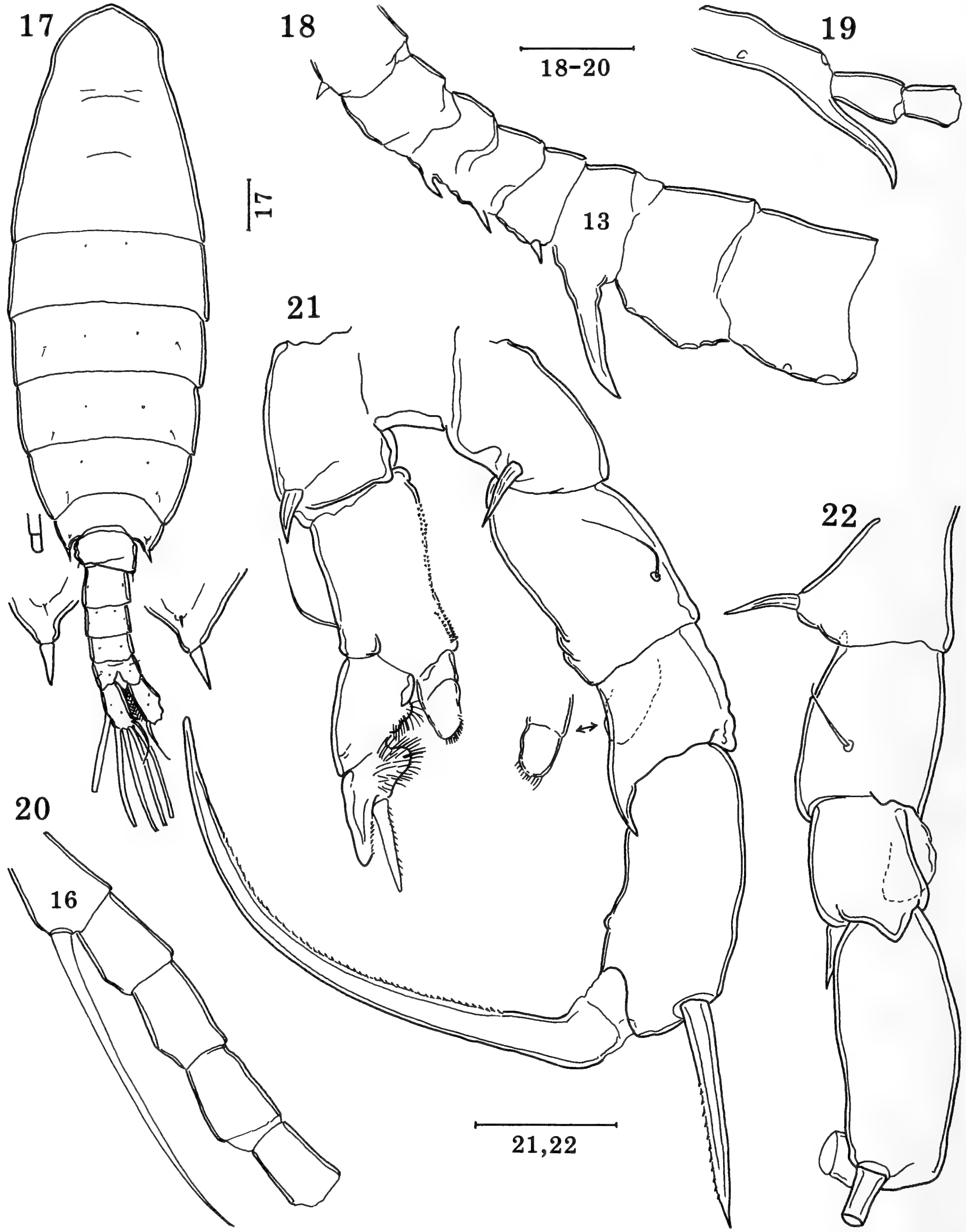
Argyrodiaptomus furcatus macrochaetus.—Dussart 1984:63.

Material examined.—♂ (fully dissected on slide), ♀ (fully dissected on slide), and 2 ♀♀ and 2 copepodids, preserved whole in ethanol, from R. W. Kiser Collection, Sample 460SM/164/520 (USNM 283139). Accompanying copepod species: *Attheyella fuhrmanni* (Thiébaud; USNM 283146), *Ectocyclops rubescens* Brady (USNM 283140), *Eucyclops ensifer* Kiefer (USNM 283141), *Mesocyclops longisetus* s.s. (USNM 283142), *Microcyclops alius* (Kiefer; USNM 283143), *Neutrocyclops brevifurca* (USNM 283145), *Paracyclops chiltoni* (Thomson; USNM 283114), and *Tropocyclops prasinus* (Fischer) s.s. (USNM 283144). ♂ and 2 ♀♀, ethanol-preserved, Kiser Collection Sample 465B/198 (USNM 283123). Accompanying copepods: *A. fuhrmanni* (USNM 283126), *Austrinodiaptomus kleerekoperi*, new species (see following section), *E. rubescens* (USNM 283125), *E. ensifer* (USNM 283119), *Macrocyclops albidus* (Jurine) s.s. (USNM 283130), *M. alius* (USNM 283121), *Microcyclops anceps* (USNM 283122), *Microcyclops* cf. *ceibaensis* (USNM 283127), *Microcyclops varicans* (G. O. Sars) s.s. (USNM 283116), *Microcyclops* sp. (USNM 283118), *P. chiltoni* (USNM 283113), and *Tropocyclops prasinus meridionalis* (Kiefer; USNM 283117). Both samples from temporary pools near Porto Alegre, Rio Grande do Sul, Brazil, Sep 1941, leg. H. Kleerekoper. (Note: the Kiser Collection material arrived at the National Museum of Natural History in xylene, and was transferred to ethanol about 1986.)

The following description refers mainly to the specimens in hand, except where information is added from the incomplete description of Brehm (1937). Because of the age and dark color of the specimens, the prosomite pores could not be reliably observed in most individuals.

Male.—Lengths in mm: 1.09 (USNM 283139), 1.2 (USNM 283123). Body (Fig. 17) slender in dorsal view. Pedigers 4 and 5 distinct. Lateral wings of pediger 5 nearly symmetrical, each with hairlike dorsal sensillum and long spiniform ventral sensillum on margin, right wing slightly longer and its ventral sensillum directed slightly more laterally. Right side of urosomite 1 slightly inflated and produced posteriorly; short hair-sensillum present on each posterior corner of urosomite 1. Metasomites, urosomites, and caudal rami with paired pores (pore pattern may be incomplete as illustrated). Caudal rami haired on medial margins only.

Antennules short, reaching posterior end of prosome. Right antennule (Figs. 18, 19) with 22 segments, geniculate between segments 18 and 19. Segment 8 and (simple) segment 12 each with small socketed spine; spiniform processes of segments 10 and 11 nearly parallel to long axis of antennule, each reaching only to proximal end of succeeding segment; spiniform process of segment 13 large; segments 14–16 without processes; antepenultimate segment with stout curved process reaching nearly midlength of segment 22 (Fig. 19). Left antennule (Fig. 20) with 25 segments; number of setae (s), spines (sp), and aesthetascs (a) of each segment as follows: (1) s + a, (2) 3s + a, (3) s + a, (4) s, (5) s + a, (6) s, (7) s + a, (8) s + sp, (9) 2s + a, (10) s, (11) s, (12) s + sp + a, (13) s, (14) s + a, (15) s, (16) s, (17) s, (18) s, (19) s + a, (20) s, (21) s, (22) 2s, (23) 2s, (24) 2s, (25) 5s + a. Seta of segment 16 reaching past midlength of segment 20, no aesthetasc at base



Figs. 17–22. *Argyrodiaptomus macrochaetus* Brehm, 1937, ♂ (17, USNM 283123; 18–22, USNM 283139): 17, Habitus, dorsal, with detail of left and right wings of pediger 5; 18, Right antennule segments 8–15 (setae omitted); 19, Right antennule terminal segments; 20, Left antennule segments 16–20 (most setae omitted); 21, Leg 5, caudal, showing Schmeil's organ; 22, Right leg 5, lateral. Scales = 100 μm.

of seta. Lengths of remaining setae similar to corresponding setae of female (Figs. 27, 28).

Antenna, mouthparts, and legs 1–4 like corresponding structures of *Austrinodiaptomus kleerekoperi*, new genus, new species (see following section). Schmeil's organ as in female (compare Fig. 29).

Leg 5 (Figs. 21, 22): each coxopodite with large spiniform sensillum on small, caudally directed lobe. Right basipodite with distal part of medial margin slightly lobate, and ornamented only with long lateral seta. Right exopodite 1 slightly longer than broad, with small blunt conical lobe on distolateral corner and long acute curved process on distomedial corner. Right exopodite 2 with small rounded process at distal ⅔ of medial margin; lateral spine subterminal, about ¾ length of segment, with serrate medial margin; terminal claw about as long as right basipodite and exopodite combined, gently curved with major curvature at distal ⅔, and serrate along medial margin (tip of claw worn, thus claw may actually be somewhat longer and possibly recurved). Right endopodite short, cylindrical, indistinctly 2-segmented, with apical row of fine hairs. Left basipodite with proximomedial corner slightly dilated, and 3 small groups of denticles on medial surface (denticles not continuing onto caudal or frontal surface). Left exopodite 1 with small haired pad on medial surface; exopodite 2 with larger haired pad on medial surface, and ending in coarsely serrate digitiform process; proximal spine longer than digitiform process, straight, with blunt tip and fine hairs along medial margin. Left endopodite indistinctly 2-segmented, with terminal row of many fine hairs.

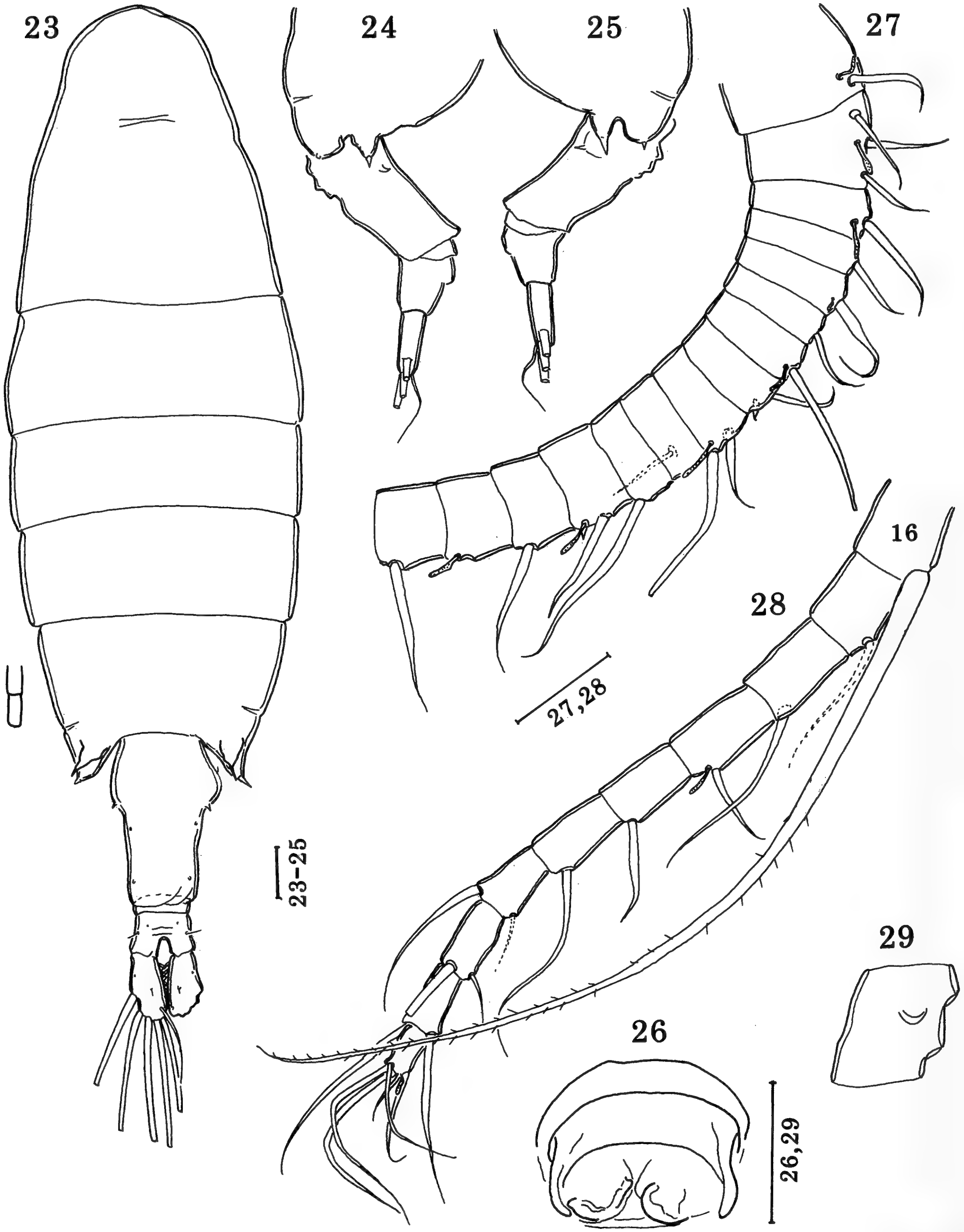
Female.—Lengths in mm: 1.6, 1.8, 2.0 (USNM 283139); 1.5, 1.7 (USNM 283123). Body (Figs. 23–25) moderately stout. Rostral points (not illustrated) acute. Pedigers 4 and 5 completely fused, line of fusion visible as lateral sulcus. Dorsal margins of pedigers 4 and 5 not elevated. Lateral wings of pediger 5 small, double, each with large dorsal and smaller ventral spiniform sensillum on margin; right wing slightly longer than left wing, with larger sensilla. Urosome of 3 segments plus caudal rami. Genital compound segment long, nearly symmetrical, except right anterior side slightly more produced than left side, and right sensillum located very slightly more posteriorly than left sensillum. Both sensilla acute (Figs. 24, 25). Genital operculum (Fig. 26) with lateral arms slightly longer than in *A. nhumirim*, otherwise similar. Urosomite 2 broader than long, telescoped into and completely covered ventrally by genital compound segment. Urosomites and caudal rami with several pairs of pores. Caudal rami haired on medial margins only.

Antennule (Figs. 27, 28) reaching only posterior end of pediger 4. Number of segments and armature as in left antennule of male, including segment 16 without aesthetasc. Seta of segment 16 extending past end of antennule.

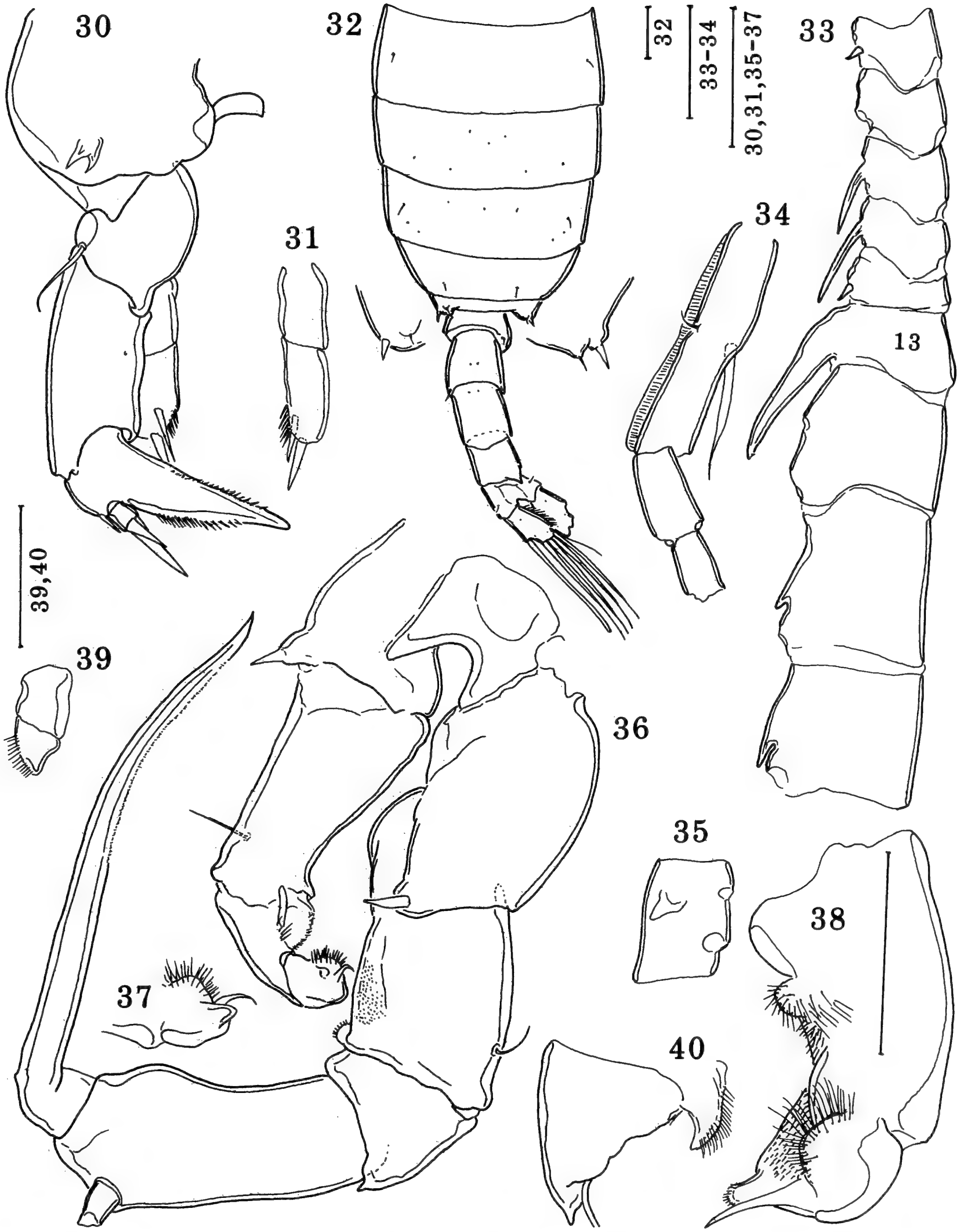
Antenna, mouthparts, and legs 1–4 like those of male. Schmeil's organ (Fig. 29) bluntly rounded, borne on caudal surface of leg 2 endopodite 2 (compare Fig. 55).

Leg 5 (Figs. 30, 31): coxopodite stout, with acutely bifid prominence on caudal surface. Basipodite with long convex medial margin, short lateral margin, and long lateral seta. Exopodite 1 slightly more than twice longer than broad, with pore on caudal surface near midlength of medial margin. Claw of exopodite 2 (of both 5th legs) broad and coarsely serrate along most of both straight margins; exopodite 2 also with slender spine at base of exopodite 3, this spine as long as and closely appressed to exopodite 3. Exopodite 3 distinct, with 2 stout terminal spines of which lateral spine is about half length of medial spine. Endopodite reaching end of medial margin of exopodite 1, distinctly 2-segmented, bearing subterminal medial row of hairs and 2 long, straight subterminal spines, distal spine especially stout.

Color of living specimens.—Notes by R. Thomsen, as reported by Brehm (1937:123,



Figs. 23–29. *Argyrodiaptomus macrochaetus* Brehm, 1937, ♀ (USNM 283139): 23, Habitus, dorsal; 24, Pedigers 4 and 5 and urosome, left lateral; 25, Pedigers 4 and 5 and urosome, right lateral; 26, Genital operculum; 27, Antennule segments 1–15; 28, Antennule segments 16–25; 29, Leg 2 endopodite 2, caudal, showing Schmeil's organ. Scales = 100 μm.



Figs. 30–40. *Argyrodiaptomus macrochaetus* Brehm, 1937, ♀ (USNM 283139): 30, Leg 5, caudal; 31, Leg 5 endopodite, frontal. Figs. 32–40. *Austrinodiaptomus kleerekoperi*, new genus, new species, holotype ♂ (MZUSP 12288): 32, Habitus, dorsal, with enlarged detail of lateral wings of pediger 5 (cephalosome broken); 33, Right antennule segments 8–16; 34, Right antennule terminal segments; 35, Leg 2 endopodite 2, caudal, showing Schmeil's organ; 36, Right Leg 5, oblique caudal; 37, Leg 5, left exopodite 2, oblique caudal; 38, Leg 5, left exopodite, caudal; 39, Leg 5, left endopodite, frontal; 40, Right leg 5, endopodite and exopodite 1, frontal. Scales = 100 μm.

translated): "The antennas of all animals are marked with 2 or 3 colored bands, each band includes 2–3 segments. Thus in some males, which I have directly under the microscope, on the antenna counting from the end, segments 6, 7, 8, 13 and 14 have a deep red coloration, which can be nearly black, while the other segments remain clear. Also the body shows these remarkable bands: segment 6 and 5 dark, 4 and 3 light, 2 again dark. A female is, in contrast, grass-green." Brehm (1937) confirmed this banding in his preserved specimens, but their color had changed to brownish red. The present, long-preserved specimens are light to dark brown with no trace of color banding.

Discussion and comparisons.—Brehm (1937) gave a cursory description of *A. furcatus* var. *macrochaetus*, with only two partial figures of the antennule and fifth leg of the female. Nevertheless, most characters mentioned by Brehm, including (in the male) the lack of spiniform processes on the right antennule segments 14 and 15, and the lateral spine of the right fifth leg exopodite 2 being much shorter than the segment, and (in the female) the long, strong subterminal spine of the leg 5 endopodite, and especially the strikingly long seta of antennule segment 16 agree exactly with the present specimens. Brehm (1937) stated that leg 5 endopodite of the female had three spines, but he probably mistook the rather stout proximalmost hairs of the subterminal hair row for a spine.

In other respects, as observed by Brehm, *A. macrochaetus* does indeed resemble *A. furcatus* and *A. furcatus* f. *exilis*. Important differentiating characters of *A. macrochaetus* include the long setae (especially on segment 16) of the antennule of both sexes; in males, the antennule lacking spiniform processes on segments 14 and 15 and with a long process on the antepenultimate segment, and, in the fifth leg, the large spiniform sensilla on the coxopodites, the small proximomedial lobe of the left basipodite, the long acute distomedial process of the right exopodite 1, and the relatively short lateral spine of the right exopodite 2; in females, the double lateral wings of pediger 5, and in the fifth leg, the bifid prominence of the coxopodite and the relatively long, two-segmented endopodite with two strong spines. These distinctive attributes fully justify raising the taxon to species rank.

Argyrodiaptomus macrochaetus has been reported only from the original collection, near the mouth of the La Plata River, Uruguay. The find near Porto Alegre extends its range northeastwards. Brehm (1937) did not specify the habitat, except that it was in fresh water. Apparently this is a species of temporary pools.

Cicchino (1994) pointed out the potential utility of the genital operculum in the taxonomy of diaptomids. She described the genital operculum structure in 10 South American species belonging to 6 genera, not including *Argyrodiaptomus*. The opercula of *A. nhumirim* and *A. macrochaetus* differ from all these in having a narrow proximal plate and broad distal plate with prominent lateral arms. The shape of the distal plate and its lateral arms resembles most that of species of *Notodiaptomus* Kiefer, 1936, but in *Notodiaptomus* the proximal plate is about as broad as the distal plate, and subrectangular (Cicchino 1994).

Austrinodiaptomus, new genus

Diagnosis.—Diaptomidae, Diaptominae. Species of temporary ponds. Left antennule of male and both antennules of female with 2 setae on segment 11 and 1 seta on each of segments 13–19; no setae with hooked ends, but several setae of terminal segments stout, with blunt tips. Legs 1–4 with lateral spine on each exopodite segment, except leg 1 exopodite 2 lacking spine. Schmeil's organ present on leg 2 endopodite 2. Male: urosomite 1 (genital somite) with small hair-sensillum on right distal margin. Right antennule with socketed spine on each of segments 8 and 12, and spiniform process on each of segments 10, 11, 13, 15, and 16;

antepenultimate segment with hyaline membrane along nearly entire length, but without process. Right leg 5, coxopodite not markedly expanded medially, caudal surface with large, distally directed protrusion bearing spiniform sensillum; basipodite produced posteriorly, ornamented only with tiny granules; endopodite of 1 short segment; exopodite 1 short and broad, exopodite 2 slightly expanded distally, bearing subterminal lateral spine and long slender terminal claw. Left leg 5, coxopodite with small protrusion bearing spiniform sensillum; basipodite slender, lacking surface ornament except lateral seta; endopodite of 2 short segments; exopodite 1 more than twice as long as exopodite 2, bearing medial haired pad; exopodite 2 narrow, with medial haired pad and ending in short stubby digitiform process and slightly longer proximal spine. Female: Pedigers 4 and 5 distinct, without dorsal process; lateral wings double, nearly symmetrical, each with 2 large spiniform sensilla. Urosome of 3 segments plus caudal rami, urosomite 2 short. Leg 5, coxopodite with large spiniform sensillum borne on conical protrusion on caudal surface, and with or without accessory spiniform process on anterolateral surface; basipodite with lateral seta inserted directly on segment, not on protrusion; exopodite 1 usually without ornament except for medial pore (1 specimen of *A. kleerekoperi* with lateral spiniform process on 1 leg), exopodite 2 with lateral spine, and exopodite 3 distinct, with 2 terminal spines; endopodite shorter than or equal to exopodite 1, with 2 or 3 short subterminal spines and subterminal oblique row of hairlike spinules.

Etymology.—From the Latin *austrinus*, south, prefixed to *Diaptomus*; gender masculine.

Type species.—*Austrinodiaptomus kleerekoperi*, new species.

Additional species.—*Austrinodiaptomus inexspectatus* (Brehm 1958), new combination.

Discussion and comparisons.—A combination of several characters makes it impossible to assign the new species to any existing genus of the family, particularly the several genera that include medium to large diaptomids of temporary ponds. These characters are, in both sexes, the two setae on antennule segment 11 and one seta on segments 13–19, the lack of hooked setae and the presence of stout blunt setae on some segments of the antennule, and the presence of Schmeil's organ on leg 2 endopodite 2. Characters of the male include the right antennule without a spiniform process on segment 14 or a process on the antepenultimate segment, and in leg 5, the short endopodites, the narrow left exopodite, and the right coxopodite without a large medial expansion. Characters of the female include the lack of a dorsal projection on pedigers 4 or 5, and in leg 5, the short stout spines on the endopodite, the presence of a lateral spine on exopodite 2, and the distinct exopodite 3.

Of the South American diaptomid genera, several (*Argyrodiaptomus*, *Colombodiaptomus* Gaviria 1989, *Dasydiaptomus* Defaye & Dussart, 1993, *Notodiaptomus* Kiefer 1936, *Prionodiaptomus* Light 1939, *Rhacodiaptomus*, and *Scolodiaptomus* Reid 1987) possess only 1 seta on antennule segment 11, among other differences. Other genera for which the antennular setation is undescribed (*Calodiaptomus* Kiefer 1936, *Dactylodiaptomus* Kiefer 1936) differ in having the male with spiniform processes on segment 14 and the antepenultimate segment of the right antennule, and the female with leg 5 exopodite 3 fused to exopodite 2, among other features. In *Aspinus* Brandorff, 1973b, exopodite 1 of legs 1–4 lacks a lateral spine. Females of *Idiodiaptomus* Kiefer, 1936 have one subterminal spine on the leg 5 endopodite; males possess a spiniform process on right antennule segment 14. Females of *Odontodiaptomus* Kiefer, 1936 have single pediger 5 wings and the leg 5 endopodite with only one subterminal spine; males have the right leg 5 endopodite long, and complex lobing on the basipodite and exopodite. In females of *Tumeodiaptomus* Dussart, 1979 the urosomite 2 is longer than broad and expanded, and in males there is a pectinate process on the antepenultimate segment of the antennule and the lateral spine of the right leg 5 exopodite 2 is inserted in the proximal half of the segment. Therefore, the new genus *Austrinodiaptomus* is proposed to accommodate the new species and the similar *D. inexspectatus*.

Austrinodiaptomus kleerekoperi, new species

Figs. 32–59

Diaptomus s.l. *inexspectatus* Brehm, 1958.—Brandorff 1972:50 (partim).—Brandorff 1973a:342 (partim).

Diaptomus s.l. *inexpectatus*.—Brandorff 1976:618 (partim).—Dussart & Defaye 1983:64 (partim).—Dussart 1984:64 (partim).—Battistoni 1995:958 (partim).

Rhacodiaptomus inexspectatus.—Brehm 1965:3, 11–14, fig. 1 (partim).

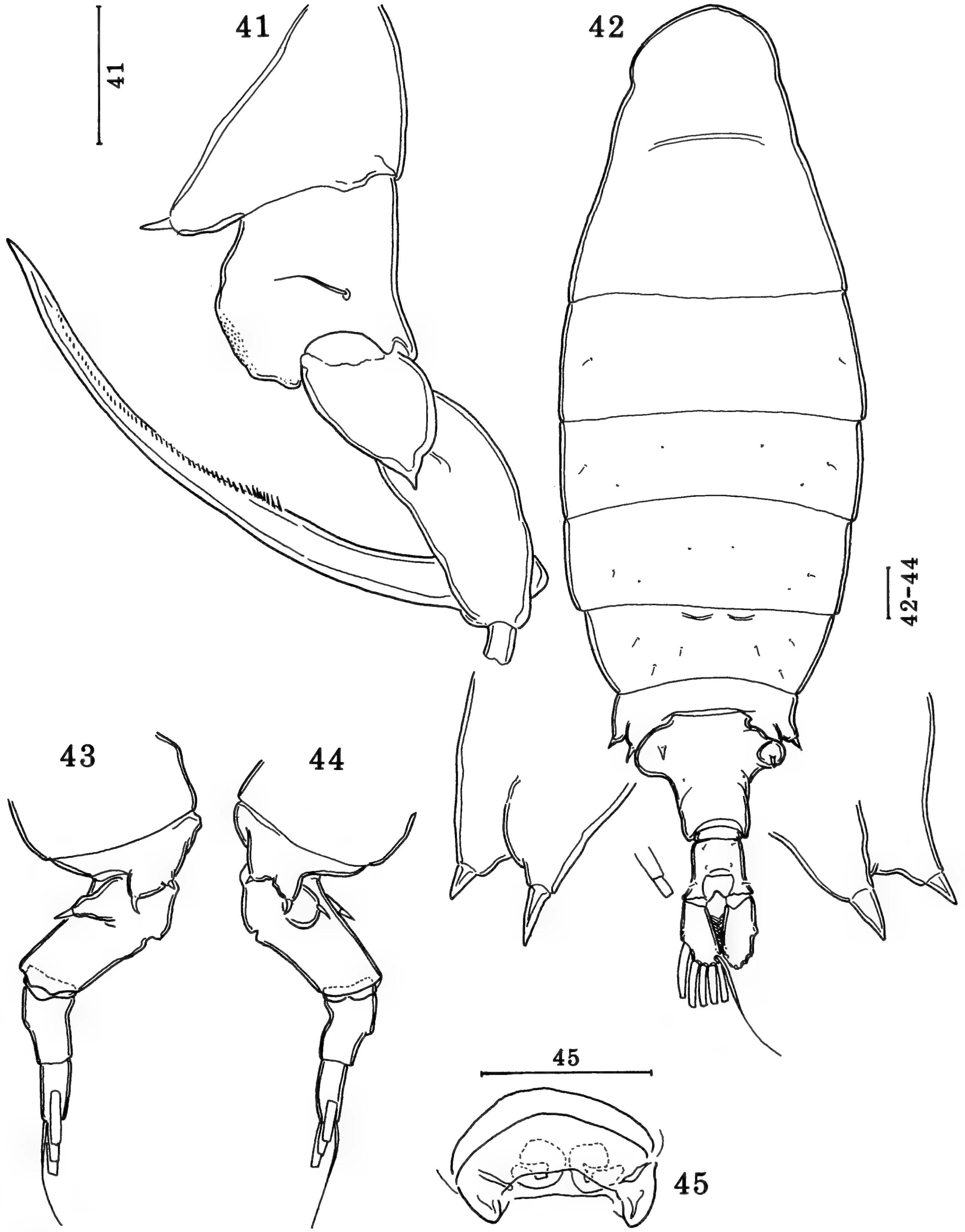
Material examined.—♂ holotype (MZUSP 12288) and ♀ allotype (MZUSP 12289), each fully dissected on slide. Paratypes: 2 ♀♀, ethanol-preserved (MZUSP 12290); ♀, dissected on slide, and 2 ♀♀ (1 broken) and 1 copepodid, ethanol-preserved (USNM 283124). All from R. W. Kiser Collection, Sample 465B/198, temporary pool near Porto Alegre, Rio Grande do Sul, Brazil, Sep 1941, leg. H. Kleerekoper. Accompanying fauna: see description of *A. macrochaetus*.

Male.—Length 1.2 mm. Body (Fig. 32) slender. Rostral points (not illustrated) acute. Pedigers 4 and 5 distinct. Lateral wings of pediger 5 small, nearly symmetrical, each with dorsal hair-sensillum and ventral spiniform sensillum, sensilla of right wing slightly larger. Right side of urosomite 1 slightly inflated and posteriorly produced, with short sensillum on distal corner. Right posterior corner of urosomite 4 produced in triangular process. Cephalosome broken; metasomites, most urosomites, and caudal rami with paired pores. Caudal rami haired on medial margins only.

Antennules reaching posterior end of anal somite. Right antennule (Figs. 33, 34) with 22 segments, geniculate between segments 18 and 19. Segments 8 and 12 each with small socketed spine; slender spiniform processes of segments 10 and 11 extending slightly outward from long axis of antennule and the latter well past base of next process; process of segment 13 large, with tiny subterminal hook; segment 14 without process, but segments 15 and 16 each with small spiniform process, process of segment 16 about twice as long as that of segment 15; antepenultimate segment lacking distal process, but with broad hyaline membrane extending along nearly entire length of segment (Fig. 34). Left antennule as in female. Seta on segment 16 broken, but reaching at least end of segment 19.

Schmeil's organ (Fig. 35) mammiform, located on caudal surface of leg 2 endopodite 2 (compare Fig. 55).

Leg 5 (Figs. 36–41): each coxopodite with large sensillum on lobe on caudal surface, left lobe small, right lobe large and produced distally (Fig. 41). Right coxopodite with distomedial margin not much expanded. Right basipodite with proximal part of medial margin slightly expanded, and distal part of caudal surface expanded, with field of tiny granules; lateral seta inserted at distal ⅔. Right exopodite 1 slightly broader than long, lateral margin about twice as long as medial margin, and distolateral corner produced in small, distally directed mammiform swelling. Right exopodite 2 lacking notable surface ornamentation, with distal half of medial margin expanded, broken lateral spine inserted subterminally, and partly serrate terminal claw, gently curved with recurved tip. Right endopodite represented by short conical protrusion with row of hairs along medial surface. Left basipodite long, proximomedial corner slightly expanded, surface smooth except for lateral seta inserted at distal ¾. Left exopodite



Figs. 41–45. *Austrinodiaptomus kleerekoperi*, new genus, new species; 41, holotype ♂ (MZUSP 12288): 41, Right leg 5, lateral; 42–45, allotype ♀ (MZUSP 12289): 42, Habitus, dorsal, showing tip of antennule and enlarged details of wings of pediger 5; 43, Posterior pedigers and urosome, right lateral; 44, Posterior pedigers and urosome, left lateral; 45, Genital operculum. Scales = 100 μm.

(Fig. 38) of 2 segments, exopodite 1 about twice as long as segment 2 and bearing medial haired pad; exopodite 2 bluntly quadrate, with field of tiny hairs on medial surface, medial pad with long hairs, slender, curved, naked proximal spine, and short, stubby, finely haired digitiform process. Left endopodite (Fig. 39) of 2 segments, endopodite 2 with row of hairs along medial surface.

Female.—Lengths of allotype 1.75 mm, of paratypes 1.72, 1.72, and 1.80 mm. Body (Figs. 42–44) stout; metasomites and urosome with several pairs of dorsal pores. Rostral points (not illustrated) acute. Pedigers 4 and 5 distinct. Pedigers 4 with pair of thick transverse bars near anterodorsal margin (Fig. 42) and slightly elevated posterodorsal margin (Figs. 43, 44). Lateral wings of pediger 5 large, approximately symmetrical, double, each wing with 2 large spiniform sensilla, dorsal sensillum ventrally curved (Figs. 43, 44). Urosome of 3 segments plus caudal rami. Anterior half of genital compound segment much expanded, conical right expansion directed dorsally and posteriorly, left expansion spherical, each with large acute spiniform sensillum; right posterior margin of segment extended in shallow trapezoidal process (Fig. 43). Genital operculum (Fig. 43). Genital operculum (Fig. 45) with narrow crescentic proximal plate, broad distal plate, and broad, prominent lateral arms set wide apart. Urosomite 2 broader than long, but narrower than other urosomites. Anal somite broadened posteriorly. Caudal rami haired on medial margins only.

Antennule (Figs. 46–48) reaching caudal rami, with 25 segments. Number of setae (s), spines (sp), and aesthetascs (a) of each segment as follows: (1) s + a, (2) 3s + a, (3) s + a, (4) s, (5) s + a, (6) s, (7) s + a, (8) s + sp, (9) 2s + a, (10) s, (11) 2s, (12) s + sp + a, (13) s, (14) s + a, (15) s, (16) s + a, (17) s, (18) s, (19) s + a, (20) s, (21) s, (22) 2s, (23) 2s, (24) 2s, (25) 5s + a. Seta of segment 16 reaching end of antennule. Larger setae of segments 18, 21, and 23–25 stout, with blunt tips; smaller setae of segments 22, 23, and 25 short and slender.

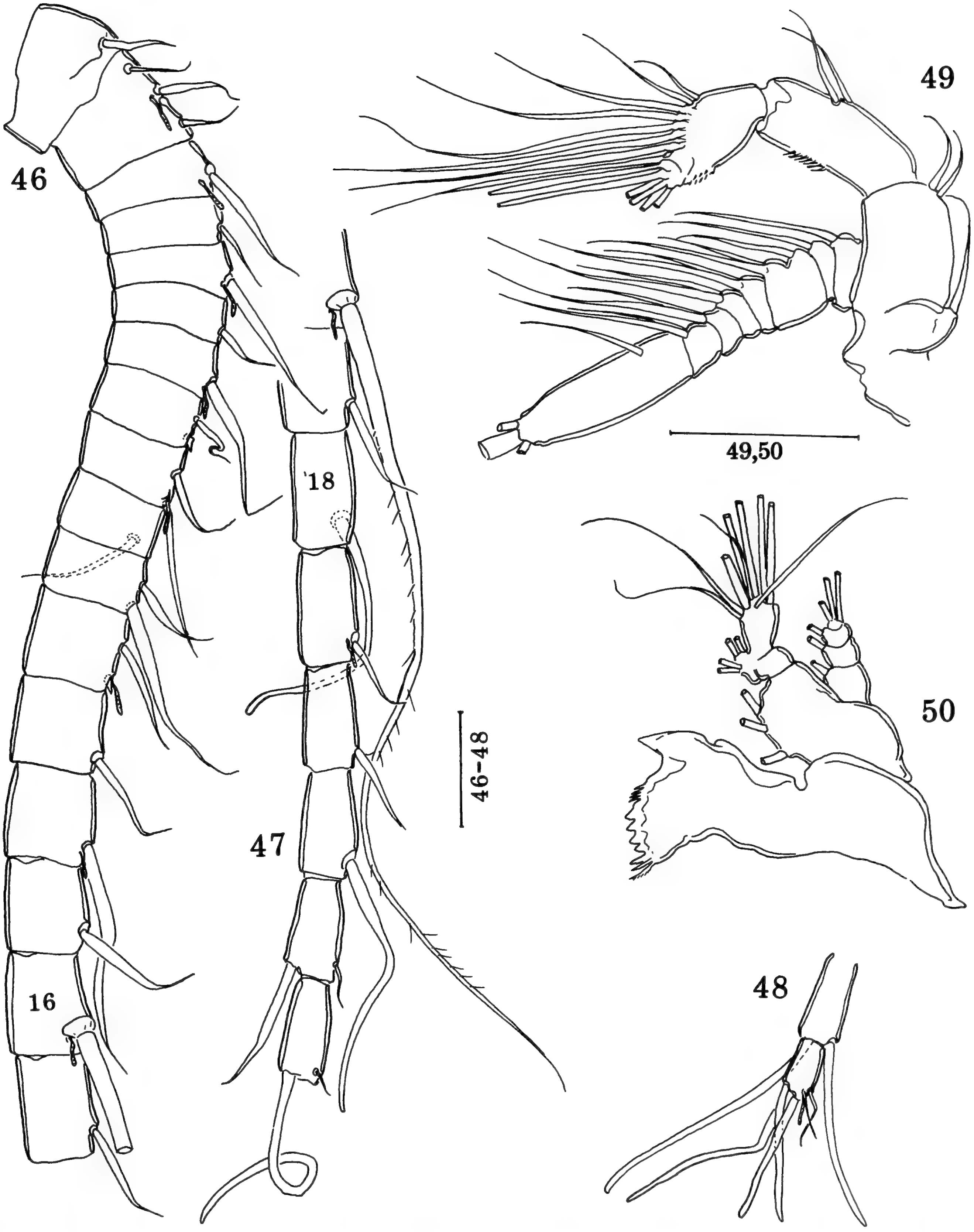
Antenna, mandible, maxillule, maxilla, and maxilliped (Figs. 49–53) of usual structure in family.

Leg 1 (Fig. 54) with 3-segmented exopodite and 2-segmented endopodite, exopodite 2 lacking lateral spine. Leg 2 (Fig. 55) with both rami 3-segmented and bluntly rounded Schmeil's organ (Fig. 56) borne on caudal surface of endopodite 2. Legs 3 and 4 (not illustrated) similar to leg 2 except slightly larger and lacking Schmeil's organ.

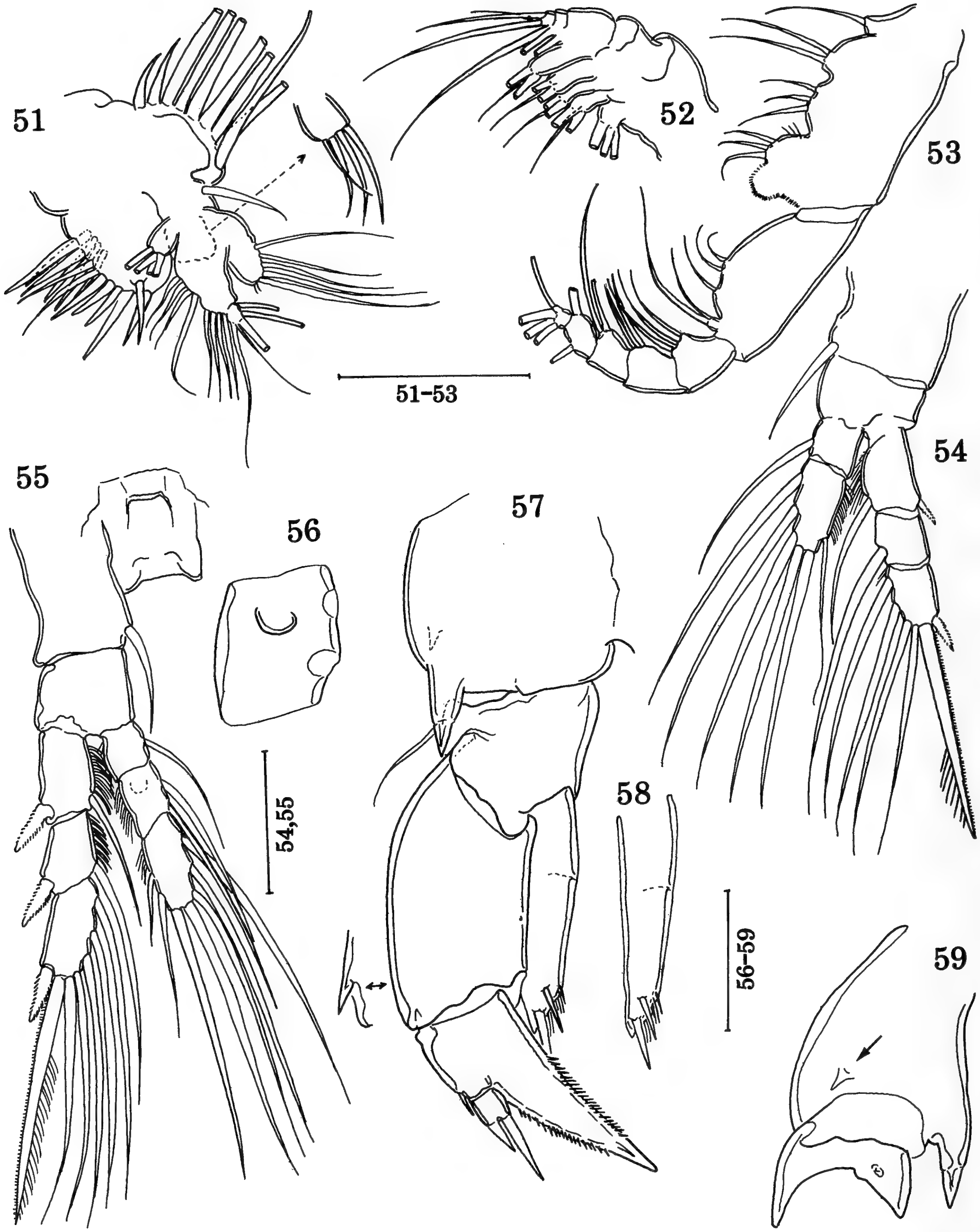
Leg 5 (Figs. 57–59): coxopodite stout, with large spiniform sensillum borne on coniform expansion on caudal surface, and spiniform process on anterolateral surface (indicated by arrow in Fig. 59). Basipodite with lateral seta inserted directly on segment, not on expansion. Exopodite 1 in most specimens without ornament except medial pore; allotype female with lateral spiniform process on 1 leg, as in detail of Fig. 57. Exopodite 2 with narrow lateral spine reaching midlength of exopodite 3, and stout claw serrate along most of each margin. Exopodite 3 distinct, with 2 stout terminal spines, lateral spine half length of medial spine. Endopodite as long as exopodite 1, indistinctly divided at proximal ⅓, with 2 short subterminal spines and oblique subterminal row of fine hairs.

Etymology.—This species is dedicated to Herman Kleerekoper, whose early investigations of southern Brazilian continental waters formed much of the basis for the subsequent development of the science of limnology in that country.

Discussion and comparisons.—Diaptomus s.l. *inexspectatus* was incompletely described from Argentinian material by Brehm (1958, repeated 1960). Later, Brehm (1965) made additional comments on supposed *D. inexspectatus* from old manuscript notes on female specimens collected from Las Garcias, Corrientes, Argentina, and (by H. Kleerekoper) near Porto Alegre, Brazil, and gave a sketch of a female from Porto



Figs. 46–50. *Austrinodiaptomus kleerekoperi*, new genus, new species; 46–48, allotype ♀ (MZUSP 12289); 49, 50, paratype ♀ (USNM 283124): 46, Antennule segments 1–17; 47, Antennule segments 16–23; 48, Antennule segments 24–25; 49, Antenna; 50, Mandible. Scales = 100 μm.



Figs. 51–59. *Austrinodiaptomus kleerekoperi*, new genus, new species; 51–55, paratype ♀ (USNM 283124); 56–59, holotype ♀ (MZUSP 12289): 51, Maxillule; 52, Maxilla; 53, Maxilliped; 54, Leg 1, frontal; 55, Leg 2, frontal; 56, Leg 2 endopodite 2, caudal, showing Schmeil's organ; 57, Leg 5, caudal, with detail of aberrant spiniform process on exopodite 2, found on one specimen; 58, Leg 5 endopodite, caudal; 59, Leg 5 coxa-basipodite, left lateral. Scales = 100 μm.

Alegre. Brehm (1965) claimed that his specimens from Brazil corresponded exactly with the Argentinian species. Certainly, Brehm's descriptions of the female of *D. inexspectatus* agree with the Brazilian specimens in hand regarding the distinctive double wings of pediger 5, the lobate genital compound segment, and certainly the leg 5 exopodite structure and ornament. However, there are several discrepancies. According to Brehm's (1958, 1960) descriptions, in females of the Argentinian population, the antennules reach the end of the caudal setae, the leg 5 endopodite is about ⅔ the length of exopodite 1 and bears three spines, the lateroterminal spine of exopodite 3 is about ⅙ as long as the medioterminal spine, and Brehm saw no spiniform sensillum on the left expansion of the female genital compound segment. Brehm's (1958, 1960) representations of the right leg 5 of the Argentinian male correspond with some features of the Brazilian specimen, such as the general proportions of the segments and terminal claw, the large coxopodite lobe, and the placement of the lateral exopodite spine. However, other features such as the right basipodite and exopodite 1 processes, and especially the left fifth leg exopodite do not correspond at all. Similarly, Brehm described the male right antennule as having a long segment 15 spiniform process (¾ the length of the process of segment 13). Even though Brehm had difficulty in describing the single, poorly preserved male, these discrepancies are difficult to explain as lapses of observation, and appear significant at the species level. Therefore it seems justifiable to propose a new taxon for the Brazilian population, pending redescription of the Argentine species and improvements in knowledge of variation.

Brehm (1965) transferred *D. inexspectatus* to the genus *Rhacodiaptomus* Kiefer, 1936, on the basis of the lobate genital compound segment of the female, while admitting that the structure of the male leg 5 did not agree with the diagnosis of *Rhacodiaptomus*. Subsequent authors (Brandorff 1972, 1973a, 1976; Dussart & Defaye 1983; Dussart 1984; Battistoni 1995) preferred to retain the species in *Diaptomus* Westwood, 1836 s.l.

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Literature Cited

Baird, W. 1850. The natural history of the British Entomostraca. The Ray Society, London, 364 pp. + pls. 1–36.

Battistoni, P. A. 1995. Crustacea Copepoda. Pp. 953–971 *in* E. C. Lopretto & G. Tell, eds., Ecosistemas de Aguas Continentales: Metodologías para su Estudio. Vol. 3, Ediciones Sur, La Plata.

Brandorff, G.-O. 1972. Ein Beitrag zur Calanidenfauna (Crustacea Copepoda) des Amazonasgebietes, mit einem Überblick über die Diaptomidae (Crustacea Copepoda) Sulamerikas. Unpublished Diplomarbeit, Max-Planck-Institut für Limnologie, Plön, 57 pp.

———. 1973a. Die neotropischer Gattung *Rhacodiaptomus* Kiefer (Crustacea, Copepoda), mit der Beschreibung von zwei neuen Arten.—Amazoniana 4:341–365.

———. 1973b. Neue freilebenden calanoide Copepoden (Crustacea) aus dem Amazonasgebiet.—Amazoniana 4:205–218.

———. 1976. The geographic distribution of the Diaptomidae in South America (Crustacea, Copepoda).—Revista Brasileira de Biologia 36: 613–627.

Brehm, V. 1933. *Argyrodiaptomus granulosus* nov.

spec., ein neuer Diaptomus aus Uruguay.—Zoologischer Anzeiger 104:283–287.

———. 1937. Weitere Mitteilungen über die Süsswasserfauna Uruguays. I. Teil.—Zoologischer Anzeiger 120:120–125.

———. 1958. Bemerkungen zu einigen Kopepoden Südamerikas.—Sitzungsberichten der Österreichischen Akademie der Wissenschaften, Mathematische-naturwissenschaftliche Klasse, I, 167:139–171.

———. 1960. Sobre los copepodos hallados por el Profesor Biraben en la Argentina. 6ª. Comunicación.—Neotrópica 6(20):49–54.

———. 1965. Bericht über eine unvollendet gebliebene Untersuchung der Argentinischen Kopepodenfauna.—Sitzungsberichten der Österreichischen Akademie der Wissenschaften, Mathematische-naturwissenschaftliche Klasse, I, 174:1–15.

Cicchino, G. 1994. Importance of the genital operculum in the taxonomy of South American Diaptomidae (Copepoda, Calanoida).—Hydrobiologia 292/293:143–147.

Daday, E. von. 1905. Untersuchungen über die Süsswasser-Mikrofauna Paraguays.—Zoologica 18(44):1–374 + pls. 1–23.

Defaye, D., & B. H. Dussart. 1993. *Dasydiaptomus* nom. nov. for *Trichodiaptomus* (Copepoda, Calanoida, Diaptomidae).—Hydrobiologia 257: 127.

Dussart, B. H. 1979. Algunos copépodos de América del Sur.—Publicación Ocasional del Museu Nacional de Historia Natural, Santiago de Chile 30:3–13.

———. 1984. Some Crustacea Copepoda from Venezuela.—Hydrobiologia 113:25–67.

———. 1985a. Another new diaptomid (Crustacea, Copepoda) from the Brazilian Amazon.—Amazoniana 9:275–280.

———. 1985b. Sur quelques copépodes d'Amérique du Sud. V. Diaptomidae.—Archiv für Hydrobiologie 103:201–215.

———, & D. Defaye. 1983. Répertoire mondial des crustacés copépodes des eaux intérieures. I.—Calanoïdes. Éditions du Centre National de la Recherche Scientifique, Paris, 224 pp.

Gaviria, S. 1989. The calanoid fauna (Crustacea, Copepoda) of the Cordillera Oriental of the Colombian Andes.—Hydrobiologia 178:113–134.

Kiefer, F. 1932. Versuch eines Systems der Diaptomiden (Copepoda, Calanoida).—Zoologisches Jahrbuch für Systematik 63:451–520.

———. 1936. Über die Systematik der südamerikanischen Diaptomiden (Crustacea, Copepoda).—Zoologischer Anzeiger 116:194–200.

Light, S. F. 1939. New American subgenera of *Diaptomus* Westwood.—Transactions of the American Microscopical Society 58:473–484.

Pesta, O. 1927. Ein Beitrag zur Kenntnis der Copepodenfauna von Argentinien.—Zoologischer Anzeiger 73:67–80.

Reid, J. W. 1987. *Scolodiaptomus*, a new genus proposed for *Diaptomus* (*sensu lato*) *corderoi* Wright, and description of *Notodiaptomus brandorffi*, new species (Copepoda, Calanoida), from Brazil.—Journal of Crustacean Biology 7: 364–379.

———, & I. H. Moreno. 1990. The Copepoda (Crustacea) of the southern Pantanal, Brazil.—Acta Limnologica Brasiliensia 3:721–739.

Richard, J. 1897. Sur quelques entomostracés d'eau douce des environs de Buenos Aires.—Anales del Museo Nacional de Buenos Aires 5:321–332.

Sars, G. O. 1901. Contributions to the knowledge of the fresh-water Entomostraca of South America as shown by artificial hatching from dried material. II. Copepoda—Ostracoda.—Archiv for Mathematik og Naturvidenskab 24:3–52 + pls. 1–8.

———. 1903. An account of the Crustacea of Norway. 4. Copepoda Calanoida. Bergen Museum, Bergen, 171 pp. + pls. 1–102, suppl. pls. 1–6.

Shen, C. J., & A. Y. Tai. 1964. Descriptions of eight new species of freshwater Copepoda (Calanoida) from the Delta of the Pearl River, South China.—Acta Zoologica Sinica 16:225–246. (in Chinese; English summary.)

———. 1965. Descriptions of six new species of freshwater copepods chiefly from the Pearl River Delta, South China.—Acta Zootaxonomica Sinica 2:126–140. (in Chinese; English summary.)

Van Douwe, C. 1911. Neue Süsswasser-Copepoden aus Brasilien.—Zoologischer Anzeiger 37:161–163.

———. 1912. Zur Kenntnis der Süsswassercopepoden von Brasilien.—Archiv für Hydrobiologie 7:309–321.

Westwood, J. O. 1836. *Cyclops* (Muller).—British Cyclopaedia of Natural History 2:227–228.

Wright, S. 1935. Three new species of *Diaptomus* from Northeast Brazil.—Annaes da Academia Brasileira de Sciencias 7:213–233 + pls. 1–4.

———. 1938. A review of the *Diaptomus bergi* group, with descriptions of two new species.—Transactions of the American Microscopical Society 57:297–315.

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Lophogaster muranoi, a new species of mysid from the coastal waters of Argentina (Crustacea: Mysidacea: Lophogastridae)

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Abstract.—*Lophogaster muranoi*, a new species, is described from the coastal waters of Argentina. This new species is characterized by the medium-sized median rostral spine extending slightly beyond the apex of the antennular lobe, the presence of a pair of the postorbital spines on the carapace, and the telson armed with 4 pairs of lateral spines and a narrow apical median plate. This is the third species of the genus *Lophogaster* from the South Atlantic Ocean.

The genus *Lophogaster* comprises 18 species and 1 subspecies to date, all from tropical to temperate waters of the world. Among them, only two species, *L. spinosus* Ortmann, 1906 and *L. challengeri* Fage, 1940, have been represented in the South Atlantic Ocean, the former was recorded from mid-Atlantic waters (Fage 1942) and off Rio de Janeiro (O. Tattersall 1955) and the latter from coastal waters of South Africa (G. Sars 1885, Fage 1942, O. Tattersall 1955) and Cape of Lopez, West Africa (O. Tattersall 1955).

An undescribed species of *Lophogaster* collected from coastal waters of San Matías Gulf and Río de la Plata estuary, Argentina, is the first species of the genus from Argentine waters. In this paper a description of the new species is given.

The type specimens are deposited in the National Science Museum, Tokyo (NSMT).

Lophogaster muranoi, new species
Figs. 1–4

Type series.—Holotype (NSMT-Cr 11994), adult male (19.2 mm, tip of the median spine of the rostrum to the posterior end of the telson except apical spines); allotype (NSMT-Cr 11995), adult female (18.8 mm); paratypes (NSMT-Cr 11996), 1 adult male (18.0 mm) and 1 adult female (16.0 mm); San Matías Gulf (42°09′S, 64°32′W); depth 170 m; 11 to 22 May 1991.

Other material.—1 adult male (16.0 mm), 1 adult female (16.0 mm), 1 immature male (13.4 mm) and 2 immature females (13.0 and 14.4 mm); same as type specimens. 1 adult male (15.8 mm), 2 adult females (13.4 and 16.0 mm), 1 immature male (13.0 mm) and 3 juveniles (7.8-9.6 mm); Río de la Plata estuary (35°32′S, 53°18′W); depth 52 m; 12 Oct 1995; collected with a Bongo net, 45–0 m oblique tow by the R/V *Oca Balda* of the INIDEP, Mar del Plata, Argentina.

Description.—Carapace covered with minute tubercles on anterior half of dorsal surface; rostrum covering eyestalks and proximal 2 segments of antennular peduncles, tridentate anteriorly, median process medium-sized extending slightly beyond apex of antennular lobe, lateral spines short; lateral margin of rostrum concave, minutely serrate (Fig. 1A, B); posterior margin of carapace deeply emarginate, leaving eighth or seventh and eighth thoracic somites exposed dorsally, furnished dorsally with fine setae; postero-lateral angles of carapace terminating in comparatively long, slightly upward spine (Fig. 4C); pair of prominent postorbital spines present (Fig. 1A, B).

Antennular peduncle robust; first segment as long as broad; second segment short, with outer distal corner produced and tipped with 2 plumose setae; third segment slightly shorter than first and second segments combined, distal margin produced into 2 blunt processes with spinules frontally (Fig. 1A, B); antennular lobe from third segment with finely serrated and rounded anterior margin with slight median depression armed with 2 unequal setae (Fig. 1C).

Antennal scale cordiform, 1.8 times as long as widest part; outer margin slightly convex, armed with 5 denticles in holotype and 6 in allotype on distal 0.7, terminating in long, straight, acute spine; inner margin setose (Fig. 1B, D). Antennal peduncle composed of 3 segments; first segment with acutely pointed small process at inner distal corner, third segment longer than proximal 2 segments combined, inner distal corner ending in long, outwardly curved spine (Fig. 1D).

Labrum triangular, produced anteriorly into acute spinose process. Mandibular palp long and slender, second segment longest, 6 times as long as broad, third segment 0.7 of second segment in length, armed densely with short setae on distal 0.8 (Fig. 1E). Maxillule with outer lobe armed with 13 strong spines on terminal margin and 1 long seta on basal part, inner lobe rounded with 7 long and 8 short setae (Fig. 1F). Maxilla with exopod oval, armed with many plumose setae on whole margin, second segment of endopod twice as long as broad at its base (Fig. 1G).

Each sternum of second to seventh thoracic somites with 2 acutely pointed spine-like processes on midline; anterior one short, posterior one long and forward-directed.

First thoracic limb short and robust; exopod short, leaf-like, 2-segmented, without setae, endopod with expanded merus and carpopropodus armed with 3 stout setae each on inner margin in addition to slender setae, dactylus with stout claw; epipod large (Fig. 2A). Second thoracic limb slender; exopod short, about half length of endopod; endopod setose on inner margin, dactylus with small curved claw (Fig. 2B). Third and fourth thoracic limbs long and slender, exopod similar to that of second limb (Fig. 2C, E); endopod of third limb with dactylus armed with 3 hooked spines on distal half and 3 ordinary spines on proximal half of inner margin (Fig. 2D); endopod of fourth limb with merus armed densely with short and slender spines on distal half of inner margin (Fig. 2F), dactylus without spines as seen in third limb. Fifth thoracic limb robust, exopod 14-segmented; endopod with merus longest, 1.2 times longer than carpopropodus and dactylus combined (Fig. 2G). Sixth to eight thoracic limbs stout, exopod 9-16-segmented; endopod with merus short, 0.6 as long as carpopropodus (Fig. 3A–C).

Marsupium of female composed of 7 pairs of brood lamellae.

Each abdominal somite with well-developed pleural plate; first to fifth somites with short, acutely pointed, median process; sixth somite armed posteriorly with pair of sharp denticles about half length of apical spines of telson (Fig. 4A).

Pleopods in both sexes well-developed and biramous; exopods 23–26 segments, longer than 13–19 segments of the endopods (Fig. 3D–H).

Uropods shorter than telson; exopod undivided, outer margin naked, terminating in tooth, inner margin setose; endopod slightly longer than exopod, both inner and outer margins setose (Fig. 4A).

Telson 2.2 times longer than last abdominal somite, about 3 times as long as broad at its base; lateral margin armed with 4 spines; subapical one long, half the length of apical spines and located away from proximal 3 arranged at regular intervals; apical margin narrow, with pair of strong spines at corners, median plate, 4 spinules, narrow, and pair of plumose setae present

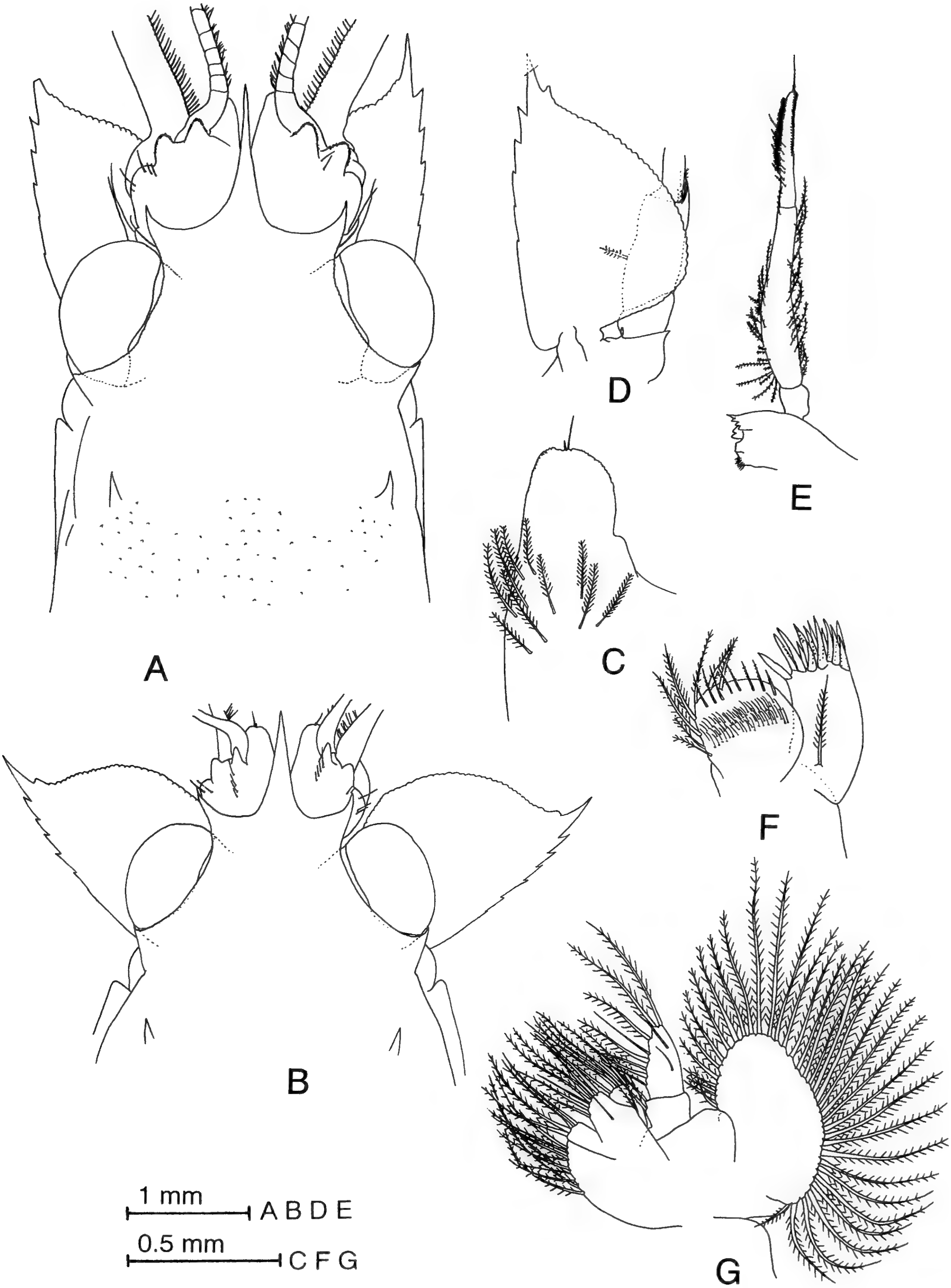

Fig. 1. *Lophogaster muranoi*, new species. A, C–G: holotype (male); B: allotype (female). A, Anterior end, dorsal view; B, anterior end, dorsal view; C, antennular lobe, ventral view; D, antenna; E, mandible; F, maxillule; G, maxilla.

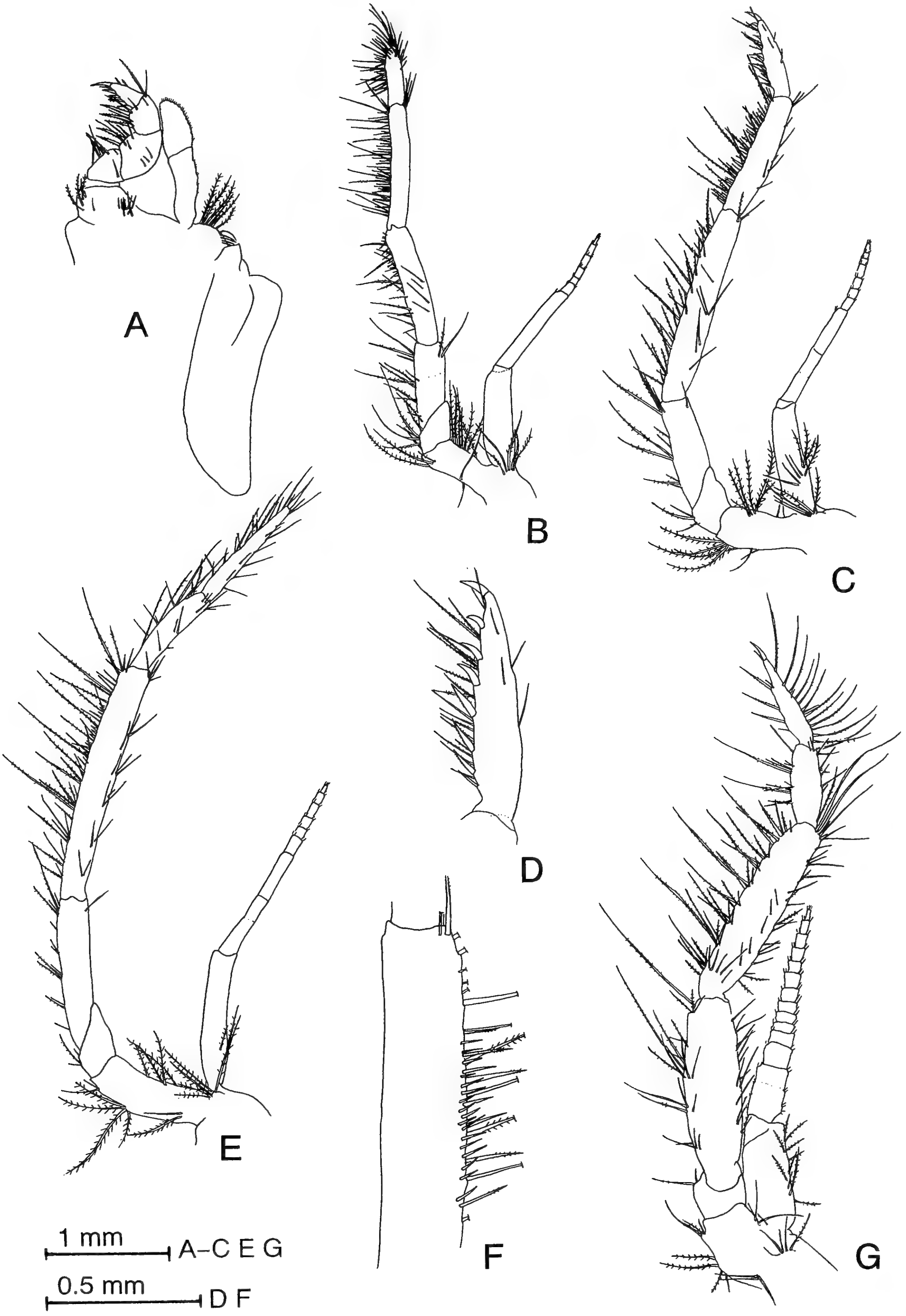

Fig. 2. *Lophogaster muranoi*, new species. Holotype (male). A, First thoracic limb; B, second thoracic limb; C, third thoracic limb; D, dactylus of third thoracic limb; E, fourth thoracic limb; F, merus of fourth thoracic limb; G, fifth thoracic limb.

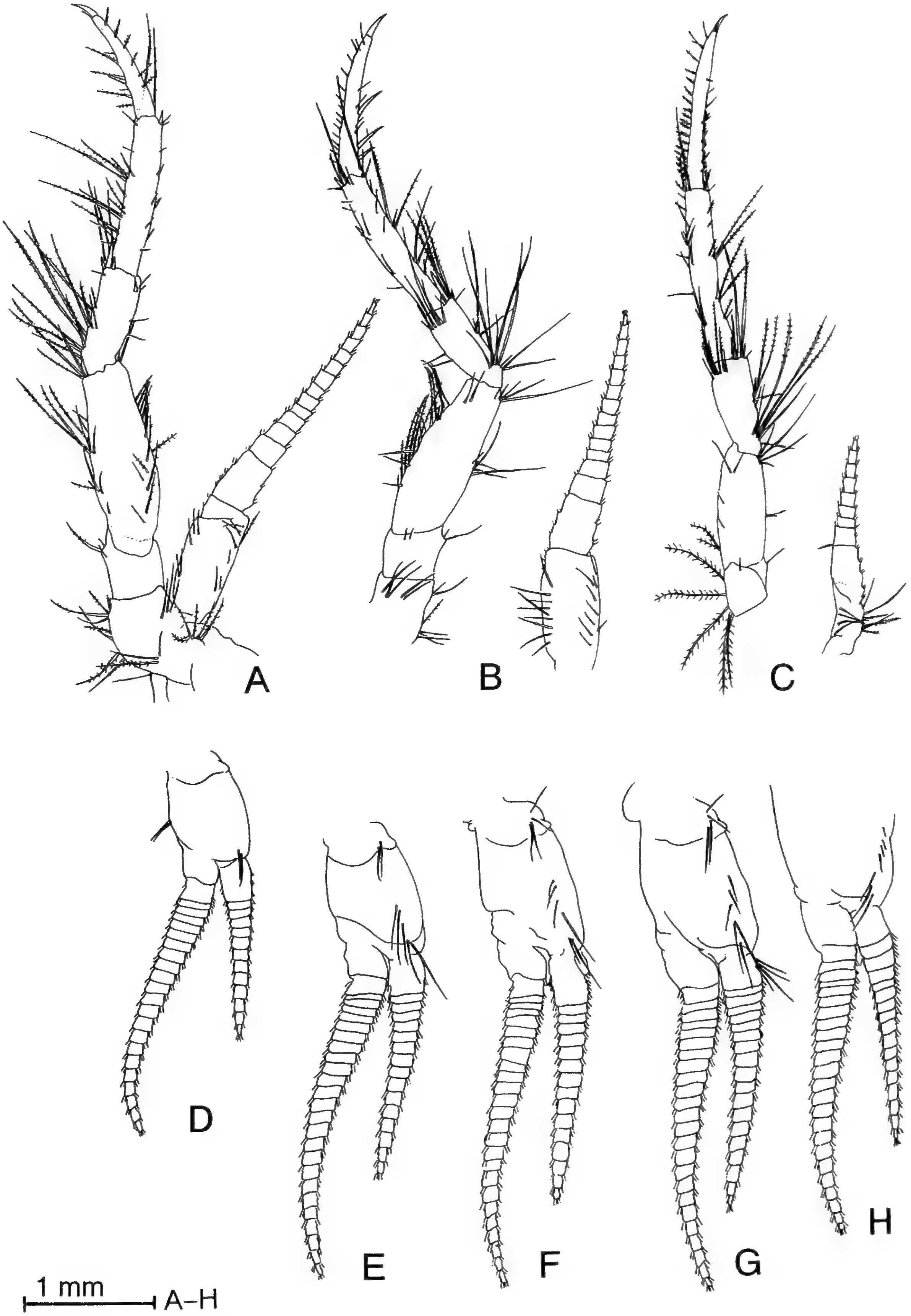

Fig. 3. *Lophogaster muranoi*, new species. Holotype (male). A–C, Sixth to eigth thoracic limbs; D–H, first to fifth pleopods.

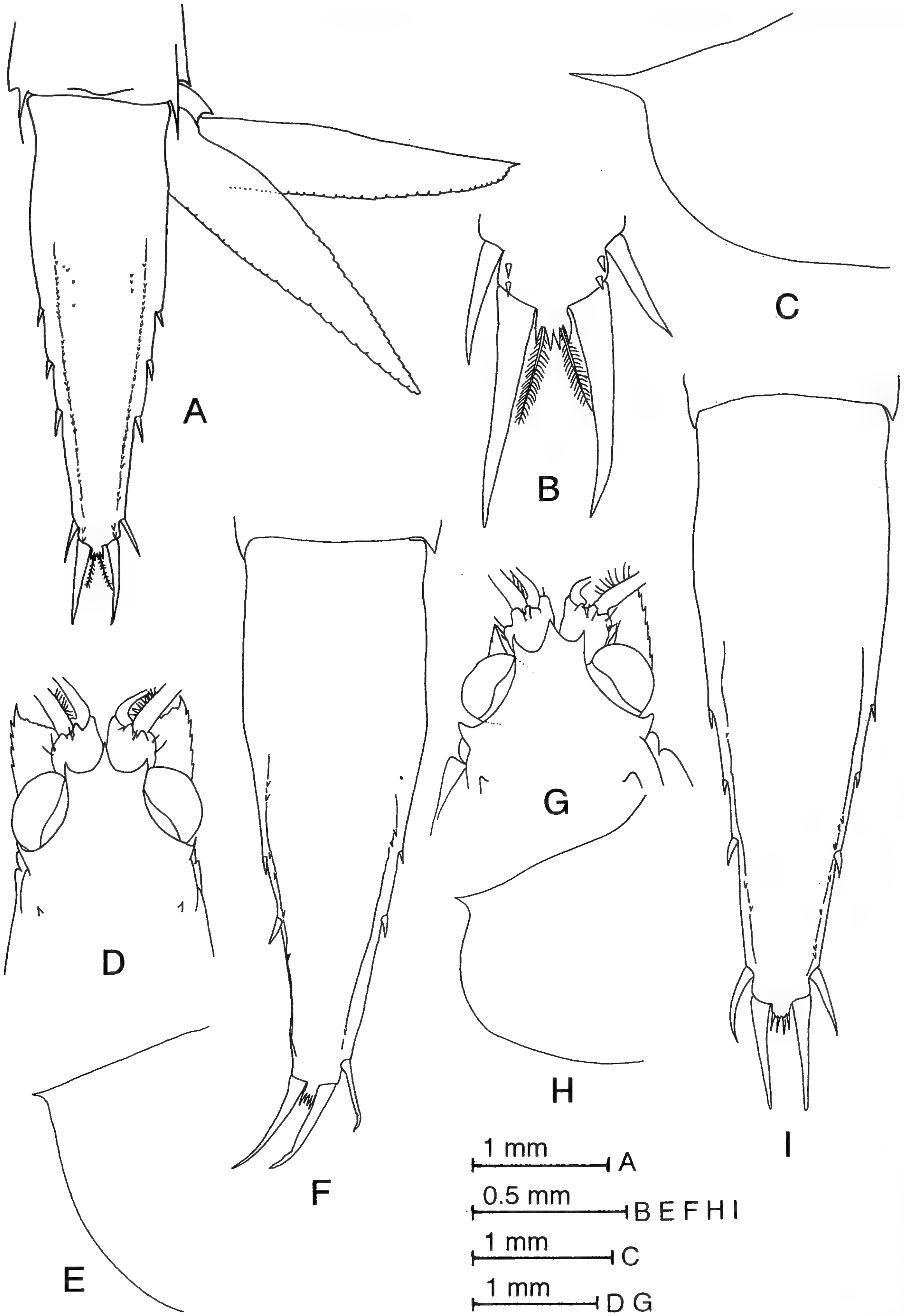

Fig. 4. *Lophogaster muranoi*, new species. A–C: holotype (male); D–F: young specimen (7.8 mm); G-I: young specimen (8.0 mm). A, Telson and uropod; B, apical part of telson; C, right postero-lateral part of carapace; D, anterior end, dorsal view; E, postero-lateral part of carapace; F, telson; G, anterior end, dorsal view; H, right postero-lateral part of carapace; I, telson.

between outer 2 indentations of median plate; 2 spinose dorsal keels present on posterior 0.8 of telson (Fig. 4A, B).

Morphological change with growth.—In many species of the genus *Lophogaster*, geographical variation, sexual dimorphism and morphological change with growth have been observed in several characters (Hansen 1910, Fage 1942, O. Tattersall 1960, Casanova 1993, 1996). In this new species morphological change with growth was observed in the lengths of the median rostral spine and the postero-lateral spine of the carapace, and in the number of lateral spines of the telson (Fig. 4D–I). The median rostral spine of young specimens is much shorter as compared to adults and extends only to the middle of the third segment of the antennular peduncle. The postero-lateral spine of the carapace is also shorter in young specimens than in adults. Three lateral telson spines are present in the smallest specimen (7.8 mm body length) compared to 4 in larger specimens. The microscopic tubercles on the carapace become noticeable in older specimens. The antennular lobe, the postorbital spines on the carapace, and the apical plate of the telson do not change with growth or gender.

Etymology.—Named in honor of Dr. Masaaki Murano.

Remarks.—*Lophogaster muranoi*, new species, is related to *Lophogaster typicus* in respect to the rounded antennular lobe, the presence of a pair of the postorbital spines, and the armature of the telson, but differs from the latter species in the following ways. The median rostral spine extends beyond the apex of the antennular lobe in *L. muranoi*, while it ends in the middle of the distal segment of the antennular peduncle in *L. typicus*, the spine at postero-lateral angle of the carapace is much longer in *L. muranoi* than in *L. typicus*, and in *L. muranoi* the apical margin of the telson between the pair of the long apical spines forms a narrow projecting plate while the apical margin does not protrude to a plate in *L. typicus*.

Tattersall & Tattersall (1951) observed that for *L. typicus* the coarse serrations on the antero-lateral margin of the rostrum, which is seen in younger specimens, is gradually lost as growth proceeds and completely disappears at a length of 13 mm. In *L. muranoi* the minute serrations on the lateral margin of the rostrum are retained continuously from the younger stage (7.8 mm) to the adult (19.2 mm).

Lophogaster muranoi is easily distinguishable from the two known species from the South Atlantic Ocean, *L. challengeri* and *L. spinosus*, by the presence of the postorbital spines on the carapace.

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Literature Cited

Casanova, J.-P. 1993. Crustacea Mysidacea: Les Mysidacés Lophogastrida et Mysida (Pethalophthamidae) de la région néo-calédonienne. *in* A. Crosnier, ed., Résultats des Campagnes MUSORSTOM, Volume 10.—Mémoires du Museum national d'Histoire naturelle 156:33–53.

———. 1996. Crustacea Mysidacea: Les Lophogastridés d'Indonésie, de Nouvelle-Calédonie et des Îles Wallis et Futuna. *in* A. Crosnier, ed., Résultats des Campagnes MUSORSTOM, Volume 15.—Mémoires du Museum national d'Histoire naturelle 168:125–146.

Fage, L. 1942. Mysidacea Lophogastrida II. The Carlsberg Foundation's oceanographical expedition round the world 1928–1930 and previous "Dana" expeditions under the leadership of Prof. Johannes Schmidt.—Dana Report 23:1–67.

Hansen, H. J. 1910. The Schizopoda of the Siboga expedition.—Siboga-Expeditie 37:1–123.

Sars, G. O. 1885. Crustacea I. *in* Den Norske Nordhavs-Expedition, 1876–78, Christiana, 14, Zool.: 1–280. (not seen)

Tattersall, O. S. 1955. Mysidacea.—Discovery Report 28:1–190.

———. 1960. Notes on mysidacean crustaceans of the genus *Lophogaster* in the U. S. National Museum.—Proceedings of the United States National Museum 112:527–547.

Tattersall, W. M., & O. S. Tattersall. 1951. The British Mysidacea.—The Ray Society, London, Volume 136:1–460.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(4):608–616. 1997.

A new species of troglobitic crayfish of the genus *Cambarus*, subgenus *Aviticambarus* (Decapoda: Cambaridae), endemic to White Spring Cave, Alabama

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Abstract.—*Cambarus* (*Aviticambarus*) *veitchorum* is a rare, diminutive species of troglobitic crayfish endemic to White Spring Cave in the Tennessee River Valley, Limestone County, Alabama. It is most closely related to *C.* (*A.*) *hamulatus*, which occurs in subterranean waters of the Sequatchie Uplift in Alabama and Tennessee, and is less closely related to *C.* (*A.*) *jonesi*, with which it is syntopic and whose range encompasses both sides of the Tennessee River in Alabama. The new species differs from the other *Aviticambarus* in the relationships of the terminal elements of the gonopod (male first pleopod); the shape of the abdominal pleura and presence of spines at their caudoventral angles; the lack of spines or prominent tubercles on the mesial surface of the carpus; the attenuated podomeres of the pereiopods, especially of the cheliped; the morphology of the epistome; and the structure of the annulus ventralis of the female.

Six species of troglobitic crayfishes, four described and two undescribed, are known to live in subterranean waters of northern Alabama. The described species are *Cambarus* (*Aviticambarus*) *hamulatus* (Cope 1881), which occurs in caves of the Sequatchie Uplift in Blount, Jackson, and Marshall counties; *Cambarus* (*Aviticambarus*) *jonesi* Hobbs & Barr, 1960, whose range encompasses both sides of the Tennessee River Valley, from Madison County west into Colbert and Lauderdale counties; *Orconectes* (*Orconectes*) *australis australis* (Rhoades 1941), known only from Jackson and Madison counties; and *Procambarus* (*Remoticambarus*) *pecki* Hobbs, 1967, reported from three caves along the Tennessee River, one each in Colbert, Lauderdale, and Morgan counties (see Hobbs et al. 1977). *Cambarus jonesi*, *P. pecki*, and the two unnamed species are endemic to Alabama, but the ranges of *C. hamulatus* and *O. a. australis* extend north into Tennessee. Each of the two undescribed forms is known from but a single cave, one in Madison County and the other in Limestone County. The description of the former species has been submitted for publication, and the latter is described herein. Only seven specimens of this rare crayfish, six adults and a juvenile, have been collected.

Cambarus (*Aviticambarus*) *veitchorum*, new species
Fig. 1

"Three new species."—Cooper & Cooper, 1966:39 (p. p.); Cooper, 1967:14 (p. p.).
Cambarus (*Aviticambarus*) sp. A.—Bouchard, 1976:14, 15.
"Two crayfishes of subgenus *Aviticambarus*."—Hobbs et al., 1977:5 (p. p.).
"Two undescribed troglobites."—Hobbs et al., 1977:75 (p. p.).
C. (*A.*) sp. A.—Fitzpatrick, 1990:78.

Diagnosis.—Albinistic; eyes degenerate, recessed, lacking pigment. Rostrum acarinate, excavate, margins narrow, slightly elevated, and parallel or subparallel to base of long acumen, which delimited by strong marginal spines; margins of acumen constricted at base, then broadly concave and strongly converging to acute, cephalodorsally directed apex; acumen comprising 35.0 to 43.2% ($\bar{X} = 39.4$) of rostrum length, latter constituting 23.3 to 25.9% ($\bar{X} = 24.6$) of total carapace length (TCL). Areola 5.1 to 7.4 ($\bar{X} = 6.1$) times as long as broad, constituting 40.0 to 43.1% ($\bar{X} = 41.3$) of TCL and 52.7 to 55.8% ($\bar{X} = 54.6$) of postorbital carapace length (PCL), with 4 to 5 punctations across narrowest part. Cephalothorax subovate; carapace 1.4 to 2.3 ($\bar{X} = 1.8$) times wider than deep, dorsally punctate, laterally granulate. Cervical spines strong, usually 1 or 2 on each side. Branchiostegal spine strong; hepatic region with scattered weak tubercles. Suborbital angle obsolete, margin of orbit diagonal. Postorbital ridge moderately strong, groove obsolete and represented by row of minute punctations, cephalic margin with strong spine. Antennal scale 2.5 to 2.8 ($\bar{X} = 2.7$) times as long as wide, greatest width just distal to midlength; lateral margin thickened and terminating distally in strong spine.

Chela of cheliped attenuate, width of palm 15.1 to 21.9% ($\bar{X} = 19.1$) of total length of chela, latter 58.3 to 76.0% ($\bar{X} = 64.6$) of TCL and 64.4 to 98.4% ($\bar{X} = 82.4$) of PCL; palm subovate in cross section, 1.3 to 1.9 ($\bar{X} = 1.4$) times as wide as deep, 2.3 to 3.1 ($\bar{X} = 2.6$) times as long as wide; mesial margin of palm with 2 or 3 poorly defined rows of minute tubercles, 13 to 18 (usually 15-16) in mesial row, length of margin 45.4 to 51.0% ($\bar{X} = 48.4$) of total chela length. Fingers without gape, without dense setae at opposable bases; both fingers with longitudinal ridge dorsally and ventrally; opposable margin of fixed finger usually bearing 3 to 4 tubercles in addition to usual subconical one; mesial margin of dactyl punctate, with 1 to 3 small tubercles near base; opposable margin of dactyl usually with 3 to 4 tubercles, one of which larger than others, subconical, and situated ventral to denticles; dactyl length 1.0 to 1.2 ($\bar{X} = 1.1$) times length of mesial margin of palm, 2.7 to 3.4 ($\bar{X} = 2.8$) times width of palm, and 50.1 to 59.4% ($\bar{X} = 53.8$) of total chela length. Carpus of cheliped subrectangular in dorsal outline, 1.5 to 2.5 ($\bar{X} = 2.0$) times as long as wide, mesial surface without spines or prominent tubercles. Merus of cheliped attenuate, 4.0 to 5.7 ($\bar{X} = 4.6$) times longer than deep, length 41.4 to 52.1% ($\bar{X} = 45.8$) of TCL and 54.5 to 67.4% ($\bar{X} = 60.5$) of PCL. Pleura of second through fifth abdominal segments with angular caudoventral corners, and spine at caudoventral apex of angle. Mesial ramus of uropod with foreshortened median keel, which lacking distal spine; cephalic section of telson with 2 cephalolateral spines each side.

Hook on ischium of third pereiopod, that of form I male slightly overreaching basioischial articulation, not opposed by tubercle on basis; coxa of fourth pereiopod of males with prominent caudomesial boss, which somewhat laterally compressed. Gonopods (first pleopods) of form I male symmetrical in caudal aspect, total length 21.0% of TCL, proximomesial apophyses widely separated; proximolateral lobe set off from rest of shaft by transverse groove; left gonopod in lateral aspect with moderate protuberance on cephalic border; central projection corneous, curved at greater than 90° angle to shaft, strongly tapering to subacute, proximomesially directed tip; subapical notch present, directed proximally; caudal portion of central projection with proximal margin twisted mesially; mesial process curved, somewhat expanded at base but tapering to subacute tip, which directed caudolaterally and extending caudally to level of tip of central projection or beyond; caudal knob absent; in mesial aspect, cephalic protuberance obvious, mesial surface lacking setae.

Annulus ventralis symmetrical, subovate, 1.8 times wider than long; caudal margin free, broadly convex, elevated, and dissected by sinus just dextral to midline, at which point caudosinistral terminus of wall plunging into expanded caudodextral terminus; lateral apices of caudal wall moderately expanded; cephalic margin of annulus arched, clearly delimited but fused to preannular sternite; cephalolateral margins relatively thick, slightly concave on each side of median arch; cephalic half of annulus with broad central depression, which extending into caudal half as oblique depression on each side of median C-shaped ridge surrounding caudosinistral terminus of caudal wall. Postannular sclerite about 3 times as wide as long, with sublinear caudal margin, broadly convex cephalic margin, and domed ventral surface bearing some small tubercles. Female first pleopod absent, slight protuberance at site on each side.

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

Table 1.—Measurements (mm) of types of *Cambarus* (*Aviticambarus*) *veitchorum,* new species.

	Holotype	Allotype	Morphotype
Carapace			
Total length	16.7	14.5	15.9
Postorbital length	12.9	11.0	12.1
Length cephalic section	9.5	8.6	9.2
Width	6.1	5.5	6.2
Depth	3.5	3.1	3.6
Length rostrum	4.0	3.6	3.7
Length acumen	1.4	1.4	1.6
Areola			
Length	7.2	5.9	6.7
Width	1.4	1.0	0.9
Antennal scale			
Length	3.6	3.5	3.5
Width	1.3	1.3	1.3
Abdomen			
Length	18.2	15.8	17.3
Width	5.3	4.1	5.1
Cheliped (right)			
Length lateral margin chela	12.7	8.6	10.4
Length mesial margin palm	6.1	4.2	5.3
Width palm	2.3	1.7	2.1
Depth palm	1.8	1.1	1.6
Length dactyl	6.4	4.7	5.6
Length carpus	3.7	2.9	3.2
Width carpus	2.0	1.4	1.6
Length dorsal margin merus	8.7	6.0	7.7
Depth merus	1.9	1.5	1.8
Gonopod length	3.4	NA	3.4

Holotypic male, form I.—Cephalothorax (Fig. 1A, D) subovate; carapace 1.7 times wider than deep. Areola 5.1 times as long as broad, constituting 43.1% of TCL (55.8% of PCL), with dense, small punctations, 5 or 6 across narrowest part; branchiocardiac grooves subparallel throughout most of length, caudally flared, with transverse eminence between caudal termini. Rostrum with narrow, somewhat elevated margins, parallel nearly to level of strong marginal spines, where moderately converging to bases of spines; margins of acumen slightly concave, converging strongly to corneous, cephalodorsally directed apical spine reaching distal margin of second article of antennular flagellum; acumen comprising 35.0% of rostrum length, latter constituting 24.0% of TCL; floor (dorsal surface) of rostrum with deep longitudinal excavation, apunctate except for small punctations proximal to marginal spines, and row of punctations bearing long, recumbent setae just mesial to each marginal ridge; subrostral ridge narrowly visible to base of marginal spines in dorsal aspect. Postorbital ridge fairly strong, groove obsolete and represented by row of small punctations; dorsal margin ridgelike, cephalic margin with strong spine. Branchiostegal spine strong; suborbital angle obsolete, orbital rim with slight concavity around base of antennal peduncle, dorsal to which rim oblique. Carapace dorsally punctate, laterally and dorsolaterally granulate; cephalic section 1.3 times longer than areola and constituting 56.9% of TCL; gastric region mostly glabrous, with some scattered punctations; carapace cephalolateral to cervical groove with small scattered tubercles, and row of same along ventral margin of cephalic portion of cervical groove. Cervical spines strong, 1 on each side. Abdomen

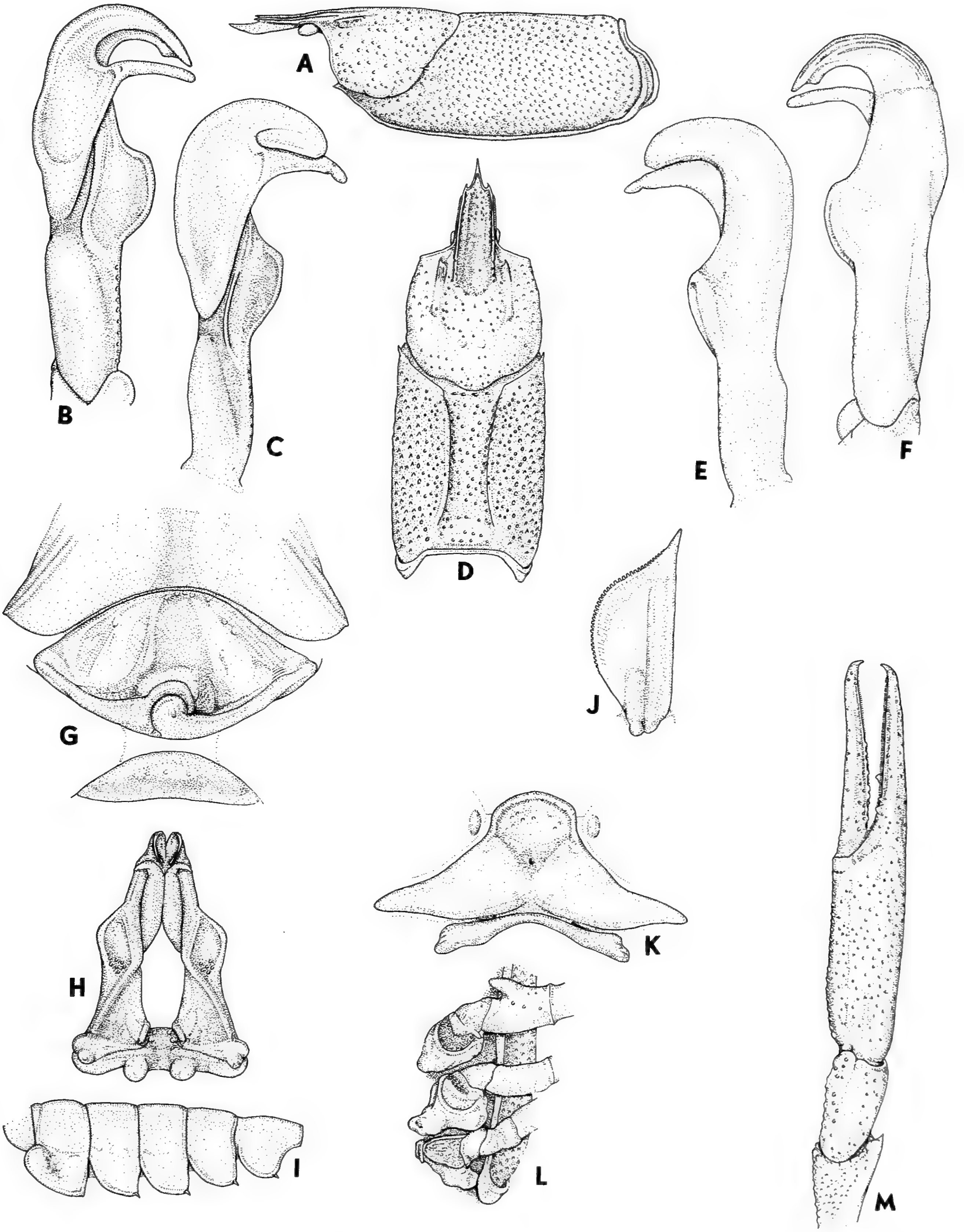

Fig. 1. *Cambarus* (*Aviticambarus*) *veitchorum*, new species (all from holotypic male, form I, except C, E, from morphotypic male, form II, and G, from allotypic female; setae not illustrated): A, lateral aspect of cephalothorax; B, C, mesial aspect of left gonopod (first pleopod); D, dorsal aspect of cephalothorax; E, F, lateral aspect of left gonopod; G, annulus ventralis and associated structures; H, caudal aspect of in situ gonopods; I, lateral aspect of abdomen; J, dorsal aspect of antennal scale; K, epistome; L, basal podomeres of third, fourth, and fifth pereiopods; M, dorsal aspect of distal podomeres of right cheliped.

narrower and slightly longer than cephalothorax. Pleura of third through fifth abdominal segments (Fig. 1I) with curved cephaloventral margins, linear caudal margins, and acute caudoventral corners; second through fifth pleura with spine at apex of caudoventral angle. Proximal podomere of uropod with strong distomedian spine on both lobes, that on mesial lobe longer; mesial ramus of uropod with foreshortened median keel, which lacking distal spine, and long distal spine on lateral margin; lateral ramus with submedian ridge of cephalic section terminating in spine at transverse flexure, latter bearing row of 12 fixed spines (14 on left) across margin, and 1 large movable spine at lateral corner. Telson with 1 long stationary and 1 smaller movable spine at each caudolateral corner of cephalic section; lateral margins of caudal section somewhat converging caudally, caudal margin rounded.

Epistome (Fig. 1K) with cephalic lobe subrectangular in outline, wider than long, margins slightly thickened; cephalic border entire, rounded, without projection; lateral margins subparallel for about ¾ of length of lobe, lateral apices not thickened; lobe without constriction at base; floor (ventral surface) of lobe with 8 minute tubercles, and central concavity extending into central depression of body; depression narrow, with shallow median fovea; lamellae with cephalolateral margins broadly concave, lateral apices narrow, subangular; zygoma weakly arched, pits short, deep. Antennal peduncle with strong, procurved cephalolateral spine on basis, and strong, erect ventral spine on ischium; antennular peduncle with strong ventral spine at base of distal ⅓ of proximal podomere. Antennal scale (Fig. 1J) 2.8 times as long as broad, widest just distal to midlength; lateral margin thickened, terminating in long distal spine (tip missing from spine on left side), which directed distolaterally, tip reaching base of distal ¼ of ultimate podomere of antennular peduncle; lamella about 2.1 times as wide as thickened lateral margin; distal margin of lamella sloping proximomesially to mesial margin, latter gently curving proximally to widest point, then curving proximolaterally to base.

Third maxilliped with distolateral margin of ischium slightly produced, not spinelike; ventrolateral margin of ischium with row of punctations bearing short setae at base of longitudinal ridge; ventral surface of lateral half with scattered punctations bearing short setae, some punctations containing small squamous tubercles; ventral surface of mesial half with long, dense setae obscuring most of proximal area; mesial margin with about 18 denticles; tip of exopodite reaching base of distal ¼ of merus of endopodite. Right mandible with incisor ridge bearing 7 denticles; molar process in two parts, caudalmost with 2 round, adjacent tubercles, cephalicmost with single tuberculiform mound.

Chela of cheliped (Fig. 1M) with palm subovate in cross section, 1.3 times wider than deep; mesial margin of palm 2.7 times longer than palm width, and length comprising about 50% of chela length; latter 76.0% of TCL (98.4% of PCL); dorsal surface of palm with small punctations bearing short setae, and several longer recumbent setae present; dorsal articular ridge fairly well defined, with subdistal clump of setae near midwidth; ventral surface of palm with small punctations bearing short setae, most punctations containing small squamous tubercles; ventral articular ridge well defined, with broad subdistal tubercle bearing several long setae at midwidth; lateral margin of palm rounded, punctate; mesial margin with 2 to 3 staggered rows of small tubercles, 18 to 19 in mesialmost row. Fingers without gape, without plumose setae at opposable bases; both fingers in dorsal aspect fairly straight, in lateral aspect gently curving distoventrally. Dactyl with longitudinal ridge dorsally and ventrally, with several small punctations on dorsal ridge near base, and 1 punctation bearing long setae at midlength; surfaces flanking ridges punctate, without grooves; mesial margin punctate, but with several minute tubercles near base; dactyl comprising 50.1% of length of chela. Fixed finger with surfaces flanking dorsal and ventral ridges punctate; lateral surface of fixed finger punctate, some median punctations large and bearing prominent setae. Opposable margin of dactyl with single row of prominent denticles on entire length of finger, 5 small tubercles on proximal ⅓ dorsal to row of denticles, and 1 larger subtriangular tubercle ventral to denticles at base of distal ⁴⁄₅ of finger; opposable margin of fixed finger with single row of prominent denticles on entire length, 3 small tubercles on proximal ⅕ of finger dorsal to denticles (second from base largest), and larger subconical tubercle ventral to denticles at base of distal ⅔ of finger.

Carpus of cheliped (Fig. 1M) subrectangular in dorsal outline, 1.9 times longer than wide; dorsal surface with shallow, nearly obsolete sulcus, mesial and lateral to which suface punctate and with short setae; ventral surface with strong distomedian spine, proximomesial to which is row of small tubercles; mesial margin without spines, with small scattered tubercles. Merus of cheliped without pronounced distodorsal spines or tubercles; dorsal ridge with 2 staggered rows of small tubercles, expanding distally into group of tubercles on dorsal, lateral, and mesial surfaces; rest of lateral and mesial surfaces with scattered small tubercles; ventrolateral ridge of merus with 16 or 17 scarcely discernible tubercles, and long distolateral spine near lateral articular prominence; ventromesial ridge with 16 or 17 small tubercles, slightly larger than those on ventrolateral ridge, and 1 long distal spine; area between ventral ridges punctate, with short setae; area between distal ends of ridges with some small tubercles. Ischium with row of 5 or 6 minuscule tubercles along ventral ridge, with several deep punctations and 2 minuscule tubercles lateral to them; dorsal surface with minuscule tubercles.

Hook on ischium of third pereiopod (Fig. 1L) simple, distally flattened and moderately acute; tip overreaching basioischial articulation, not opposed by tubercle on basis. Coxa of fourth pereiopod with prominent caudomesial boss.

See the "Diagnosis" for description of gonopod (Fig. 1B, F, H).

Allotypic female.—Except for secondary sexual characters, differing from holotype in following respects: Carapace 1.8 times wider than deep; areola 5.9 times longer than wide, constituting 40.7% of TCL (53.6% of PCL), with 3 to 4 punctations across narrowest part. Cephalic section of cephalothorax 1.5 times longer than areola and constituting 59.3% of TCL. Acumen comprising 38.9% of rostrum length, latter constituting 24.8% of TCL. Cervical spines 2 on left, 1 on right. Antennal scale 2.7 times longer than wide, tip of spine reaching distal margin of second article of antennular flagellum. Palm of chela of cheliped 1.5 times wider than deep; mesial margin of palm 2.5 times longer than palm width, and length comprising 48.8% of chela length; latter 59.3% of TCL (78.2% of PCL); mesial margin of palm with 14 to 15 minute tubercles in mesialmost row. Dactyl comprising 54.7% of chela length; mesial surface punctate, without tubercles; opposable margin with 2 small tubercles near base, and 1 small subtriangular tubercle ventral to denticles at proximal ¼ of finger. Opposable margin of fixed finger with 2 small tubercles near base, and subconical tubercle at base of distal ⅔ of finger. Carpus of cheliped 2.1 times longer than wide; ventromesial ridge of merus with 12 or 13 small tubercles, plus large distal spine. Coxa of fourth pereiopod without boss.

See the "Diagnosis" for description of annulus (Fig. 1G).

Morphotypic male, form II.—Differing from holotype in following respects: Areola 7.4 times longer than wide, constituting 42.1% of TCL (55.5% of PCL), with 4 punctations across narrowest part. Cephalic section of carapace 1.4 times longer than areola and constituting 57.9% of TCL. Acumen comprising 43.2% of TCL. Rostrum with right margin and marginal spine extending farther cephalically than left margin and spine. Single small cervical spine on left side of carapace, none on right. Antennal scale 2.7 times longer than wide, tip of spine reaching distal margin of fourth article of antennular flagellum. Palm of chela of cheliped with mesial margin 2.5 times longer than wide, chela length 65.4% of TCL (86.0% of PCL); mesial margin of palm with 14 or 15 minuscule tubercles in mesialmost row. Dactyl comprising 53.8% of chela length; opposable margin of dactyl with 3 small tubercles near base (middle one slightly larger), 1 large subtriangular tubercle ventral to denticles at base of distal ⅘ of finger, followed distally by 2 minuscule tubercles. Opposable margin of fixed finger with subconical tubercle situated just proximal to midlength. Carpus of cheliped 2.0 times longer than wide; ventrolateral ridge of merus with 14 or 15 scarcely discernible tubercles and small distolateral spine. Hook on ischium of third pereiopod moderately well developed, not overreaching basioischial articulation.

Gonopods (Fig. 1C, E) reaching just beyond midlength of coxa of third pereiopod when abdomen flexed; left gonopod in lateral aspect without juvenile suture; prominence on cephalic margin reduced; central projection noncorneous, fairly broad but tapering to rounded tip, which directed slightly proximocaudally; proximal margin of central projection slightly overlapping distal margin of mesial process; mesial process long, narrow, with constriction near tip; latter curved at slightly greater than 90° angle, tip extending well beyond apex of central projection.

Disposition of types.—The holotype, allotype, and morphotype are in the crustacean collections of the North Carolina State Museum of Natural Sciences (NCSM), Raleigh (catalogue numbers NCSM C-2544, C-2545, and C-2546, respectively), as are the following paratopotypes: 1 ♂ I, 1 ♀ (C-2547), 1 ♂ I, 1 j ♂ (C-2548).

Type locality.—Alabama, Limestone County, subterranean stream in White Spring Cave, NW of Holland Gin (Tanner 7.5′ USGS Quadrangle, Sec. 11, T.5S, R.4W). The cave is designated AL 242 in the cave cataloguing system of the Alabama Cave Survey, an official project of the National Speleological Society.

White Spring Cave is located in the Tennessee Valley north of the Tennessee River, within the southern boundaries of the Highland Rim of the Interior Low Plateaus. The cave is developed in rock of Mississippian age, probably the Fort Payne Chert. The extent of the cave is unknown because the accessible passage is only traversible for about 12 to 18 m beyond either of the two entrances. The northern entrance is at the western edge of a shallow surface depression, in which water from the cave stands during periods of elevated water level. We have observed troglobitic crayfish in the depression, where they were exposed to daylight. The stream within the cave flows generally southeast and south, and the water was moving slowly during both of our visits.

Range and specimens examined.—Known only from the type locality, where the following specimens have been collected: 2 ♂ I, 2 ♀, 24 Sep 1967, coll. J. Veitch, MRC, JEC; 1 ♂ I, 1 ♂ II, 1 j ♂, 4 Jul 1968, coll. A. Dobson, R. C. Graham, JEC.

Variations.—The range of variation in most characters is provided in the "Diagnosis" and in the discussions of the allotype and morphotype. The following additional variations have been noted. The number of tubercles on the opposable margin of the fixed finger of the chela (exclusive of the larger subconical tubercle) ranges from one in the two smallest animals, to two or three in the others; the number of tubercles on the opposable margin of the dactyl is usually greater and shows more variation, with two in the juvenile male and from three to six in the others. The number of cervical spines varies from one animal to another, and from one side of the body to the other. The juvenile male and the holotype have a single spine on each side, the other form I males have two spines on each side, the morphotype and the smallest female have one spine on the left side and none on the right, and the allotype has two spines on the left and one on the right. One of the form I males has the usual two spines in the caudolateral corner of the cephalic section of the left side of the telson, but a single spine on the right side. The margins of the rostrum are more strongly convergent in the allotype and the juvenile male, and in both these specimens the merus is slightly longer than it is in the others. Sexual dimorphism is evident in the length of the chela, with form I males having chelae that exceed 75% of TCL, while the chelae of other males and females constitute 60 to 65% of TCL.

Size.—Adult TCL ranges from 13.5 mm (a female) to 16.7 mm (a form I male). The mean TCL of the four males is 15.9 mm, and of all six adults is 15.2 mm.

Life history notes.—Form I males were found in July and September. The largest of the two females collected in September exhibited oocytes (visible through the carapace) in a late stage of development, as well as highly developed cement glands. The small female collected at the same time contained oocytes in an early stage of development. As is the case with nearly all troglobitic crayfishes, no females carrying attached ova or young have been found.

Relationships.—*Cambarus veitchorum* is closely related to *C. hamulatus* and *C. jonesi*, and is syntopic with the latter. Although the gonopods of the form I and form II males of *C. veitchorum* are more like those of *C. jonesi* than those of *C. hamulatus*, as are the relative proportions of the areola, the overall facies of the new species argues for a somewhat closer relationship to *C. hamulatus*. The rostrum of both is very similar (and unlike that of *C. jonesi*), as are the shape of the antennal scale, the general shape and proportions of the chela and the cephalothorax, and the overall structure of the annulus. In all three species the female lacks first pleopods.

Cambarus veitchorum is markedly different from both its closest relatives in the following characters: the configuration and spatial relationships of the terminal elements of the form I male gonopod, with the central projection directed caudomesially and the proximal margin of its caudal portion twisted mesially; the shape of the ventral margins of the third through fifth abdominal pleura, and the presence of a spine on the caudoventral angle of the second through fifth pleura; the absence of spines or prominent tubercles on the mesial surface of the carpus; the attenuated chela, carpus, and merus; the configuration of the cephalic lobe of the epistome; the reduced number of tubercles on the mesial surface of the dactyl; the greater number and very weak nature of the tubercles on the mesial margin of the palm and on both ventral ridges of the merus; the obsolete groove of the postorbital ridge; the very broad depression in the cephalic portion of the annulus; the lower number of tubercles on the opposable margins of both fingers; the comparative dearth of long, erect setae on the palm and fingers of the cheliped (also generally absent in *C. hamulatus*); and the diminutive adult size, with the maximum TCL of 16.7 mm, as opposed to 28.9 mm for *C. jonesi* (♂ I, NCSM C-198), and 35.2 mm for *C. hamulatus* (Hobbs et al. 1977: 76).

Crayfish associates.—The only other crayfish known to inhabit White Spring Cave is *C. jonesi*, which is far more abundant there than *C. veitchorum*. Both species were observed in very close proximity to each other, but no interactions between them were seen.

Etymology.—We take great pleasure in naming this species for John D. Veitch and Joyce Veitch of Decatur, Alabama, friends who introduced us to White Spring Cave and its owners, and who served as immensely cheerful hosts to a couple of muddy cave biologists on more occasions than they would probably care to remember.

Suggested vernacular name: White Spring Cave Crayfish.

Acknowledgments

We are very grateful to John and Joyce Veitch for their hospitality and many kindnesses; to Mr. and Mrs. Rowe Sanderson, who gave us permission to collect in White Spring Cave; and to Arthur Dobson and Richard C. Graham, who accompanied JEC on the trip that yielded the morphotype. JEC expresses his sincerest gratitude to his co-author, to R. E. Ashton, Jr., J. E. Cooper, Jr., J. Perry, and especially to D. Howard and A. L. Braswell, without whose generosity this paper could never have been completed. Joseph F. Fitzpatrick, Jr., Steve Busack, and an anonymous reviewer, provided cogent comments on the manuscript. As always, we are immensely grateful to the late Horton H. Hobbs, Jr., for the splendid lessons he taught (not all of them about decapods).

Literature Cited

Bouchard, R. W. 1976. Crayfishes and shrimps. Pp. 13–20 *in* H. Boschung, ed., Endangered and threatened plants and animals of Alabama.—Bulletin of the Alabama Museum of Natural History No. 2, 93 pp.

Cooper, J. E. 1967. Animals in Alabama caves. Pp. 14–16 *in* J. Veitch. The caves of Alabama. Huntsville Grotto, National Speleological Society, Huntsville, Alabama, 51 pp.

———, & M. R. Cooper. 1966. Comments on Alabama cave biology. Huntsville Grotto Newsletter 7(5–6):37–41. Reprinted 1969, pp. 25–30 *in* W. T. Plummer, ed., Speleo Digest, Section 2. National Speleological Society, Huntsville, Alabama.

Cope, E. D. 1881. *Orconectes hamulatus. in* E. D. Cope & A. S. Packard, Jr. The fauna of the Nickajack Cave.—American Naturalist 15:881–882.

Fitzpatrick, J. F., Jr. 1990. Decapoda. Pp. 77–80 *in* S. C. Harris, Preliminary considerations on rare and endangered invertebrates in Alabama.—Journal of the Alabama Academy of Sciences 61(2):64–92.

Hobbs, H. H., Jr. 1967. A new crayfish from Alabama caves with notes on the origin of the genera *Orconectes* and *Cambarus* (Decapoda: Astacidae).—Proceedings of the United States National Museum 123(3621):1–17.

———, & T. C. Barr, Jr. 1960. The origins and affinities of the troglobitic crayfishes of North America (Decapoda, Astacidae), I: the genus *Cambarus*.—American Midland Naturalist 64(1): 12–33.

———, H. H. Hobbs, III, & M. R. Daniel. 1977. A review of the troglobitic decapod crustaceans of the Americas.—Smithsonian Contributions to Zoology 244:1–183.

Rhoades, R. 1941. Notes on some crayfishes from Alabama caves, with the description of a new species and a new subspecies.—Proceedings of the United States National Museum 91(3129):141–148.

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Two new species and a range extension of mud shrimps, *Upogebia*, from Pacific Costa Rica and Mexico (Decapoda: Thalassinidea: Upogebiidae)

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Abstract.—Two new species of mud shrimps are described from the Pacific side of Middle America, *Upogebia baldwini* from the state of Nayarit, Mexico, and *U. vargasae* from Puntarenas Province, Costa Rica. The geographic range of the poorly known *U. burkenroadi* Williams, 1986 is extended from its type locality in the state of Sonora, Mexico to a documented Costa Rican occurrence. The new species are illustrated, and a key for identification of eastern Pacific species of *Upogebia* (Williams 1986) is amended to accommodate the new species. Cataloged lots of each species collected are listed.

Three species of mud shrimps, genus *Upogebia*, from the Pacific side of Middle America that have become known since the publication of Williams (1986) require more than routine identification. The first is a unique specimen of a new species collected in mangrove habitat from the state of Nayarit, Mexico by Aaron Baldwin in 1988. Additional material has not become available, so it seems inappropriate to delay description. A second new species, collected by Rita Vargas in 1995 from a mangrove habitat in Costa Rica, is described. Finally, specimens collected by J. Cortés from Costa Rica in 1991 are provisionally referred to *Upogebia burkenroadi* Williams, 1986 described from Sonora, Mexico, thus extending the geographic range of that species.

Specimens are deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), or returned to the University of Costa Rica Museum of Zoology (UCRMZ), San José, as indicated in the species accounts.

Upogebia baldwini, new species
Fig. 1

Material.—USNM 251486. Holotype ♀, Estero Playa Novillero, Nayarit, Mexico, dug from mangrove estero, coll. A. Baldwin, 5 Feb 1988.

Diagnosis.—Projections to either side of rostrum ending in acute spine. Postocular spine present. Abdominal sternites unarmed. Telson subrectangular, with transverse proximal ridge. Carpus of cheliped with 2 spines on mesiodistal margin, palm with row of spines on mesioventral surface. Merus of pereopod 2 with proximal mesioventral spine and subdistal dorsal spine; merus of pereopod 4 spineless.

Description.—Rostrum triangular, lateral margin shorter than basal width; lower margin nearly horizontal in lateral view but dorsal margin downturned, tip exceeding eyestalks; dorsal pair of strong subapical spines followed on each side by 4 erect marginal spines separated by subequal intervals; 3 spines mesial to marginal row at base on right side, none on left; central dorsal area hidden under setae. Rostral spines hidden by dense tufts of setae sprouting anterior to their bases, confluent with field of similar postrostral spines becoming smaller and less hidden posteriorly. Ridge lateral to field bearing crest of about 15–16 moderate to small spines,

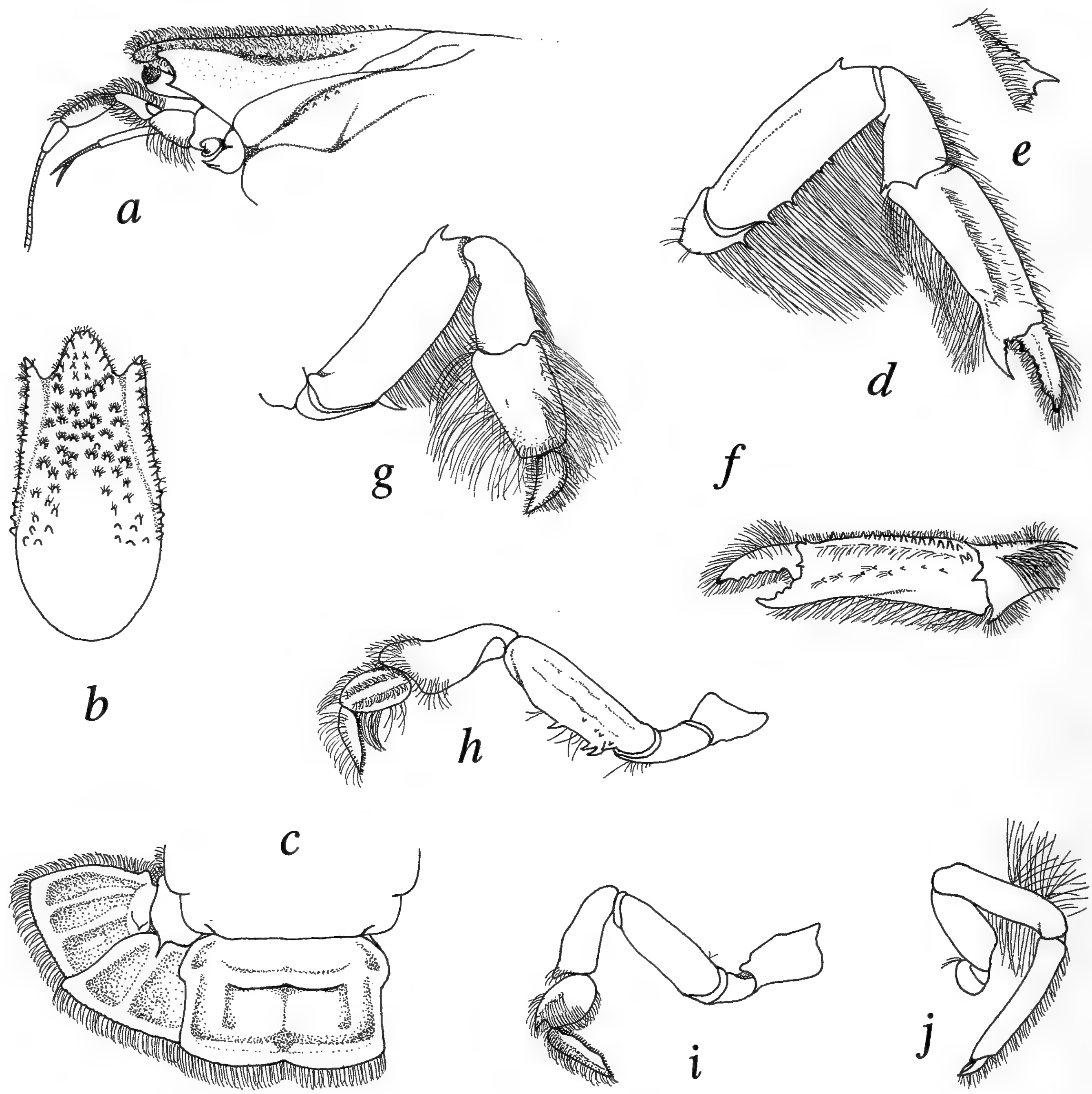

Fig. 1. *Upogebia baldwini*, USNM 251486, ♀ Holotype; *a*, cephalic region, lateral; *b*, anterior carapace, dorsal; *c*, telson, left uropod, part of abdominal segment 6, dorsal; *d*, cheliped, right lateral; *e*, crest of right cheliped carpus showing spines; *f*, chela and carpus, right mesial; *g–j*, right pereopod 2, left 3–4, right, 5.

strongest on process lateral to rostrum but decreasing posteriorly, with tendency to cluster at end of row. Shoulder lateral to cervical groove armed with tubercle on left side above intersection with thalassinidean line and with 4–9 obsolescent spines or tubercles to either side below intersection, line continuing strongly to posterior margin. Postocular spine present.

Abdomen with sternites on segments 1 and 2 wrinkled but not spined.

Telson with transverse proximal ridge confluent with low longitudinal ridge to either side.

Eyestalk stout, deepest at about midlength, convex ventrally, horizontal in repose; cornea prominent, obliquely terminal, narrower than diameter of stalk, row of tiny forward trending spines above margin of cornea on mesial aspect.

Antennular peduncle reaching slightly beyond midlength of terminal article of antennal peduncle, proximal 2 articles together slightly longer than terminal article.

Antennal peduncle with almost ⅓ of length extending beyond tip of rostrum; scale moderate, oval.

Maxilliped 3 bearing epipod.

Epistomial projection rather broad in lateral view, bearing 2 small apical projections.

Chelipeds with ventral margin of ischium bearing 1 spine. Merus with row of 5 spines on ventral margin, proximal 2–3 modest in size, distal spines smaller; single subdistal dorsal spine reaching level of postocular spine. Carpus trigonal, shallow longitudinal groove laterally, anterior ventrolateral corner bearing modest spine; mesiodorsal crest of 4 moderate spines partly obscured by setae behind prominent spine on anterior margin; 2 spines on anterodorsal margin mesial to articulation with propodus obscured by dense setae; strong spine near middle of anteromesial margin, smaller spine dorsal to it, and strong slender spine behind distoventral corner. Chela length about 5 times chela height; dorsal ridge spineless, stout spine mesial to it subdistally; mesiodorsal row of 13–14 erect to forward-hooked spines not reaching anterior part of palmar length; moderate spine below mesial dactylar condyle, single spine on margin below lateral condyle; mesial surface bearing setose longitudinal row of obsolescent spines on upper half, lower half bearing horizontal row of about 7 strong spines; transverse low ridge near proximomesial margin intersecting ventral ciliated keel. Fixed finger shorter than dactyl, continuing slightly sinuous trend of lower palmar margin and tapering to slender tip, 3 irregular teeth on proximal prehensile edge, strong double tooth in middle of row. Dactyl with corneous tip preceded on prehensile edge by crowded row of coalescent teeth ending in molariform tooth near toothless basal section; slightly enlarged tooth opposing tip of fixed finger; mesial more or less concave surface bearing few crowded pearly tubercles proximally, curved extensor surface bearing 2 rows of dense setae, with clustered granules proximally.

Pereopod 2 reaching to near midlength of cheliped palm; carpus with small acute distodorsal and subdistal ventral spines; merus with strong subdistal dorsal spine and proximal mesioventral spine. Pereopod 3 with merus bearing 4 ventral spines and clustered tubercles; coxa of female with slender spine lateral to gonopore. Pereopod 4 with spineless merus.

Uropod with acute spine on protopod above base of mesial ramus; mesial rib of lateral ramus bearing small acute proximal spine, distal margin of both rami bearing close-set row of tiny spines and spiniform granules except for short mesial sector on each.

Measurements in mm.—Holotype ♀, anterior carapace length 10.2, carapace length 15.4, chela length 7.3, chela height 2.3.

Remarks.—The specimen, dry when received, was softened in surfactant (Aerosol® OT Solution) and then preserved in 70% ethanol before study.

The eyestalks of *Upogebia baldwini* somewhat resemble those of *U. acanthops* Williams, 1986 in having an oblique anterior corneal surface, but there is no subterminal spine mesial to the cornea. Instead, there is a row of small forwardly trending spines dorsal to the cornea along its mesial margin. Other observed conspicuous differences from *U. acanthops* include: *U. baldwini* has no corneous spinules on pleura of abdominal segments 1 and 2, the rostrum has more spines on the lateral margin, the carpus of the cheliped has no spine preceding the spine at the anterolateral corner, rows of spines on the dorsal and mesial surfaces of the palm are more prominent, and the merus of leg 4 is spineless.

In comparison with similar eastern Pacific species in the genus, both *U. baldwini* and *U. longipollex* (Streets 1871) have the merus of leg 4 spineless, but *U. baldwini* is not thickly strewn with deciduous corneous spinules on its tail fan, abdominal sternites and pleura, and thoracic parts of the carapace to either side of the thalassinidean line posterior to intersection with the cervical groove as is *U. longipollex.*

Etymology.—The species is named for Aaron Baldwin, then of Sea and Shore Museum, Port Gamble, Washington, who collected this and other decapod crustaceans from Pacific Middle America.

Upogebia vargasae, new species
Fig. 2

Material.—USNM 251484. Holotype ♂, Boca Guarumal [08°52′N, 83°36′W, Puntarenas Prov.], Costa Rica, Mangroves of Terraba-Sierpe, from burrows with thick walls, coll. with *Upogebia spinigera* (Smith), Rita Vargas, 23 Nov 1995. USNM 251485. Paratypes, 1 ♂, 3 ♀ (1 ovig.), same. Both holotype and paratypes from UCRMZ, Cat. No. 2108-02; 1 ♂ and 4 ♀ returned to UCRMZ.

Diagnosis.—Projections to either side of rostrum ending in laterally divergent acute spine. Postocular spine present. Abdominal sternites armed. Telson subrectangular with strongly spined transverse proximal ridge. Carpus of cheliped with 2 spines on mesiodistal margin, palm without row of spines on mesioventral surface but with cluster of scattered spines there. Merus of pereopod 2 with proximal mesioventral spine and subdistal dorsal spine; merus of pereopod 4 spineless.

Description.—Rostrum triangular, lateral margin shorter than basal width; nearly horizontal in lateral view, tip exceeding eyestalks; dorsal pair of strong subapical spines followed on each side by 2–3 erect marginal spines separated by subequal intervals, spine mesial to marginal row at base, central dorsal area hidden under setae spineless and glabrous. Rostral spines, confluent with field of postrostral spines, hidden by dense tufts of setae sprouting anterior to their bases. Ridge lateral to field bearing crest of about 10–12 moderate to small spines, strongest on divergent process lateral to rostrum and decreasing almost to obsolescence posteriorly. Shoulder lateral to cervical groove armed with 0–2 obsolescent spines or tubercles above and 2–5 spines below its intersection with thalassinidean line, latter continuing strongly to posterior margin, additional 0–2 spines or tubercles above it on lateral aspect of head. Postocular spine present.

Abdomen armed with many spinules on sternites and few spinules on margin of pleura, mainly on segments 1 and 2.

Telson with proximal transverse proximal ridge bearing row of acute reclining spines directed posteriorly, confluent with low longitudinal ridge to either side occasionally bearing 1 or 2 spines proximally.

Eyestalk stout, deepest at about midlength, convex ventrally, angled slightly upward in repose; cornea prominent, oval, obliquely terminal, narrower than diameter of stalk, few tubercles on mesial aspect near base.

Antennular peduncle not quite reaching midlength of terminal article of antennal peduncle, proximal 2 articles together slightly longer than terminal article.

Antennal peduncle with almost ⅖ of length extending beyond tip of rostrum; antepenultimate article bearing ventral subterminal spine; scale moderate, oval.

Maxilliped 3 bearing epipod.

Epistomial projection rather broad in lateral view, bearing 2 small apical projections.

Chelipeds with ventral margin of ischium bearing 1 spine. Merus with row of 4–5 relatively strong spines on ventral margin; single subdistal dorsal spine reaching level of postocular spine. Carpus trigonal, shallow longitudinal groove laterally, anterior ventrolateral corner with strong spine preceded by 2 much smaller spines; mesiodorsal crest of 5–10 moderate spines behind prominent spine on anterior margin partly obscured by setae in proximal part of row, series often asymmetrical; 4 or fewer spines on anterodorsal margin mesial to articulation with propodus often obscured by dense setae; strong spine near middle of anteromesial

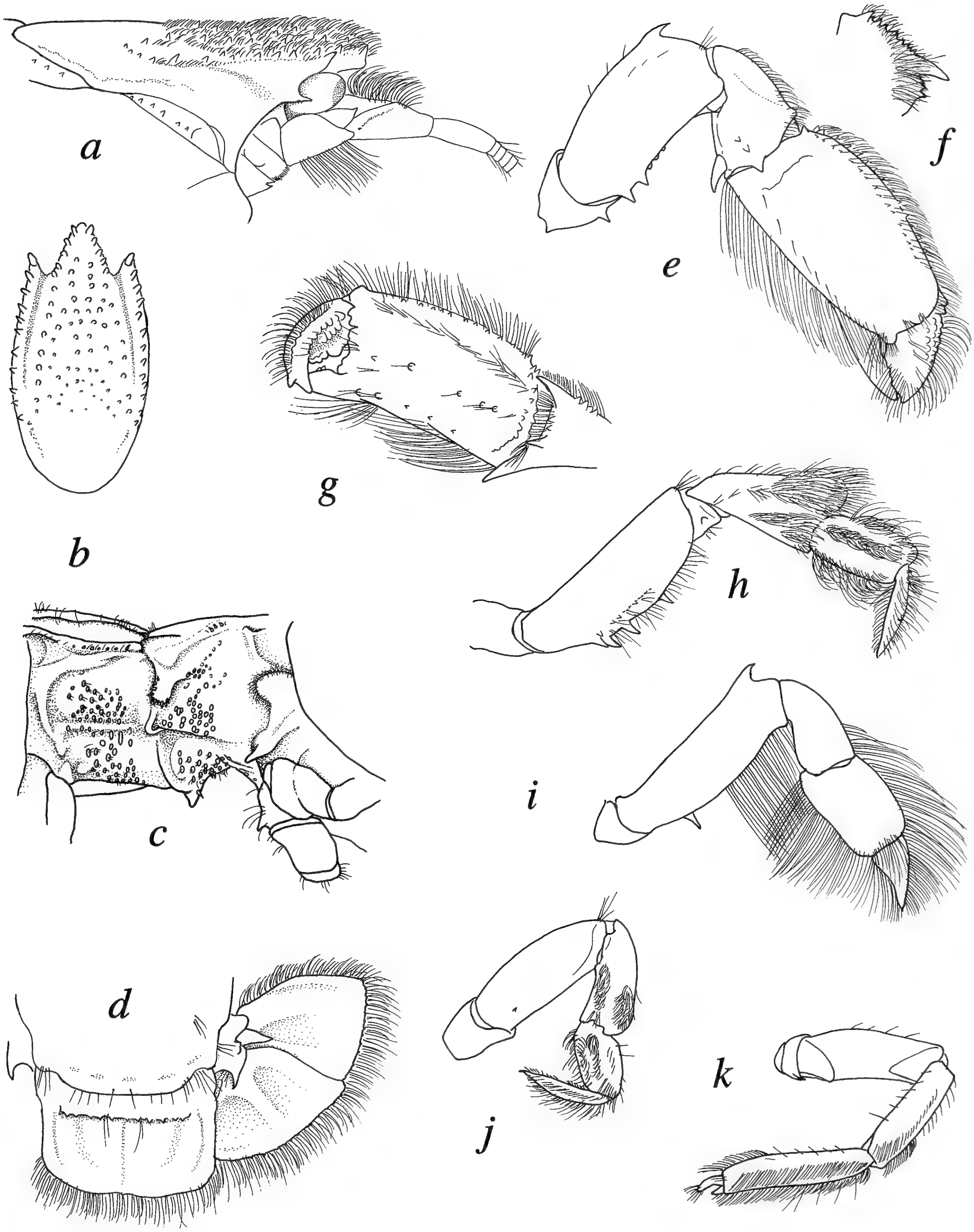

Fig. 2. *Upogebia vargasae*, USNM 251484, ♂ Holotype; *a*, cephalic region, lateral; *b*, anterior carapace, dorsal; *c*, parts of abdominal segments 1–2 showing spinules on sternites and edge of pleura, oblique view; *d*, telson, right uropod, part of abdominal segment 6, dorsal; *e*, cheliped, right lateral; *f*, crest of right cheliped carpus showing spines; *g*, chela and carpus, right mesial; *h–k*, right pereopods 2–5.

margin, smaller similar spine dorsal to it, and very strong spine behind distoventral corner. Chela length about 2.3–3.2 chela height; low dorsal ridge bearing 9–17 variable spines partly obscured by setae, spines on distal part of ridge tending to obsolescence, stout spine mesial to ridge subdistally; mesiodorsal row of about 10–12 irregularly distributed small spines or spiniform tubercles becoming reduced in size or obsolescent near distal ⅔ of palmar length and with tendency for development of scattered spines around proximal end of row; moderate spine and row of about 4–5 smaller rounded teeth below mesial dactylar condyle, single spine on margin below lateral condyle; mesial surface bearing longitudinal row of 15 spines on upper half, prominent proximally but obsolescent distally, lower half bearing about 6–8 spines variable in position but tending to arrangement in oblique line or tract, holotype male with additional 4–5 mesioventral spines near or on ventral keel; transversely sinuous granulo-tuberculate ridge near proximomesial margin intersecting ventral ciliated keel bearing 2–4 obsolescent tubercles or spines. Fixed finger shorter than dactyl and more slender, continuing slightly sinuous trend of lower margin of palm and tapering to slender tip, 2–4 irregular strong teeth on proximal prehensile edge. Dactyl with corneous tip preceded on prehensile edge by strong subdistal tooth and crowded row of 7–8 small coalescent teeth ending in much larger tooth near base, basal section toothless; mesial more or less concave surface bearing 2 rows of closely crowded tubercles, pearly on proximal half, upper row running nearly length of finger, lower row only half as long; curved extensor surface bearing 2 rows of setae, clustered rows of tubercles between them proximally.

Pereopod 2 reaching to near midlength of cheliped palm; carpus with distodorsal and subdistal ventral spines obsolescent; merus with strong subdistal dorsal spine and proximal mesioventral spine. Pereopod 3 with merus bearing 4 ventral spines, a few tubercles or spiniform tubercles and scattered setae; coxa of female with broad spine lateral to gonopore. Pereopod 4 occasionally with obsolescent, proximal, ventrolateral spine on merus.

Uropod with acute strong spine on protopod above base of mesial ramus; mesial rib of lateral ramus bearing proximal spine, distal margin of both rami bearing row of small spines and spiniform granules except for short mesial sector on each.

Measurements in mm.—Holotype ♂, anterior carapace length 11.0, carapace length 15.9, chela length 11.9, chela height 4.9; paratype ovigerous ♀, same, 10.5, 15.2, 8.2, 2.6.

Remarks.—*Upogebia vargasae* is most closely allied with *U. longipollex* and *U. spinigera* (Smith 1871), but it differs from each in having a row of strong reclining, posteriorly directed spines on the transverse proximal ridge of the telson, and all spines on the uropods are more strongly developed than in those species. *Upogebia vargasae* lacks the tiny deciduous spinules that are characteristically distributed over dorsal surfaces of the tail fan in *U. longipollex* as well as on external surfaces of its abdominal pleura and on thoracic parts of its carapace to either side of the thalassinidean line posterior to intersection with the cervical groove. *Upogebia vargasae* and *U. longipollex* have conspicuously developed spinules on abdominal sternites and pleura, but *U. spinigera* has these only on the pleura. Much like *U. longipollex, U. vargasae* usually has a spineless merus on pereopod 4, but occasionally there is an obsolescent, proximal, lateroventral spine; that of *U. spinigera* is armed with ventral and ventrolateral spines and tubercles.

Etymology.—The species is named for Rita Vargas, University of Costa Rica Biology School, who collected this and other thalassinideans from Pacific Costa Rica.

Discussion.—In a key to known Eastern Pacific species of *Upogebia* (Williams 1986:7–10), the following insertion in p. 8

will aid in identification of new species described above:

12. Eyestalks with cornea normally rounded distally 13
– Eyestalks obliquely truncate distally, cornea triangular in lateral view 12a
12a. Eyestalk bearing short subterminal spine mesial to reduced, triangular cornea; merus of leg 4 bearing ventral spines and tubercles. Panama . . . . *U. acanthops* Williams
– Eyestalk bearing row of small forward trending spines on dorsal surface mesial to margin of cornea; merus of leg 4 usually spineless. Nayarit, Mexico . . . . *U. baldwini* n. sp.
13. Telson with proximal transverse ridge spineless 13a
– Telson with proximal transverse ridge bearing row of acute reclining spines directed posteriorly; merus of leg 4 usually spineless. Costa Rica *U. vargasae* n. sp.
13a. Abdominal segments 1 and/or 2 spined ventrally on sternites or edge of pleura 14
– Abdominal segments 1 and/or 2 lacking ventral spines 15

Upogebia burkenroadi Williams, 1986

Material.—University of Costa Rica, UCR 1708. 1♂, 1 ♀, Punta Pitahaya, Guanacaste, 8–10 m, coll. J. Cortés, 15 Jun 1991. Note on back of label translated from Spanish, "Living in holes covered with mud, 5 × 5 mm, chambers approx. 5 mm diameter, connection to exterior covered with sand and some algae."

Measurements in mm.—♀, anterior carapace length 3.9, carapace length 5.3, chela length 3.3, chela height 1.0; ♂, same, 4.5, 6.5, 4.4, 1.2.

Remarks.—*Upogebia burkendroadi* Williams, 1986, described on the basis of a male (holotype) and female (paratype), with no accompanying ecological information, were the only specimens of the species known, until the material listed above came to my attention. I provisionally refer the Costa Rican material to this species after comparison with the type series. Except for smaller size, the Costa Rican specimens seem almost identical to the types, but a noticeable difference is presence of a corneous tip on the prehensile edge of the cheliped dactyl in the type specimens, whereas this feature is reduced or absent in the smaller Costa Rican specimens. Development of this feature may be an age dependent character.

Acknowledgments

I am indebted to collectors, institutions listed in Materials, and to Ana Dittel, Universities of Delaware and Costa Rica, for providing specimens that made this report possible. Keiko Hiratsuka Moore and Mollie S. Oremland enhanced the text with the excellent illustrations. Critical comments on the manuscript were provided by B. B. Collette and Ana I. Dittel.

Literature Cited

Smith, S. I. 1871. List of the Crustacea collected by J. A. McNeil in Central America. Second and Third Annual Report of the Trustees of the Peabody, Academy of Science, for the years 1869 and 1870, pp. 87–98.

Streets, T. H. 1871. Catalogue of Crustacea from the Isthmus of Panama, collected by J. A. McNeil.—Proceedings of the Academy of Natural Sciences of Philadelphia 23:238–243.

Williams, A. B. 1986. Mud shrimps, *Upogebia*, from the eastern Pacific (Thalassinoidea:Upogebiidae).—Memoirs of the San Diego Society of Natural History, 14:1–60.

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A trans-Atlantic record of the fossil tropicbird *Heliadornis ashbyi* (Aves: Phaethontidae) from the Miocene of Belgium

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Abstract.—The fossil tropicbird *Heliadornis ashbyi* Olson, previously known from the unique holotype from the middle Miocene Calvert Formation of Maryland, is here recorded from a contemporaneous site in Belgium based on a nearly complete humerus. Its trans-Atlantic occurrence at a much higher latitude suggests that *Heliadornis* may have been the higher-latitude sister group of the extant tropical genus *Phaethon*, much as within the Sulidae gannets of the genus *Morus* are the higher latitude counterparts of the tropical boobies of the genus *Sula*.

The three living species of tropicbirds (*Phaethon*, Phaethontidae) are remnants of an ancient and aberrant group that have almost always been allied with the Pelecaniformes. The best-preserved fossil associated with this group is *Prophaethon shrubsolei* Andrews (1899), from the early Eocene London Clay. This was shown to be so different from modern tropicbirds as to merit its own family, Prophaethontidae (Harrison & Walker 1976). Other very fragmentary unnamed remains of early Tertiary birds resembling tropicbirds have been reported (e.g., Olson 1994), but it is uncertain to which of the two families these may belong.

Apart from Quaternary records of extant species, the first certain fossil record of the Phaethontidae proper was based on three associated bones from the middle Miocene Calvert Formation of Maryland that were described as a new genus and species, *Heliadornis ashbyi* (Olson 1985), which was considered to have been already too specialized to be on a lineage leading to *Phaethon*. This record was somewhat anomalous geographically, as modern tropicbirds are usually found only within the tropics, an exception being Bermuda, where warm waters of the Gulf Stream have permitted *Phaethon lepturus* to colonize. That the original specimen of *Heliadornis ashbyi* was not some aberrant wanderer from the south is now confirmed by the discovery of a second specimen from a much higher latitude on the opposite side of the Atlantic.

Phaethontidae
Heliadornis Olson 1985
Heliadornis ashbyi Olson 1985

Referred material.—Left humerus lacking the area of the internal tuberosity and bicipital crest and a few fragments of midshaft, BMNH A9005 (Figs. 1, 2). Collected in 1979 and presented in 1985 by Jacques Herman of the Service Géolgique de Belgique.

Locality.—Belgium, Antwerp (Anvers) Province, Brussels-Antwerp motorway at the vicinity of the boundary between the communities of Berchem and Wilrijke. Service Géolgique de Belgique site designation 28W126′.

Horizon.—At the base of the "Sables d'Anvers" or Sands of Antwerp, Middle

Fig. 1. Left humeri of tropicbirds in anconal view: A, *Phaethon aethereus* USNM 558044; B, *Heliadornis ashbyi* BMNH A9005, referred specimen from Belgium; C, *Heliadornis ashbyi* USNM 237226, holotype. Scale = 2 cm.

Fig. 2. Left humeri of tropicbirds in palmar view: A, *Phaethon aethereus* USNM 558044; B, *Heliadornis ashbyi* BMNH A9005, referred specimen from Belgium; C, *Heliadornis ashbyi* USNM 237226, holotype. Scale = 2 cm.

Miocene. The Anversian Sands fall somewhere within European Neogene land mammal stages (MN) 6 through 8 (Cheneval 1996). The sediments at the site are glauconitic sands with phosphatic concretions. The associated vertebrate fauna consists of rare cetaceans, frequent bones of teleosts, and abundant elasmobranchs.

Measurements (mm).—Measurements in parentheses are from the holotype of *H. ashbyi*. Total length, 97.3; distance from head to distal extent of pectoralis scar 31.2 (30.2); depth through head 5.1 (5.3); proximo-distal extent of bicipital intumescence 16.1 (16.0); width and depth of shaft at midpoint, 6.5 × 5.3 (6.4 × 5.3); distal width, 14.1; greatest diameter of brachial depression, 9.7; depth through external condyle, 8.2; greatest diameter of external condyle, 7.1.

Comparisons.—As far as they preserve portions in common, both the new specimen and the holotype of *Heliadornis ashbyi* are identical to one another and distinct from *Phaethon* in the manner outlined in the original diagnosis, especially in the great difference in the shape of the pectoral crest. Compared with *Phaethon aethereus*, which is the most similar in size (*P. rubricauda* is larger, *P. lepturus* smaller), the Belgian specimen of *Heliadornis* is somewhat larger with a straighter, more robust shaft. The distal end is wider because of the greater extension of the entepicondylar area, the brachial depression is wider and deeper, and the external condyle is shorter and more ovoid.

Discussion.—The age of the Belgian specimen appears to be almost exactly equivalent to that of the holotype of *Heliadornis ashbyi*, which came from Bed 11 of the Plum Point Member of the Calvert Formation and is thus earliest Middle Miocene (Langhian) in age (Ward 1992: figs. 2, 3). The Belgian specimen, coming from the base of the Anversian Sands, is possibly equivalent to MN 6, which is also at least partially Langhian in age (Steininger et al. 1989, fig. 1). In absolute terms, this was approximately 14 million years ago. These specimens provide such a nice trans-Atlantic correlation that it is tempting to cite the ornithostratigraphy as evidence for the contemporaneity of the Calvert Formation and the Anversian Sands.

The holotype of *Heliadornis ashbyi* comes from just below 39° north latitude, whereas the Belgian specimen is from much higher, just above 51°N. Mlikovsky (1997) has described a second species in this genus, *Heliadornis paratethydicus*, based on an abraded proximal end of an ulna from the late Miocene at Brunn-Vösendorf, Austria, in a deposit that formed in the Paratethys Sea at about 48°N. This was referred to *Heliadornis* because it was generically distinct from *Phaethon* and considered a new species because it was larger than *H. ashbyi*. Thus *Heliadornis* was apparently a truly high latitude tropicbird, the scarcity of which is probably a reflection of strictly pelagic habits similar to those of modern tropicbirds of the genus *Phaethon*. In the Tertiary, the situation in tropicbirds may have paralleled that seen today in the Sulidae, in which gannets of the genus *Morus* are found in temperate waters at higher latitudes whereas boobies of the genus *Sula* occur in the tropics. *Heliadornis* may therefore have been the high latitude subtropical counterpart of the tropical *Phaethon*. The same factors, including the rigors of Pleistocene climates and the closing of the Panamanian seaway, that may have been responsible for the reduction in diversity of *Morus* from three species in the Calvert Formation to a single species in the North Atlantic today may also have brought about extinction in the higher latitude lineage of tropicbirds.

Acknowledgments

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Literature Cited

Andrews, C. W. 1899. On the remains of a new bird from the London Clay of Sheppey.—Proceedings of the Zoological Society of London 1899: 776–775.

Cheneval, J. 1996. Tertiary avian localities of Belgium. Pp. 535–540 *in* J. Mlikovsky, ed., Tertiary avian localities of Europe.—Acta Universitatis Carolinae Geologica 39 (for 1995):519–846.

Harrison, C. J. O., & C. A. Walker. 1976. A reappraisal of *Prophaethon shrubsolei* Andrews (Aves).—Bulletin of the British Museum (Natural History) Geology 27:1–30.

Mlikovsky, J. 1997. A new tropicbird (Aves: Phaethontidae) from the late Miocene of Austria.—Annalen des Naturhistorischen Museums in Wien, 98A:151–154.

Olson, S. L. 1985. A new genus of tropicbird (Pelecaniformes: Phaethontidae) from the Middle Miocene Calvert Formation of Maryland.—Proceedings of the Biological Society of Washington 98:851–855.

———. 1994. A giant *Presbyornis* (Aves: Anseriformes) and other birds from the Paleocene Aquia Formation of Maryland and Virginia.—Proceedings of the Biological Society of Washington 107:429–435.

Steininger, F. F., R. L. Bernor, & V. Fahlbusch. 1989. European Neogene marine/continental chronologic correlations. Pp. 15–46 *in* E. H. Lindsay, V. Fahlbusch, and P. Mein. European Neogene mammal chronology. New York: Plenum Press. 658 pp.

Ward, L. 1992. Molluscan biostratigraphy of the Miocene, Middle Atlantic coastal plain of North America.—Virginia Museum of Natural History Memoir 2, 159 pp.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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A new species of *Cyclemys* (Testudines: Bataguridae) from Southeast Asia

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Abstract.—A new species of batagurid turtle, *Cyclemys atripons*, is described from the mountainous areas of southeastern Thailand and adjacent Cambodia. It differs from other *Cyclemys* (herein all referred to as *C. dentata*) by the unique combination of a head mottled with black dorsally and striped laterally, a nearly immaculate chin, a distinct carapace pattern, a plastron with no or only a few coarse black rays, a coarsely and densely pigmented bridge, a narrow carapace, a long plastral hindlobe, a wide plastral forelobe, a small gular scute, and a long interhumeral seam length. Discriminant function analysis of 17 morphometric characters standardized for body size supported the distinctiveness of the new species from *Cyclemys dentata*, and indicated that other populations of this complex (on Borneo and in China) may also be morphologically distinct.

The genus *Cyclemys* is currently envisioned by most authors to comprise two species (*C. dentata* Gray 1831 and *C. tcheponensis* Bourret 1939) with very uncertain distributions (Ernst & Barbour 1989, Iverson 1992). *Cyclemys dentata* was originally described by Gray (1831:20) as *Emys Dhor* (type locality: "Bengal . . . Java"), but he corrected the name to *Emys dentata* in the Errata of that publication. However, for the next 100 years the species name *dhor* was used by most authors (including Gray on occasion, e.g., 1870 and 1872). During that period several additional names (now recognized as synonyms) were applied to this taxon: *Cyclemys orbiculata* Bell 1834; *Cistudo diardi* Duméril & Bibron 1835; *Cyclemys oldhami* Gray 1863; *Cyclemys ovata* Gray 1863; and *Cyclemys bellii* Gray 1863. Stejneger (*in* Barbour 1912:143) and Smith (1930:8) both argued that the correct species name is *dentata* and nearly all authors subsequent to Smith have used the latter name. As defined by Smith, *C. dentata* ranges from northeastern India to southwestern China, and through southeast Asia to Sumatra, Java, Borneo and the Philippines (Taylor 1920, Smith 1930, Zhao & Adler 1993).

In 1939, Bourret recorded *C. dentata* from Hanoi, Vietnam, but described *Geoemyda tcheponensis* from central Vietnam, based on a juvenile in the Hanoi Museum. Wermuth & Mertens (1961) first recognized the similarity of *G. tcheponensis* and *C. dentata* (even though the two species were originally described in separate genera) and synonymized the former under the latter. In a comprehensive study of the generic relationships among all the pond turtles (emydines and batagurines), McDowell (1964) supported that synonymy. However, in 1976, after examining 16 pet trade or market specimens of *Cyclemys*, McMorris argued that *tcheponensis* and *dentata* were distinct species characterized by color pattern differences (the former having a head mottled dorsally and striped laterally, and the latter lacking head and neck stripes and having the dorsum of its head uniform brown). During the following 20 years, most authors have cautiously recognized both, pending further study (e.g., Pritchard 1979, Ernst & Barbour 1989, Iverson 1992). A single anomalous specimen of *Cyclemys* with only 11 marginal scutes per side was described from southern Yunnan, China by Kou (1989) as *C. tiannanensis*, but that name was quickly synonymized with *dentata* by Das (1991:80) and Zhao & Adler (1993:167).

In 1994, distinctive turtles labelled as *Cyclemys dentata* began appearing in the pet trade from southeast Asia. According to the exporters, these turtles originated from Tonle Sap, near Phnom Penh, Cambodia (Anson Wong, pers. comm.). These unique turtles clearly belonged to the genus *Cyclemys* (sensu McDowell 1964), but in order to compare them with other *Cyclemys* we began examining variation across all known populations of the genus. Our full analysis of variation is not yet complete (Iverson, McCord, van Dijk, Das, and Moll, pers. comm.), but our preliminary morphometric comparisons of over 180 *Cyclemys* representing all known areas of the range, of most of the type specimens, and of all phenotypes from typical *tcheponensis* to typical *dentata* (sensu McMorris 1976) revealed the existence of an unnamed population apparently associated with the Cardamom uplift in southeastern Thailand and adjacent Cambodia; indicated that *tcheponensis* is apparently not *morphometrically* distinct from *dentata*; and suggested that populations on Borneo and from China may also each be distinctive.

Although the new taxon seems to have a very limited distribution, it is now exported from Cambodia in great numbers. Therefore, it seems appropriate to name it now, before our full analysis of variation in the genus is complete, so that it might soon be given appropriate legal protection.

Materials and Methods

Shell and scute measurements (to the nearest 0.1 mm) were recorded from all available museum and pet trade specimens of *Cyclemys* (*sensu* McDowell 1964). Because we observed specimens with both the *tcheponensis* and *dentata* phenotypes from nearly everywhere across the composite range and because specimens without heads could not be allocated confidently to either phenotype, we lumped specimens by geography, establishing ten populations for analysis: India and Burma (0), northern Cambodia/Laos/Vietnam (1), southeastern Thailand and adjacent Cambodia (2), Thailand (3, excluding southeast Thailand), China (4), Malay Peninsula (5), Borneo (6), Sumatra (7), Java (8), and Philippines (9).

Preserved material was borrowed from the American Museum of Natural History (AMNH), the British Museum of Natural History (BMNH), the California Academy of Sciences (CAS), the Field Museum of Natural History (FMNH), the Museum of Comparative Zoology at Harvard (MCZ), the National Museum of Natural History in Paris (MNHN), the Oxford University Museum (OUM), the National Museum of Natural History in Leiden (RMNH), the Florida Museum of Natural History at the University of Florida (UF), the University of Kansas Museum of Natural History (KU), and the United States National Museum (USNM), and living material was available in McCord's private collection (WPM) (Fig. 1). Recorded measurements included maximum (not midline) carapace length (CL), maximum carapace width (CW), maximum carapace height (CH), maximum (not midline) plastron length (PL), maximum (not midline) length of the plastral forelobe from the interabdomino-interpectoral junction to a line across the anterior ends of the gular scutes (FL), maximum (not midline) length of the plastral hindlobe from the interabdominal-interfemoral junction to a line across the posterior ends of the anal scutes (HL), minimum (median) length of the plastral hindlobe from the interabdominal-interfemoral junction to the anal notch (NHL), plastral forelobe width at the level of the junction of the humeropectoral seam and the plastral margin (PWA), anterior

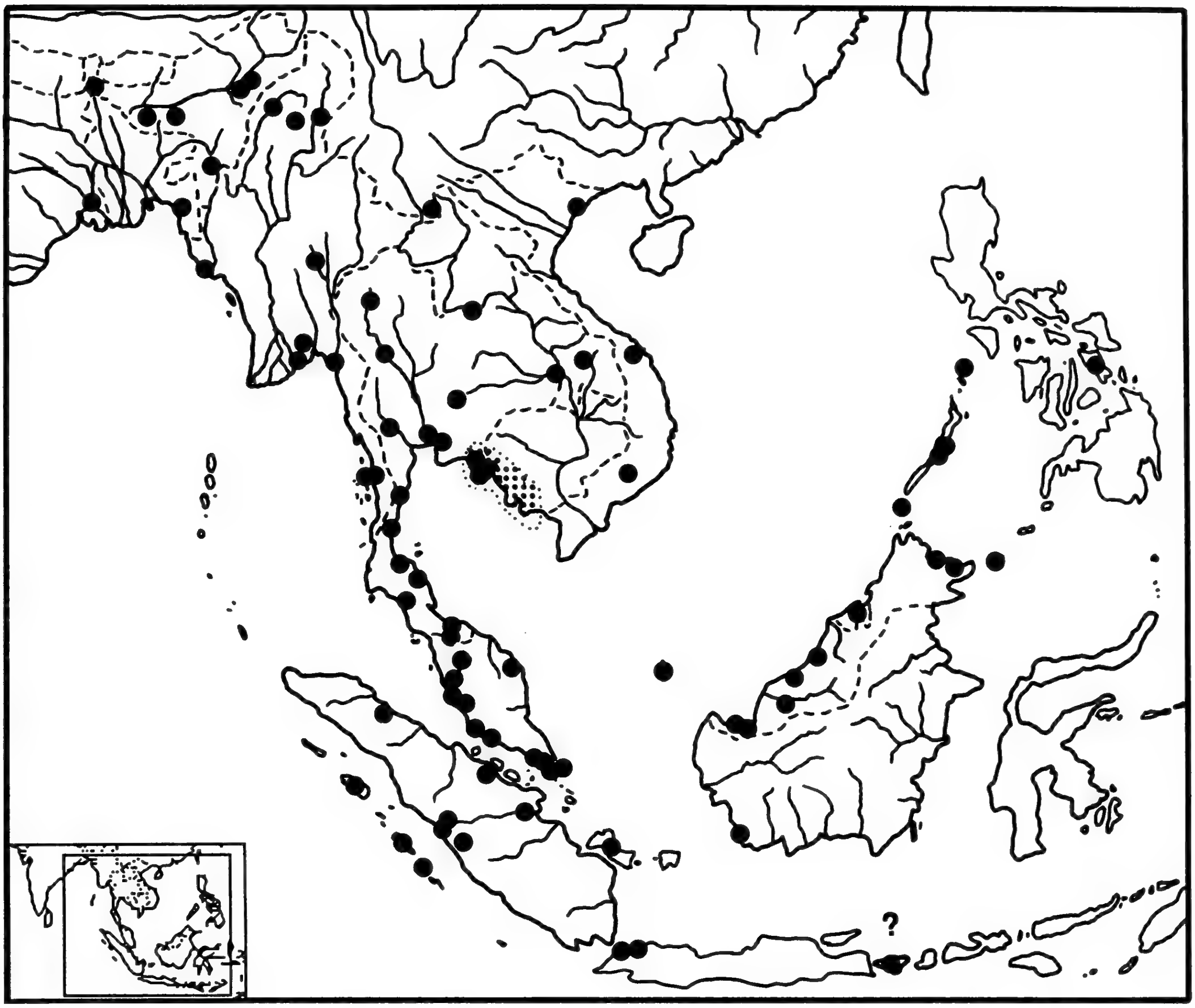

Fig. 1. Composite range map of *Cyclemys* in southeast Asia (from Iverson, 1992, and unpublished). Dots represent literature or museum locality records. Hatched area in Thailand and Cambodia encircles hypothesized range of *Cyclemys atripons*.

plastral hindlobe width at the level of the junction of the abdominofemoral seam and the plastral margin (PWC), posterior plastral hindlobe width at the level of the junction of the femoroanal seam and the plastral margin (PWD), left bridge length from axilla to inguinal pocket (BL), maximum ventral width across gular scutes (GW), maximum (not midline) length of right gular scute (GL), and lengths of right interhumeral (IH), interpectoral (IP), interabdominal (IAB), interfemoral (IF), and interanal (IAN) seams. Although there is some sexual dimorphism in some of these characters, females and males were analyzed together in order to include dried museum specimens lacking soft parts and subadults that could not be sexed confidently. Only adult and subadults (>110 mm CL) were included in this preliminary analysis.

The data were standardized for body size by division by carapace length. Although concerns have been expressed about the statistical validity of using ratios rather than residuals in quantitative analyses (Atchley et al. 1975, 1976; among others), multivariate analyses of ratios of turtle morphometric data have not yielded results that differed from those employing residuals (e.g., Berry 1978, McCord & Iverson 1991). In addition, the use of ratios offers the advantage of working with parameters that can be directly measured and/or compared; it is not possible to compare raw measurements

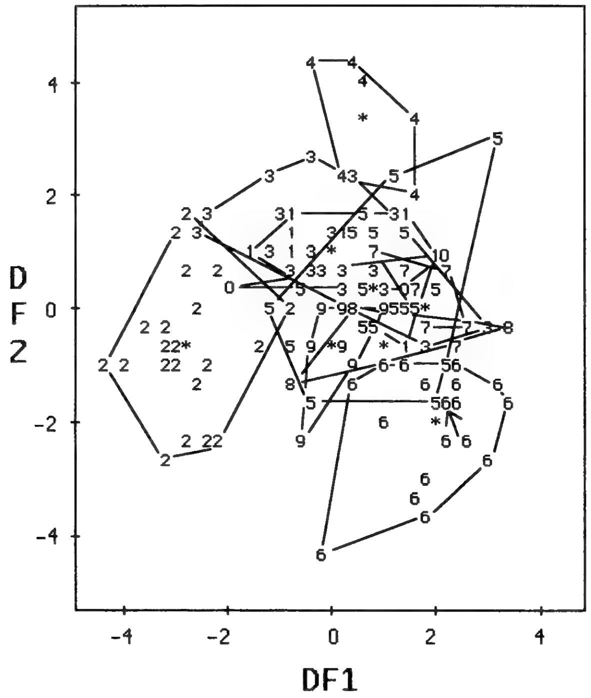

Fig. 2. Plot of first two canonical axes (discriminant functions DF1 and DF2) for specimens of *Cyclemys* based on discriminant function analysis of the ratios of 17 characters (listed in Table 1). First and second axes account for 44.9% and 27.2% of the variation, respectively. Country codes are India and Burma (0), northern Cambodia/Laos/Vietnam (1), southeastern Thailand and adjacent Cambodia (2), Thailand (3, excluding southeast Thailand), China (4), Malay Peninsula (5), Borneo (6), Sumatra (7), Java (8), and Philippines (9). The arrow marks the adult syntype of *Cyclemys ovata* Gray, which is grouped among the other Borneo turtles with a probability of 93%.

directly to mean values of a residual. The 17 character ratios produced by this standardization were then submitted to discriminant function analysis (DFA) with SPSS software (SPSS, Inc. 1983). ANOVA and pairwise population comparisons for the ratios of each variable to CL were made with Fisher's (protected) least significant difference (PLSD) test with STATVIEW software (Abacus Concepts 1992).

Results and Discussion

Both the discriminant function analysis (DFA; Fig. 2) and the analyses of variance of the ratios for the various populations of *Cyclemys* (Table 1) demonstrated that the population in southeast Thailand and adjacent Cambodia is morphometrically the most distinct of all populations. They also suggested that turtles from Borneo and those from China are divergent. The analyses revealed that, compared to other *Cyclemys* populations, those from SE Thailand/Cambodia tend to have a narrower carapace, a longer plastral hindlobe, a wider plastral forelobe, a narrower and shorter gular scute, and a longer interhumeral seam length; those from Borneo tend to have a deeper shell, a longer hindlobe, a longer gular scute, a shorter interhumeral seam length, a longer interfemoral seam length, and a shorter interanal seam length; and those from China tend to have a very narrow shell, a shorter and narrower plastral forelobe, a narrower plastral hindlobe, and a wider gular scute.

Untransformed data for the characters that varied most significantly in the ANOVA's and DFA (Table 1) were recombined into character ratios and examined to summarize variation within the genus *Cyclemys* (Table 2). That analysis reinforced the distinctiveness of the Thailand/Cambodia population and demonstrated significant overlap among most of the other populations; however, confirmation of the uniqueness of the Borneo and/or Chinese populations must await our additional analyses. Because the Thailand/Cambodia population is both allopatric and morphometrically distinct from other populations of *Cyclemys*, and because that population also differs in color patterns of the head and shell, we here describe it as:

Cyclemys atripons, new species

Black-bridged leaf turtle

Fig. 3.

Holotype.—USNM 81865, a dried shell of a female with limbs but no head, from Thailand, Krat [=Trat], Kao [=Mt.] Kuap (=Khao Kuap), collected 24 December 1929 by Hugh M. Smith.

Paratypes.—USNM 94745, an unsexed juvenile from Thailand, Chanthaburi, Kao [Mt.] Sabab (=Khao Sabap) collected 20

Table 1.—Results of univariate analysis of variance of ratios of 17 characters to carapace length across 10 populations of *Cyclemys* and for *Cyclemys atripons* (n = 29) versus all other populations (n = 106).

Character	Across all populations		*C. atripons* vs. others	
	f	*P*	*f*	*P*
Maximum carapace width (CW)	7.7	<0.0001	8.1	0.005
Maximum carapace height (CH)	8.1	<0.0001	11.0	0.0011
Maximum plastron length (PL)	1.9	0.06	6.5	0.012
Maximum forelobe length (FL)	0.6	0.78	1.4	0.24
Maximum hindlobe length (HL)	3.2	0.0017	5.8	0.018
Medial hindlobe length (NHL)	3.4	0.001	9.7	0.0022
Plastral width (PW1)	4.1	<0.0001	12.3	0.0006
Plastral width (PW3)	5.2	<0.0001	0.3	0.61
Plastral width (PW4)	2.6	0.008	0.4	0.55
Bridge length (BL)	2.2	0.029	4.7	0.032
Gular width (GW)	2.8	0.0046	9.5	0.0025
Gular length (GL)	2.1	0.032	8.3	0.0046
Interhumeral seam length (IH)	3.0	0.0025	14.1	0.0003
Interpectoral seam length (IP)	1.2	0.28	2.5	0.12
Interabdominal seam length (IAB)	3.1	0.0022	1.7	0.20
Interfemoral seam length (IF)	4.2	<0.0001	0.03	0.87
Interanal seam length (IAN)	4.3	<0.0001	4.0	0.047

November 1931 by Hugh M. Smith. USNM 53423, a dried shell of a female with separate head, limbs, and viscera in alcohol, and USNM 53424, an unsexed juvenile preserved in alcohol, from Thailand, Trat, Koh [= Ko = island] Chang, both collected in December 1914 by C. B. Kloss (see Smith & Kloss 1915). MCZ 29571, an unsexed juvenile preserved in alcohol, and MCZ 29572, a subadult (possibly male) in alcohol from Thailand, Gulf of Siam, Koh Kong (=Ko Chang), both donated in 1930 by Malcolm Smith. USNM 79515, a complete, mummified adult female from Thailand, Trat, Koh Kut (=Ko Kut), Gulf of Thailand collected 21 May 1929 by Hugh M. Smith. KU 47171 (formerly MCZ 29558), a dried shell of an adult, from "Bangkok, Siam" (certainly the shipping point rather than the actual collection locality), donated in 1930 by Malcolm Smith. UF 105992, an adult male preserved in alcohol, and UF 105993, a dried skeleton of an unsexed subadult; reported to have been collected from Tonle Sap, Phnom Penh, Cambodia [=Kampuchea], but purchased from local people in Phnom Penh by Mr. Anson Wong in the spring of 1994.

Table 2.—Morphometric characters useful in distinguishing *Cyclemys atripons* (n = 29) from other *Cyclemys* (n = 106). Character abbreviations are maximum carapace width (CW), maximum shell height (SH), width of anterior plastral lobe (PWA), median length of plastral hindlobe (NHL), maximum gular width (GW), maximum gular length (GL), and interhumeral seam length (IH). Values are means followed by range in parentheses. All character ratios are highly significantly different (P < 0.0001) by Fisher's (protected) least significant difference test.

Character	*Cyclemys atripons*	Other *Cyclemys*
IH/SH	0.293 (0.176–0.425)	0.231 (0.095–0.529)
IH/CW	0.132 (0.088–0.199)	0.106 (0.045–0.186)
PWA/CW	0.598 (0.503–0.671)	0.554 (0.451–0.651)
GL/NHL	0.278 (0.201–0.308)	0.305 (0.228–0.377)
GW/PWA	0.414 (0.335–0.503)	0.452 (0.371–0.562)

Diagnosis.—A medium-sized species of *Cyclemys* (carapace to 224 mm, but usually less than 200; to at least 250 mm in other *Cyclemys*) with an elongate, basically tricarinate carapace having an obvious middorsal keel and weak lateral keels and being nearly flat dorsally in adults; a plastron hinged between the pectoral and abdominal scutes (hyoplastral and hypoplastral bones); a very weakly hooked upper tomium with a medial shallow notch or cusp; a relatively wide carapace (maximum width averages 78% of carapace length [CL] in *C. atripons*; 82% in other *Cyclemys*); a relatively low carapace (maximum shell height averages 35% of CL in *C. atripons*; 37% in other *Cyclemys*); a relatively wide plastral forelobe (posterior width averages 46% of CL in *C. atripons*; 45% in other *Cyclemys*); a relatively long plastral hindlobe (median length averages 50% of CL in *C. atripons*; 49% in other *Cyclemys*); a small gular scute (maximum length and width average 19% and 14% of CL, respectively, in *C. atripons*; 20% and 15%, respectively, in other *Cyclemys*); and a relatively long interhumeral seam (length averages 10% of CL in *C. atripons*; 8.5% in other *Cyclemys*) [see also Table 2 and Fig. 3]; a light cream to brown temporal and postorbital stripe on each side of head extending posteriorly onto the neck (flushed with salmon in juveniles), and a third narrower light stripe extending from the angle of the jaw to the ventral margin of the tympanum (sometimes connected to the postorbital stripe by a short vertical branch along the anterior margin of the tympanum) (basic pattern is similar to that in other *Cyclemys*); a nearly immaculate cream or yellow chin, lightly flushed with salmon in juveniles and sometimes with a few vague black flecks (darkly mottled to almost completely black in other *Cyclemys*); carapace light olive to brown to nearly black, with coarse black rays radiating from the areolae, but the lateral rays on C1–C3 disappearing with age, leaving the anterior rays in a bold, dense triangular concentration on the anterodorsal half of C1–C3 (carapacial rays, if visible, evenly distributed across costal scutes in other *Cyclemys*); the plastron with no or only a few coarse black rays on a cream to yellow-brown to horn-colored background, but with the bridge coarsely and densely flecked or streaked with black (entire plastron almost always heavily streaked with black [sometimes completely brown or black] in other *Cyclemys*).

Description (based on the type series as well as 12 adult females, 8 adult males, 6 unsexed subadults or juveniles alive in McCord's collection).—Carapace length to at least 191 mm in males and at least 224 mm in females, elongate, moderately tricarinate with a prominent medial keel and weak lateral keels, not domed (maximum shell height/CL = 0.308–0.395; mean = 0.352), nearly flat dorsally in full adults, widest at marginal M7 (maximum carapace width/CL = 0.703–0.898; mean = 0.781), with a slightly serrated posterior margin, and with moderately obvious growth annuli (least obvious in old individuals). Marginals all fairly uniform in length (along carapace margin); M5, 6.7, or 12 tallest; M9–11 usually flared. Cervical scute medium in size, usually longer than wide, indented medially along the posterior margin, and occasionally wider posteriorly than anteriorly. Vertebrals V2–5 wider than long; V1 usually wider than long, but not contacting seam between M1 and M2; V5 not even close to contacting M10. Prominent medial keel most pronounced on V4 and V5, but also obvious on V1 and V3; lateral keels weak, but most pronounced on costal C3. Carapace olive to brown to nearly black, with seams more darkly marked; coarse black rays radiate from the areolae; however, rays extending to the marginals on costals C1–C3 fade with age such that adults appear to have a dense triangular concentration of black streaks on the anterodorsal half of C1–C3 (Fig. 3); carapacial keels not distinctly colored unless due to abrasion, but medial keel in subadults and most adults tending to lack black pigment, giving the impression of a weak, light midvertebral stripe (particularly evident on the nuchal scute).

Maximum plastron length shorter than carapace length (PL/CL = 0.899–1.039; mean = 0.975). Plastron very slightly upturned anteriorly, with hinge present between the hyoplastral and hypoplastral bones (approximately aligned with the seam between the pectoral and abdominal

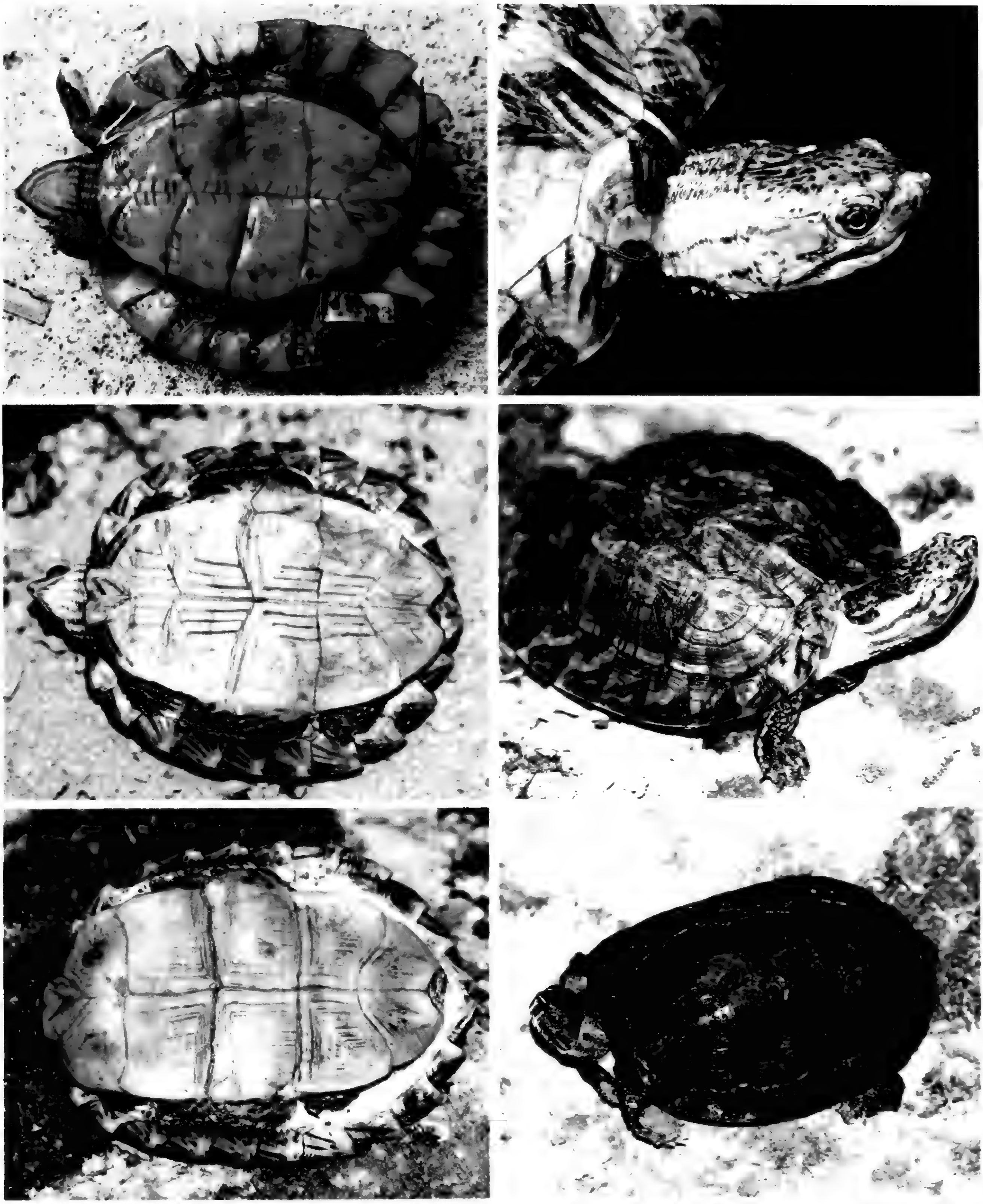

Fig. 3. *Cyclemys atripons*. Left (plastral views; top to bottom): carapace of first year turtle, USNM 94745, 78 mm carapace length (CL); subadult, WPM 001, 132 mm CL; adult, WPM 003, 191 mm CL. Right (top to bottom); juvenile, WPM 002, 135 mm CL; subadult, WPM 001, 132 mm CL; adult female, WPM 004, 196 mm CL.

scutes). Plastral forelobe width (PWA) at level of junction of humeropectoral seam and lateral plastral margin relatively wide (PWA/CL = 0.420–0.507; mean = 0.464). Median length of plastral hindlobe lobe (NHL) relatively long (NHL/CL = 0.441–0.536; mean = 0.501). Plastral hindlobe with relatively shallow anal notch. Bridge moderately long (BL/CL = 0.304–0.360; mean = 0.336); axillary and inguinal scutes very reduced or absent. Gular scute relatively small (GW/CL = 0.162–0.216; mean = 0.192; GL/CL = 0.108–0.163; mean = 0.139), but interhumeral seam relatively long (IH/CL = 0.065–0.155; mean = 0.103). Average plastral formula (see also Table 2 and Fig. 1 for diagnostic ratios): interpectoral seam (IP) > interabdominal seam (IAB) ≃ interanal seam (IAN) ≫ gular length (GL) ≃ interfemoral seam (IF) ≥ interhumeral seam (IH). Plastron cream, yellow-brown, or horn colored, with seams more darkly marked with brown; no or only a few short, coarse, black flecks or rays present (Fig. 3); bridge area with obvious coarse black rays or flecks radiating anteriorly and laterally (not medially) from the scute areolae. Ventral surfaces of M4–M7 more boldly marked with black rays or flecks than on other marginals.

Head of medium width; upper jaw weakly hooked, but with a shallow median notch; triturating surfaces narrow. A few small tubercles evident between angle of jaw and tympanum. Dorsum of head coarsely flecked with black on a greenish-brown background. A light cream to brown temporal and postorbital stripe on each side of head, extending posteriorly onto the neck (flushed with salmon in juveniles), and a third narrower light stripe extending from the angle of the jaw at least to the ventral margin of the tympanum (sometimes connected to the postorbital stripe by a short vertical branch along the anterior margin of the tympanum); these stripes darken with age but are still evident even in old individuals (see Fig. 3). Chin cream or yellow (lightly flushed with salmon in juveniles), with a few or no vague black markings; most frequent black mark on chin a short, thin median line subequal to orbit diameter. Neck with six vague light stripes ventrally (parallel to and between the stripes extending posteriorly from the angle of the jaws). Tomia cream to yellow brown to dark gray with several coarse black streaks. Vague black horizontal line across eye (through pupil); iris light green to brown.

Anterior surface of antebrachium covered with large, imbricate scales, the largest of which are crescent to spade-shaped; largest scales on hindlimb at heel, but generally smaller than largest forelimb scales. Upper parts of limbs and tail covered with fine scales. Exposed dorsal parts of forelimbs dark brown (rarely almost black) with black flecks; ventral surfaces cream to yellow and unmarked; dorsal surface of digits generally lighter in color than lateral surfaces. Dorsal surface of hindlimbs dark gray-brown to black; ventral surfaces cream colored. Narrow cream colored stripe on posterior margin of each hind limb, extending at least to heel; dark stripe immediately ventral to it, extending to anal region in all but the oldest specimens. Cream colored soft parts between hindlimbs and tail washed with salmon in some juveniles. Recessed areas of inguinal and axillary regions and between neck and forelimbs uniform cream color. Tail (even in males) relatively short, dark gray to brown, with a black middorsal stripe and a ventrolateral dark brown stripe on each side.

Males and females both with a flat or slightly convex plastron. Males with a slightly longer tail than females; vent generally at level of posterior carapace margin in males and anterior to it in females.

The single available, incompletely prepared skull associated with UF 105993 has the maxillae separated anteriorly by the premaxillae; pterygoid barely in contact with the jugal; foramen posterius palatinum small and similar in size to the foramen orbitonasale; fissura ethmoidalis extremely narrow ventrally, distinctly key-hole shaped; cranial cavity not ventrally narrowed by the processi inferiores parietales; and quadratojugal present as part of postorbital bar.

Etymology.—From the Latin, *atri*, meaning black, and *pons*, meaning bridge, in reference to the darkly pigmented bridge in this species that contasts so strongly with the usually unmarked plastron.

Other material.—Twenty-six live specimens in the collection of William P. McCord (WPM 1–26), to be deposited on death in the UF collection.

Distribution.—Apparently restricted to the isolated hill country of extreme southeastern Thailand and southwestern Cambodia, in association with the Cardamon mountain range, including the Gulf of Thailand islands of Koh Chang and Koh Kut (the two largest and most mountainous islands in the area). Recent pet trade specimens, said to be coming from Tonle Sap, a lowland wetland near Phnom Penh, Cambodia, more likely came from the hill country to the southwest. The nearest confirmed record for *Cyclemys dentata* is from Sakaeret, Thailand (FMNH 183723-39; Inger & Colwell 1977), ca. 275 km to the north-northwest.

Remarks.—Our preliminary analyses support the suggestion by Das (1995a, 1995b) that the population on Borneo is distinctive. Should our further analysis confirm its distinctiveness, the name *Cyclemys ovata* (Gray 1863:178 from Sarawak) is available (see also Fig. 2). If our preliminary results regarding the distinctiveness of the Chinese population are confirmed, the name *Cyclemys tiannanensis* Kou 1989:193 (from Yunnan) may be applicable to the Chinese population we sampled, even though the name was based on a single aberrant specimen. In our preliminary analysis we could find no morphometric character to distinguish *tcheponensis* from *dentata*. It has been suggested that color pattern differences between these two may reflect altitudinal variation more than regional variation (Frank Yuwono, pers. comm.). However, our final conclusion on the validity of *tcheponensis* must await completion of our broader analysis (including juveniles).

Zoogeography.—*Cyclemys atripons* is apparently not the only species endemic to the hill country of southeastern Thailand and adjacent Cambodia. According to Peter Paul van Dijk (pers. comm.), at least the following two frogs and two lizards are endemic to the same area: *Rana fasciculispina*, *Rana kohchangae*, *Isopachys roulei*, and *Pseudocalotes floweri*.

Comparative material examined: *Cyclemys dentata* (sl): India (BMNH 1930.6.8.4, OUM 8502 [syntype of *Cyclemys orbiculata*], OUM 8513 [syntype of *Cyclemys orbiculata* and holotype of *Cyclemys bellii*], RMNH 6073, and USNM 293726); Burma (AMNH 58423, BMNH 1947.3.5.63 [syntype of *Cyclemys oldhami*]); China (WPM 6 specimens); Thailand (BMNH 1947.3.4.26 [syntype of *Cyclemys oldhami*], BMNH 62.8.18.20, FMNH 183727–728, 183730, 183732, 183735, 183737–738, MCZ 29561–566, 29568–570, 29573, 43066–067, 43084, USNM 26249, 94602, 269918–919, WPM 3 specimens); Laos (USNM 103016); Vietnam (MNHN 1948.38, RMNH 4751, USNM 95100, WPM 12 specimens); Malay Peninsula (AMNH 49933, FMNH 142501, 166553, 224081–082, 224085–092, 251501, 251508, USNM 30961, 30964, WPM 8 specimens); Sumatra (BMNH 1979.221, CAS-SU 8615, RMNH 3838, USNM 37792, WPM 11 specimens); Java (BMNH 1946.1.22.62 and 1946.1.22.63 [syntypes of *Emys dentata*], MNHN 9107 [syntype of *Cistudo diardii*], USNM 62576, WPM 2 specimens); Philippines (AMNH 90102, CAS 62166, 134331–332, 157280, FMNH 51598, KU 47172, 79176, MCZ 25569, USNM 229500–501, 496884); and Borneo (BMNH 63.6.21.1 [syntype of *Cyclemys ovata*], FMNH 14974, 63276–278, 128257, 128259, 151015, 166554, MCZ 11244, USNM 38534, WPM 16 specimens).

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Literature Cited

Abacus Concepts. 1987. Statview. Abacus Concepts, Inc., Berkeley, California, 466 pp.

Atchley, W. R., C. T. Gaskins, & D. Anderson. 1975. Statistical properties of ratios of biological data.—American Zoologist 15:829.

———. 1976. Statistical properties of ratios I. Empirical results.—Systematic Zoology 25:137–148.

Barbour, T. 1912. A contribution to the zoogeography of the East Indian islands.—Memoirs of the Museum of Comparative Zoology 44:1–203.

Bell, T. 1834. Characters of a new genus of freshwater tortoises (*Cyclemys*).—Proceedings of the Zoological Society of London 1834:17.

Berry, J. F. 1978. Variation and systematics in the *Kinosternon scorpioides* and *K. leucostomum* complexes (Reptilia: Testudines: Kinosternidae) of Mexico and Central America. Unpublished Ph. D. dissertation, University of Utah, Salt Lake City, 325 pp.

Bourret, R. 1939. Notes herpétologiques sur l'Indochine française. XVI. Tortues de la collection du Laboratoire des Sciences Naturelles de l'Université. Description d'une espèce nouvelle.—Annexe au Bulletin Général de l'Institution Publique (Hanoi) 1939(6):1–34.

Das, I. 1991. Colour guide to the turtles and tortoises of the Indian subcontinent. R & A Publ., Avon, England, 133 pp.

———. 1995a. An illustrated key to the turtles of insular south-east Asia.—Hamadryad 20:27–32.

———. 1995b. Turtles and Tortoises of India. Oxford University Press, Bombay, India, 176 pp.

Duméril, A.-M.-C., & G Bibron. 1835. Erpétologie Générale ou Histoire Naturelle des Reptiles. Tome Second, Roret, Paris, 680 pp.

Ernst, C. H., & R. W. Barbour. 1989. Turtles of the World. Smithsonian Institution Press, Washington, D.C., 313 pp.

Gray, J. E. 1831. Synopsis Reptilium, or short description of the species of reptiles. Treuttel, Wurtz & Co., London, 85 pp.

———. 1863. Observations on the box tortoises, with descriptions of three new Asiatic species.—Proceedings of the Zoological Society of London 1863:173–179.

———. 1870. Supplement to the catalogue of shield reptiles in the collection of the British Museum. Part I. Testudinata (Tortoises). Taylor and Francis, London, 120 pp.

———. 1872. Appendix to the catalogue of shield reptiles in the collection of the British Museum. Part I. Testudinata (Tortoises). British Museum, London, 28 pp.

Inger, R. F., & R. K. Colwell. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand.—Ecological Monographs 47: 229–253.

Iverson, J. B. 1992. A revised checklist with distribution maps of the turtles of the world. Iverson Publishing, Richmond, Indiana, 363 pp.

Kou, Z. 1989. *Cyclemys* from Yunnan, a description of a new species and a new record to China (Testudinata:Emydidae).—Current Herpetology in East Asia: 193–197.

McDowell, S. B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae.—Proceedings of the Zoological Society of London 143:239–279.

McCord, W. P., & J. B. Iverson. 1991. A new box turtle of the genus *Cuora* (Testudines: Emydidae) with taxonomic notes and a key to the species.—Herpetologica 47:407–420.

McMorris, J. R. 1976. The generic reassignment of *Geoemyda tcheponensis* Bourret.—Chelonia 3(2):10–11.

Pritchard, P. C. H. 1979. Encyclopedia of Turtles. T. F. H. Publ., Inc., Neptune, New Jersey, 895 pp.

Smith, M. A. 1930. The Reptilia and Amphibia of the Malay Peninsula from the Isthmus of Kra to Singapore, including the adjacent Islands (A Supplement to Dr. G. A. Boulenger's Reptilia and Batrachia, 1912).—Bulletin of the Raffles Museum, Singapore, Straits Settlements 3:1–138.

———, & B. Kloss. 1915. On reptiles and batrachians from the coast and islands of south–east Siam.—Journal of the Natural History Society of Siam 1:237–249.

SPSS, Inc. 1983. SPSS^{X} User's Guide. McGraw-Hill, New York, 949 pp.

Taylor, E. H. 1920. Philippine Turtles.—The Philippine Journal of Science 16(2):111–144.

Wermuth, H., & R. Mertens. 1961. Schildkröten, Krokodile, Brückenechsen. G. Fischer, Jena, 422 pp.

Zhao, E.-M., & K. Adler. 1993. Herpetology of China.—SSAR Contributions to Herpetology 10:1–522.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
110(4):640–680. 1997.

Morphological differentiation among Subsaharan and North African populations of the *Lemniscomys barbarus* complex (Rodentia: Muridae)

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Abstract.—Morphometric evaluation discloses patterns of craniodental variation which demonstrate that populations currently assigned to *Lemniscomys barbarus* consist of two species: *L. barbarus* (Linnaeus 1766) and *L. zebra* (Heuglin 1864). One species-group epithet is herein allocated to the junior synonymy of *L. barbarus* (*ifniensis* Morales Agacino 1935), ten to *L. zebra* (*spekei* De Winton 1897, *dunni* Thomas 1903, *convictus* Osgood 1910, *albolineatus* Osgood 1910, *manteufeli* Matschie 1911, *oweni* Thomas 1911b, *nigeriae* Thomas 1912, *olga* Thomas & Hinton 1921, *nubalis* Thomas & Hinton 1923, and *orientalis* Hatt 1935), and a lectotype is designated for *Mus zebra* Heuglin (1864). No subspecies are recognized for either species, but the substantial heterogeneity documented within *L. zebra* advises continued study of those populations. The geographic occurrence of *L. barbarus* is restricted to scrub vegetation along a narrow coastal strip in Morocco, Algeria, and Tunisia; whereas, *L. zebra* is widely distributed over dry grassland and savanna biomes south of the Sahara Desert, from Senegal in West Africa to central Sudan in East Africa, and southwards to northcentral Tanzania. *Lemniscomys hoogstraali* Dieterlen (1991), known only by the holotype from eastcentral Sudan, is retained as a third member of the *barbarus* group. The species *L. barbarus* represents another example of small mammal endemic to the Barbarian province (Maghreb) of northwest Africa.

African grass mice of the genus *Lemniscomys* have been conventionally arranged into three species groups or complexes–*barbarus*, *griselda*, and *striatus*–defined principally by the striping pattern of the dorsal pelage (Hollister 1919, Ellerman 1941, Van der Straeten & Verheyen 1980). While the *griselda* and *striatus* species groups have attracted much revisionary attention over the past 20 years (Van der Straeten 1975, 1976, 1980a, 1980b, 1981; Van der Straeten & Verheyen 1978, 1979, 1980), the *barbarus* complex, or striped grass mice, has yet to receive the same careful review, an oversight which this study begins to redress.

As with other taxa named in the late 1800s through the early 1900s, forms eventually associated under *Lemniscomys barbarus* had been first described as full species (for example, *zebra* Heuglin 1864; *spekei* De Winton 1897, and *dunni* Thomas 1903). In 1910, however, Osgood diagnosed two new races of striped grass mice from British East Africa (*albolineatus* and *convictus*) that he assigned to *Arvicanthis barbarus* and at the same time reassociated *zebra* Heuglin and *spekei* De Winton as subspecies of *A. barbarus*. Whether or not he was continuing the polytypic approach advanced in his 1909 revision of *Peromyscus*, Osgood's nomenclatural assessments

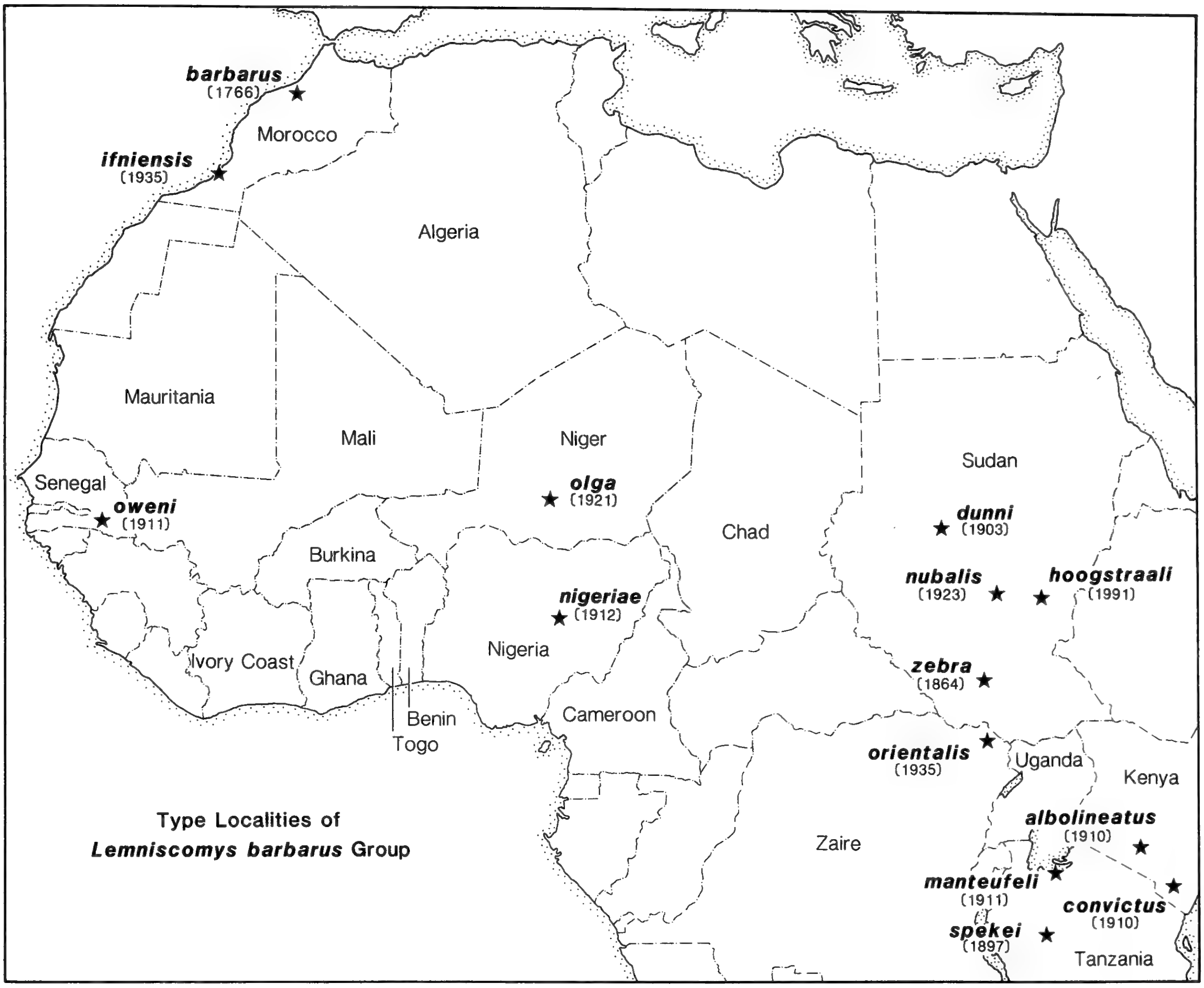

Fig. 1. Map of North and Central Africa depicting the type localities (stars) of the fourteen species-group taxa allocated to striped mice of the *Lemniscomys barbarus* species group. The date in parenthesis below each name indicates the year of the description.

established the precedent for treating striped grass mice south of the Sahara Desert as geographic representatives of Linnaeus' (1766) *Mus barbarus*, a form described from the Barbary Coast of northwest Africa. The new trinomials that appeared in the early 1900s–*b. manteufeli* Matschie (1911) and *b. nigeriae* Thomas (1912)—observed Osgood's delineation of specific boundaries, and Thomas' (1916) subsequent designation of a type species and emended diagnosis stabilized the contents and usage of *Lemniscomys* for African grass mice.

Still, an inclusive species definition was not universally or immediately adopted. By the time of Allen's (1939) systematic checklist of African mammals, three nominal species of the *barbarus* complex were thought to inhabit Subsaharan savannas: *L. barbarus* proper (including *albolineatus*, *convictus*, *ifniensis*, *manteufeli*, *nigeriae*, *spekei*, and *zebra*), *L. dunni* (including *nubalis* Thomas & Hinton 1923, and *olga* Thomas & Hinton 1921), and *L. oweni* (including *orientalis* Hatt 1935). Ellerman (1941), as he did for so many sweeping formulations of species limits of African small mammals, adopted a broad definition of *L. barbarus* and so consolidated most of these regional epithets as geographic races (Fig. 1). As an exception, he retained, without explanation, *L. olga* as a species with a restricted distribution in Niger and left the final nomenclatural step to Rosevear, who in

1969 ranked *olga* as a subspecies of *L. barbarus*.

Ellerman's (1941) influential classification of *L. barbarus*, amplified by Rosevear's (1969) later reassignment of *olga*, is generally observed in recent African catalogues and mammalian checklists (Misonne 1974, Honacki et al. 1982, Corbet & Hill 1991, Musser & Carleton 1993). The only other currently recognized species allocated to the *barbarus* group is *L. hoogstraali*, a member from southern Sudan recently described by Dieterlen (1991) and known only by the holotype (Fig. 1). Dieterlen, however, did not address the substantial variation apparent within *L. barbarus*, a widely distributed species with isolated populations in northwest Africa and with others occurring over savannas south of the Sahara Desert, from western (Senegal) to eastern Africa (Kenya and Tanzania). The appreciable variation across this region was remarked upon by Lamine Cheniti & Sami (1989), who noted that their Tunisian specimens of *L. barbarus* more closely resembled Central African *L. striatus* in size than West African *L. barbarus* (*b. nigeriae*, *b. olga*, and *b. oweni*). In this study, we examine the level of differentiation between the northwestern and Subsaharan moieties, the former the geographic source ("Barbaria") of *Mus barbarus* Linnaeus (1766), the type species of the genus, and the latter known by many regional epithets, the oldest of which is *Mus zebra* Heuglin (1864).

Materials and Methods

Approximately 650 specimens, representing about 170 principal collecting localities (Appendix 1), form the basis of this report. Specimens examined consist principally of skins with associated skulls contained in the museums, universities, or private collections listed below, each preceded by their institutional abbreviation. Except for *Mus barbarus* Linnaeus, which probably does not exist, type specimens of all species-group taxa we associate with the *Lemniscomys barbarus* complex (Table 4) have been examined and measured by Van der Straeten.

AMNH	American Museum of Natural History, New York City
BEL	Bellier Collection, presently housed in the Universitair Centrum, Antwerpen
BMNH	The Natural History Museum, London
BZM	Museum für Naturkunde der Humboldt-Universität, Berlin
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	The Field Museum of Natural History, Chicago
HAP	D. C. D. Happold Collection of Mammals, Canberra
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel
KMMA	Koninklijk Museum voor Midden Afrika, Tervuren
MAKB	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
MCZ	Museum of Comparative Zoology, Harvard University
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Museum National d'Histoire Naturelle, Paris
NHRS	Naturhistoriska Riksmuseet, Stockholm
RUCA	Universitair Centrum, Antwerpen
SMF	Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt
SMNS	Staatliches Museum für Naturkunde, Stuttgart
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C.
ZMA	Zoologisch Museum, Amsterdam
ZMK	Zoologisk Museum, København

Fourteen cranial and two dental dimensions, distilled from a larger suite of variables previously defined by Van der Straeten & Van der Straeten-Harrie (1977), were recorded in millimeters (mm) to analyse

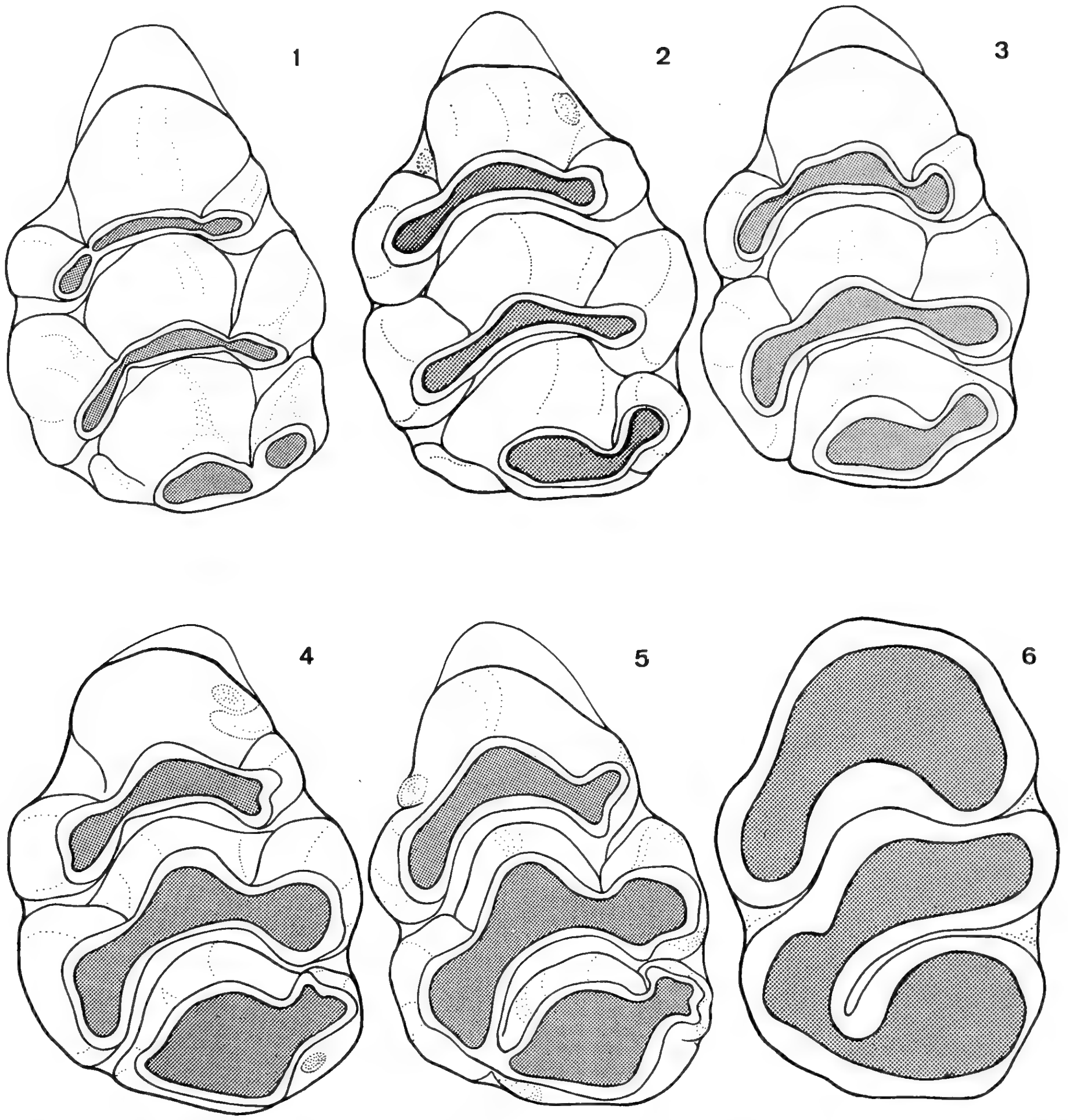

Fig. 2. Six age-classes based on toothwear stages, as defined by Van der Straeten (1980a:Fig. 1) for specimens of *Lemniscomys*.

univariate and multivariate variation within and between the populations sampled. To assess variation due to sexual dimorphism or post-weaning growth, gender was recorded from skin tags and specimens were assigned to one of six age classes. The age classes (Fig. 2) correspond to progressive wear patterns of the upper first molar as recognized by Van der Straeten (1980a).

Crania were viewed under a stereomicroscope when measuring the craniodental variables to 0.01 mm using hand-held digital calipers accurate to 0.03 mm. These 16 measurements, and their abbreviations as used herein, include (see Fig. 3 for landmarks): occipitonasal length (ONL); greatest zygomatic breadth (ZB); breadth of the braincase (BBC); breadth across the occipital condyles (BOC); least interorbital breadth (IOB); length of nasals (LN); breadth of the rostrum (BR); postpalatal length (PPL); length of the bony palate (LBP); length of the upper diastema (LD); length of the incisive foramen (LIF); breadth across the upper first molars (BM1s); breadth of the zygomatic plate (BZP); length of the auditory bulla (LAB); alveolar length of the maxillary toothrow (ALM); and coronal width of the first upper molar (WM1). In addition, standard external dimensions and weight (in grams) were transcribed from skin tags as given by the

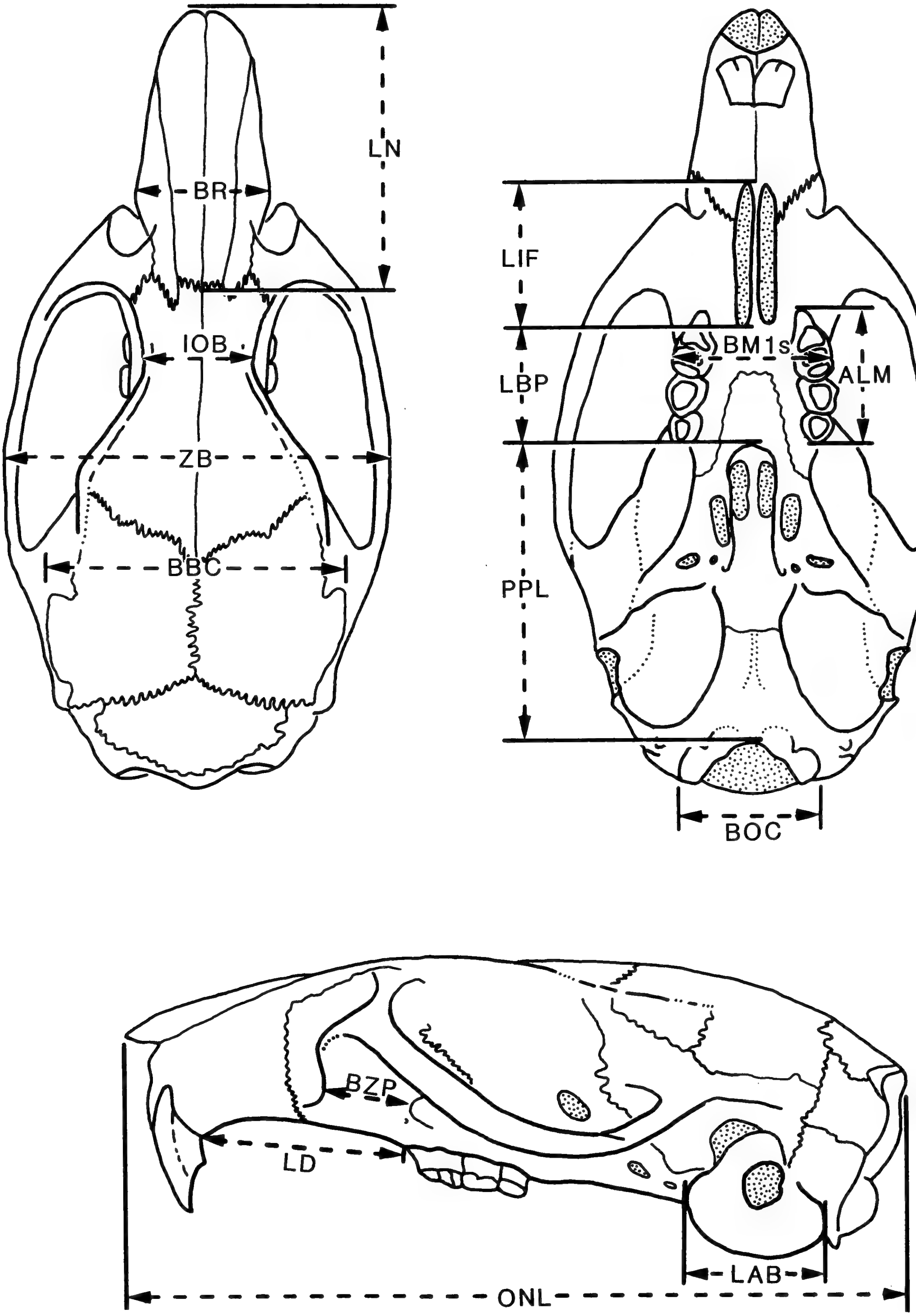

Fig. 3. Landmark points for 15 cranial measurements recorded in this study, as portrayed on dorsal, ventral, and lateral views of a schematic *Lemniscomys* skull (adapted from Van der Straeten & Van der Straeten-Harrie 1977:Fig. 1).

collector: total length (TOTL), tail length (TL), hindfoot length (HFL), and ear length (EL); subtraction of TL from TOTL yielded head-and-body length (HBL).

Several authors have commented on the relative scarcity of individuals of *Lemniscomys barbarus* in the field and the difficulty of obtaining them in adequate series (for example, Saint Girons & Petter 1965, Rosevear 1969, Happold 1987). We formed a similar impression based on the character of the museum samples we encountered, in which striped grass mice are usually represented by only one to a few specimens from a collecting locality. For certain multivariate analyses, specimens from localities over a general region were necessarily grouped as eleven operational taxonomic units (OTUs). These OTUs, arranged from northwestern toward eastern Africa, and their sample sizes are:

OTU (1).—*n* = 44, from Morocco, Agadir Province (USNM 475125–475148, 475150–475169);

OTU (2).—*n* = 15, from Morocco, Khouribga and Rabat provinces (USNM 475121, 475122, 475170–475182);

OTU (3).—*n* = 9, from Senegal, all localities (USNM 376529–376536, 380463);

OTU (4).—*n* = 24, from Ivory Coast and western Burkina Faso (FMNH 105180; USNM 465398–465400, 465413, 466674–466676, 466678–466693);

OTU (5).—*n* = 32, from Ghana and Togo, all localities (USNM 412746, 412747, 420570–420585, 435400–435405, 438311–438314, 466694–466697);

OTU (6).—*n* = 49, from eastern Burkina Faso, Benin, and westernmost Nigeria (USNM 397647, 404085–404087, 422058–422064, 422066–422083, 439580–439586, 450852–450855, 465401, 465404–465412);

OTU (7).—*n* = 51, from Nigeria, Jos Plateau, Panyam and vicinity (USNM 404020, 404022–404028, 404030–404039, 404044, 404046–404048, 404050, 404052–404056, 404058–404064, 404065–404069, 404071–404073, 404075–404078, 404080–404084);

OTU (8).—*n* = 11, from Zaire, Faradje and Niangara (AMNH 49610–49612, 49614, 49615, 49623, 49624, 49627, 49630, 49632, 49633);

OTU (9).—*n* = 13, from Uganda, Rhino Camp (AMNH 180121; CM 2850; USNM 165191, 165193, 165194, 165198, 165200–165205, 165422);

OTU (10).—*n* = 23, from Sudan, Equatorial Province, various localities (FMNH 35313, 35314, 66853, 66854, 66857, 66859, 66860, 67171, 67172, 67175, 67293, 79500–79502; USNM 165192, 299764–299766, 299768–299771, 318003);

OTU (11).—*n* = 15, from southcentral Kenya, various localities (AMNH 114446–114448, 187678, 187679; CM 57977, 98258, 102462, 102463; USNM 162884, 181737–181740, 437394).

Standard descriptive statistics (mean, range, standard deviation, coefficient of variation) were derived for the OTUs. One- and two-way analyses of variance, discriminant functions, and principal component analyses were computed using the 16 craniodental variables, all of which were first transformed to natural logarithms. Principal components were extracted from the variance-covariance matrix, and loadings are expressed as Pearson product-moment correlation coefficients of the components with the original cranial variables. Means and ranges of external variables are provided as a guidance in identification (see Appendix 2) but were not considered in multivariate analyses. Except for the a posteriori input of type specimens (all measured by Van der Straeten) to a discriminant function analysis (OTU series measured by Carleton), numerical results presented in the various tables and figures are not based on intermixture of craniodental data collected individually by the authors. All analytic procedures were conducted using Systat (Version 6.0, 1996), a series of statistical routines programmed for microcomputers.

Results

Morphometric analyses.—Patterns of variation contingent upon age and gender cohorts within local samples of *Lemniscomys* generally conform to those presented for other species of African muroids (Van der Straeten & Verheyen 1978, Carleton & Robbins 1985, Carleton & Martinez 1991). That is, significant age-related size variation is apparent for certain variables, notably those measured at the cranial extremes (ONL, ZB) or on the rostrum (LN, BR, LIF, LD); whereas, *f* values of age effects derived from ANOVAs are smaller and typically insignificant for dimensions taken across the braincase (BBC, IOB, BOC) and on the molars (ALM, WM1). Sexual dimorphism in size or age-sex interactions contribute little to mensural variation within OTUs (Table 1). Critical estimation of such influences upon sample variation is sensitive to sample size and particularly to the balance of age and sex representation among the specimens available for measurement (Voss & Marcus 1992). Our inability to achieve these sampling ideals with the real museum series at hand presumably accounts for certain inconsistencies and differences in probability levels attained for our two largest OTUs (Table 1). Notably, the lack of significant mean size differences among age cohorts for external skin variables (TOTL, TAIL, HFL) and the occurrence of same for the alveolar molar length of the Moroccan sample (OTU 1) seem counterintuitive and at odds with previous studies.

Table 1.—*f*-values from two-way ANOVAs (sex and age cohort) for 3 external and 16 cranial dimensions in two large OTUs of the *Lemniscomys barbarus* group.

	OTU 1 (25 M, 19 F)			OTU 6 (26 M, 23 F)		
	Age	Sex	Interaction	Age	Sex	Interaction
TOTL	2.6	0.0	0.6	0.1	0.0	1.1
TAIL	2.3	0.1	0.2	1.1	0.8	1.3
HFL	0.6	1.3	0.2	0.1	0.1	0.4
ONL	5.2**	0.1	1.2	9.4***	0.1	1.7
ZB	8.2***	0.5	1.1	2.4	0.4	2.1
BBC	4.6*	5.7*	0.0	1.5	3.2	0.2
IOB	1.2	0.1	0.7	1.1	0.5	0.1
LN	1.2	0.1	0.8	6.4**	0.6	4.1*
BR	8.2***	1.5	0.7	4.5*	0.2	0.3
PPL	1.9	0.5	0.3	9.4***	1.3	2.1
LBP	4.5*	0.1	1.2	0.2	0.2	0.9
LIF	0.9	0.4	1.8	3.8*	0.2	0.3
LD	4.3*	0.1	1.9	10.2***	0.0	1.3
BM1s	5.0*	0.2	3.1	8.9***	4.1*	0.2
BZP	2.2	0.1	0.4	9.3***	0.0	1.0
LAB	1.2	0.6	0.2	2.2	0.2	1.4
BOC	0.5	0.3	1.3	1.5	0.2	1.0
ALM	0.7	0.7	0.8	8.7***	1.0	0.4
WM1	1.5	1.2	1.1	0.7	1.1	0.1

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

For the two largest, geographically homogeneous samples–Morocco (OTU 1) and Nigeria (OTU 7)—nearly all cranial variables (except WM1) contribute substantially and positively to variation (74.1%) summarized by the first principal component (Table 2). Their covariation accounts for the uniformly higher scores and right-oriented dispersion of the Moroccan specimens relative to those from Nigeria (Fig. 4A). Pearson correlation coefficients of the original variables and the second principal component are consistently smaller and occasionally negative; no biologically meaningful segregation of specimen scores is apparent among the minor variation (6.0%) represented by this axis. Age-related size increase may account for some dispersion along the first component within each geographic sample (Fig. 4B); however, for the comparison of these two samples, age-class influence is statistically negligible (f = 1.99, P = 0.09) relative to the pronounced locality effect (f = 121.1, $P \leq 0.001$) upon PC I scores.

Little overlap of individual scores between the Moroccan and Subsaharan sam-

Table 2.—Results of principal component analysis performed on OTU 1 (Morocco, $n = 43$) and OTU 7 (Nigeria, $n = 51$), the two largest samples available for the *Lemniscomys barbarus* complex (see Fig. 4).

Variable	PC I	PC II
ONL	0.99	−0.02
ZB	0.94	0.09
BBC	0.81	0.05
IOB	0.75	0.29
LR	0.91	−0.13
BR	0.83	0.10
PPL	0.94	−0.08
LBP	0.80	0.47
LD	0.97	−0.11
LIF	0.86	−0.47
BM1s	0.85	0.06
BZP	0.87	0.17
LAB	0.74	0.15
BOC	0.74	−0.02
ALM	0.67	0.05
WM1	0.19	0.02
Eigenvalue	0.049	0.004
% Variance	74.1	6.0

ples is observed in plots of the first two canonical variates derived from discriminant function analysis of the 11 defined OTUs (Fig. 5A, B). Again, the uniformly larger skull dimensions of the Moroccan series are emphasized by the high, positive loadings of nearly all cranial variables on the first canonical variate (Table 3); the width of the first molar as in the principal component analysis, is least influential in affecting the segregation of group means along the first canonical axis. Unlike the clearcut separation of the two Moroccan samples, those drawn from West (OTUs 3–7) and East (OTUs 8–11) Africa display appreciable intermixture of individual specimen scores projected upon the first two canonical variates (Fig. 5A).

Cluster diagrams generated either from Mahalanobis distances among group centroids (Fig. 6A) or from log-transformed OTU means (Fig. 6B) similarly underscore the strong phenetic separation of the Moroccan samples from those found south of the Sahara Desert. Among the latter, the clustering patterns suggest some association according to geographic propinquity, but certain OTUs (Senegal and Kenya) discordantly merge with far distant samples.

Posthoc numerical classification of ten type specimens with suitably intact crania was effected using the discriminant function statistics computed from analysis of the 11 OTUs. Of the nine types representing taxa described from Subsaharan Africa, none was "correctly" classified with the OTU closest to their geographic origin; for example, *albolineatus* and *convictus*, both named from Kenya, were predicted to have membership in Ivory Coast-West Burkina Faso (OTU 4) and East Burkina Faso-Benin (OTU 6), respectively, and *manteufeli*, named from Tanzania, was allocated to Sudan (OTU 10). Nevertheless, all type specimens were sensibly associated within the range of multivariate dispersion exhibited by specimens from the general region of their collection: namely, Morocco (*ifniensis*) or the Subsahara (the remaining nine) (Fig. 7).

In summary, ordination analyses, whether extracting principal components from original measurement data or canonical variates from the centroids of 11 predefined geographic samples, reveal the more robust crania typical of the Moroccan samples as compared to striped grass mice from East and West Africa (Fig. 8). In contrast to our experience with other morphologically similar, congeneric species, features of shape or proportion are not evidenced by the dispersion of scores along the secondary axis of ordination; that is, the cranium of Moroccan *barbarus* seems to be an isometrically oversized version of that characterizing populations broadly distributed across Subsaharan savannas. Although not used in multivariate computations, parameters of bodily dimension and mass also convey the exceptional size of the Moroccan populations (Fig. 9, Appendix 2).

Pelage comparisons.—The upperparts of members of the *L. barbarus* complex are marked by longitudinally continuous, alternating dark and light stripes, a distinctive

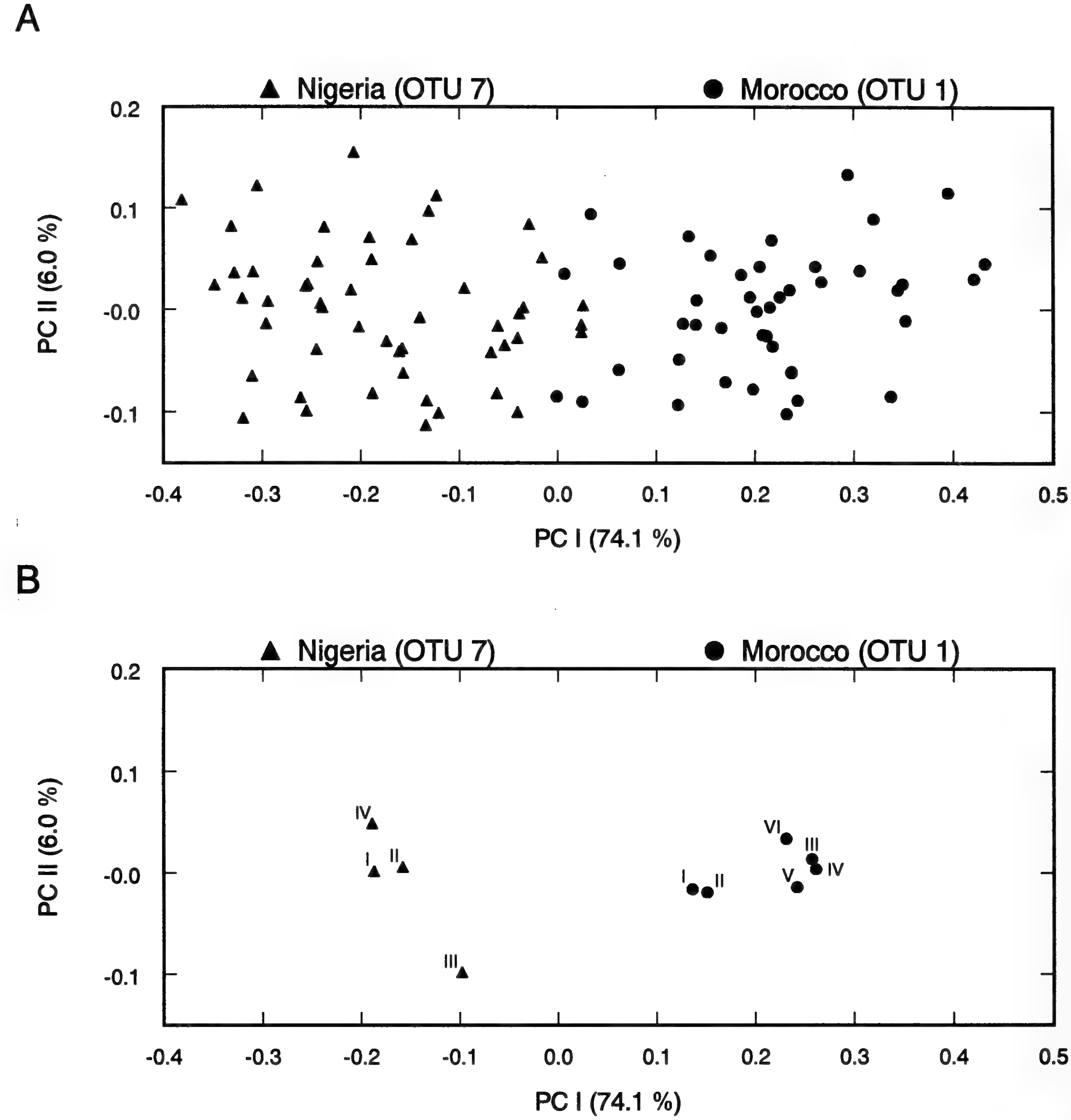

Fig. 4. Results of principal component analysis performed on 16 log-transformed craniodental variables measured on 94 specimens representing Moroccan (OTU 1, n = 43) and Nigerian (OTU 7, n = 51) samples of the *Lemniscomys barbarus* complex: A, projection of individual specimen scores on the first two principal components extracted (see Table 2); B, projection of centroids, as calculated a posteriorly, representing six age classes within each OTU on same principal components (age classes V and VI not represented in the Nigerian sample).

pattern which readily contrasts to the single mid-dorsal line of the *L. griselda* group (single-striped grass mice) or to the variably interrupted or punctulated lines of the *L. striatus* group (spotted grass mice). Attention is here given to qualitative description of chromatic and pattern variation of the upperparts because such traits have historically received prominence in the diagnoses of taxa, whether named as species or subspecies.

General characterization of the pelage in the *L. barbarus* group follows (Fig. 9). The single vertebral line, which extends from the middle crown to the rump, typically possesses a deeper hue than that of the lat-

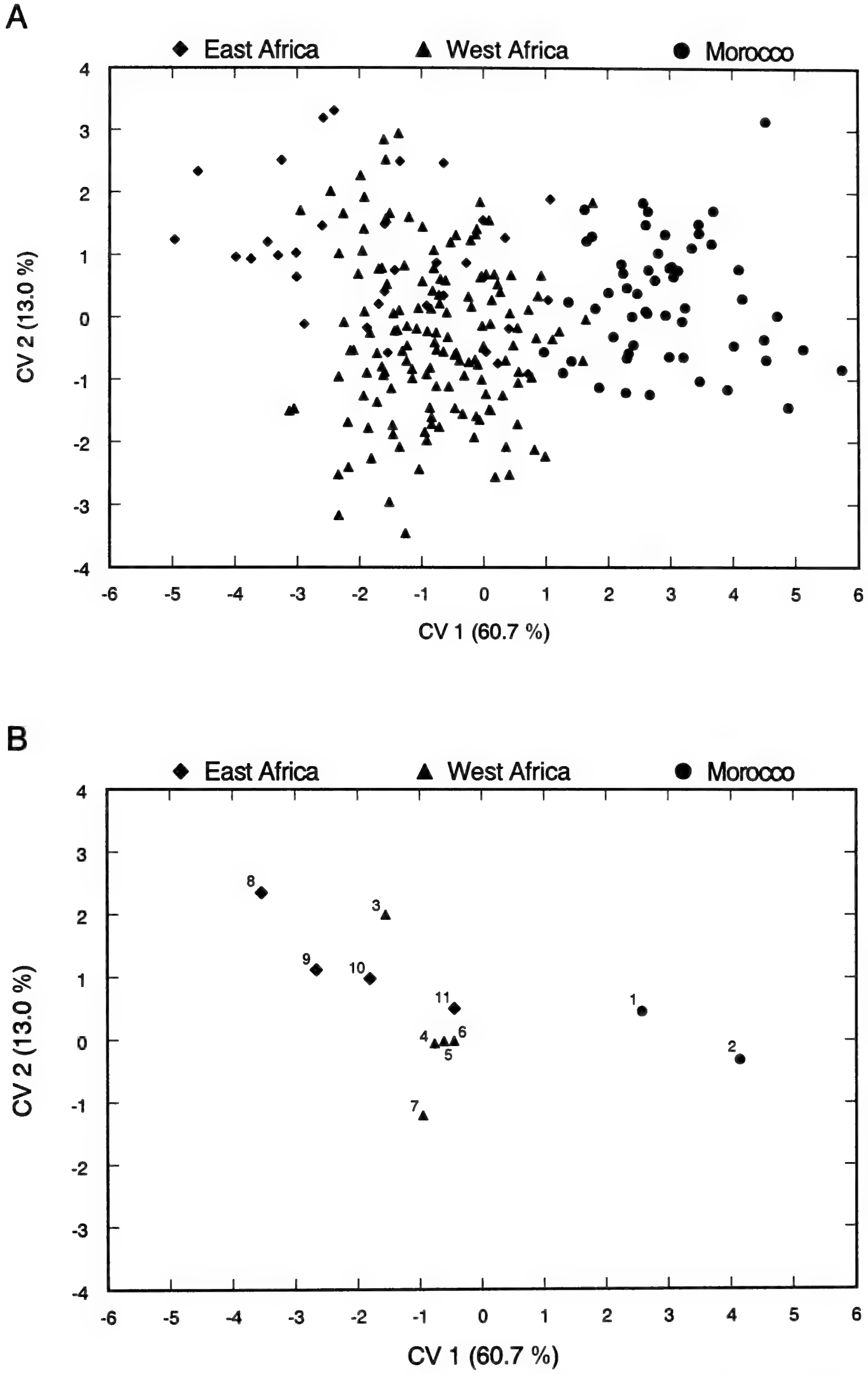

Fig. 5. Results of discriminant function analysis performed on 16 log-transformed craniodental variables measured on 235 intact specimens representing 11 OTUs of the *Lemniscomys barbarus* complex (see Table 3): A, Projection of individual specimen scores on first two canonical variates extracted; B, Projection of group centroids on first two canonical variates extracted.

Table 3.—Results of discriminant function analysis performed on intact specimens ($n = 235$) representing 11 OTUs of *Lemniscomys* (see Fig. 5).

Variable	CV I	CV II	*f*(OTU)
ONL	0.94	0.14	49.0***
ZB	0.94	−0.08	53.2***
BBC	0.75	−0.04	21.3***
IOB	0.70	0.04	19.2***
LR	0.87	−0.03	33.2***
BR	0.76	−0.06	21.5***
PPL	0.84	0.28	33.6***
LBP	0.75	0.16	18.0***
LD	0.91	0.23	43.7***
LIF	0.79	0.19	29.9***
BM1s	0.82	−0.21	29.9***
BZP	0.70	0.14	14.9***
LAB	0.70	−0.13	16.3***
BOC	0.65	0.23	13.4***
ALM	0.70	−0.09	15.4***
WM1	0.45	−0.49	9.3***
Canonical correlation	0.87	0.64	
Eigenvalue	3.25	0.69	
% Variance	60.7	13.0	

* = $P \leq 0.05$; *** = $P \leq 0.001$.

eral dark stripes, appearing black as compared to dark gray or brown. To either side of the mid-dorsal line occur four to six primary pairs of alternating light and dark stripes (as observed over the lumbar-rump region), whose definition more or less abruptly degrades toward the sides; the dark lines are usually wider than the intervening light ones. The venter is much lighter and unmarked, ranging from dull to bright white, and a clear buff lateral line may demarcate the dorsal-ventral pelage transition. Fine tawny to rufescent hairs densely clothe the pinnae and accent their contrast to the crown and dorsal pelage. Tops of the fore and hindfeet are covered with white to pale buff hairs. The tail is indistinctly bicolored, the dorsal hairs black and those underneath ochraceous to rufous, resembling the color of the pinnae.

Within and among locality samples of the *L. barbarus* group, one can discern several thematic variations around the chromatic groundplan described above. The distinctiveness of the mid-dorsal line varies with respect to the dark lateral stripes, a consequence of its color (brown to dusky to black) and width. Thus, the mid-dorsal stripe may appear densely black and relatively wide (Figs. 9A, C) or brown and notably thin (Fig. 9B). The boldness of the striping pattern is modulated by the color of the dark bands (medium brown to black) in relation to the purity of the pale bands (clear white to warm buff or dull ochraceous) and by the degree of ochraceous suffusion over the middle dorsum. These chromatic subtleties interact to heighten or lessen the sharpness of the linear contrast (compare Figs. 9A to 9C, & D). The fine aural hairs range from nearly cinnamon, setting the pinnae conspicuously apart from the general dorsum (Fig. 9D), to dull ochraceous, lessening the visual distinction of the pinnae (Fig. 9A).

An important pelage variation involves the number of dorsal stripes, counts of which were mentioned regularly by the early describers. For example, Thomas (1903: 297) noted that *dunni* possesses "on each side, five uninterrupted buffy stripes, separated from each other by broad brown bands, each of which is divided down the centre into two by an uninterrupted band of light." Osgood (1910:11) characterized *convictus* as having: "Light stripes pale ochraceous buff and numbering 5–6 of the heavier or primary ones and 4–5 of the secondary ones on each side;" and "Four definite primary dark stripes on each side, each divided by a secondary light stripe." And Hatt (1935:2) cited the "six pairs of lateral dark stripes . . . distinctly split by secondary light stripes" in describing *orientalis*. The number of stripes is an inexact impression largely mediated by the development of these secondary light lines within the first, and sometimes the second, pair of primary dark lateral stripes (as numbered away from the unpaired vertebral stripe). Individuals with strongly penetrant secondary light stripes appear to be finely streaked with more and narrower light and dark stripes, especially over the middle dorsum (Figs.

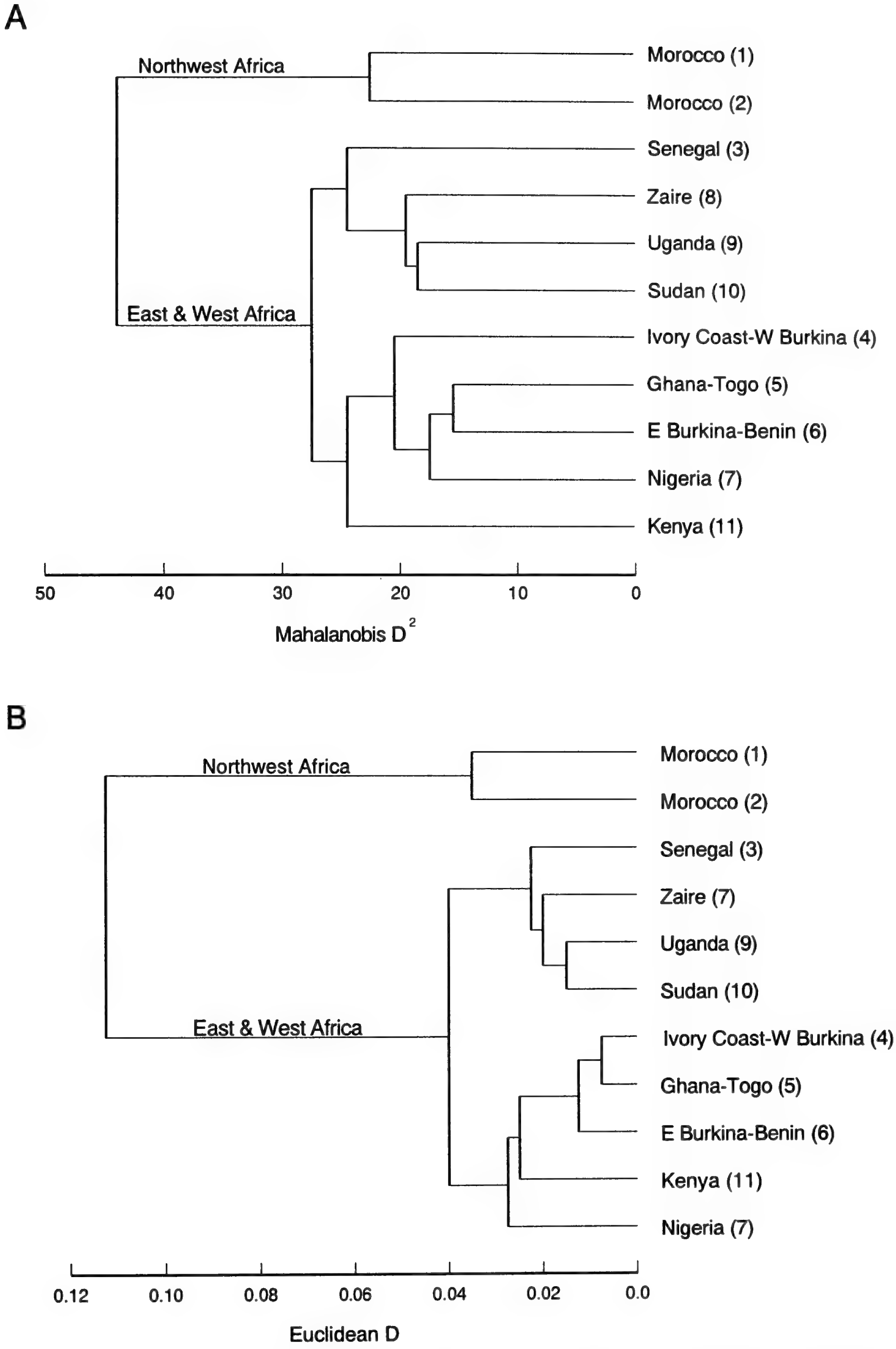

Fig. 6. Clustering (UPGMA) of 11 geographic samples representing the *Lemniscomys barbarus* complex, as derived from: A, Mahalanobis' distances (D^2) among the OTU centroids (see Fig. 4); B, Euclidean distances between OTUs based on means of the 16 log-transformed craniodental variables.

9B, D); whereas, those that have obscurely defined secondary lines seem to have fewer and broader dark stripes on their upperparts (Figs. 9A, C—the latter specimen was purposefully selected for its extreme expression of this consolidated pattern.).

The pelage characteristics reviewed above undoubtedly seemed easily definable

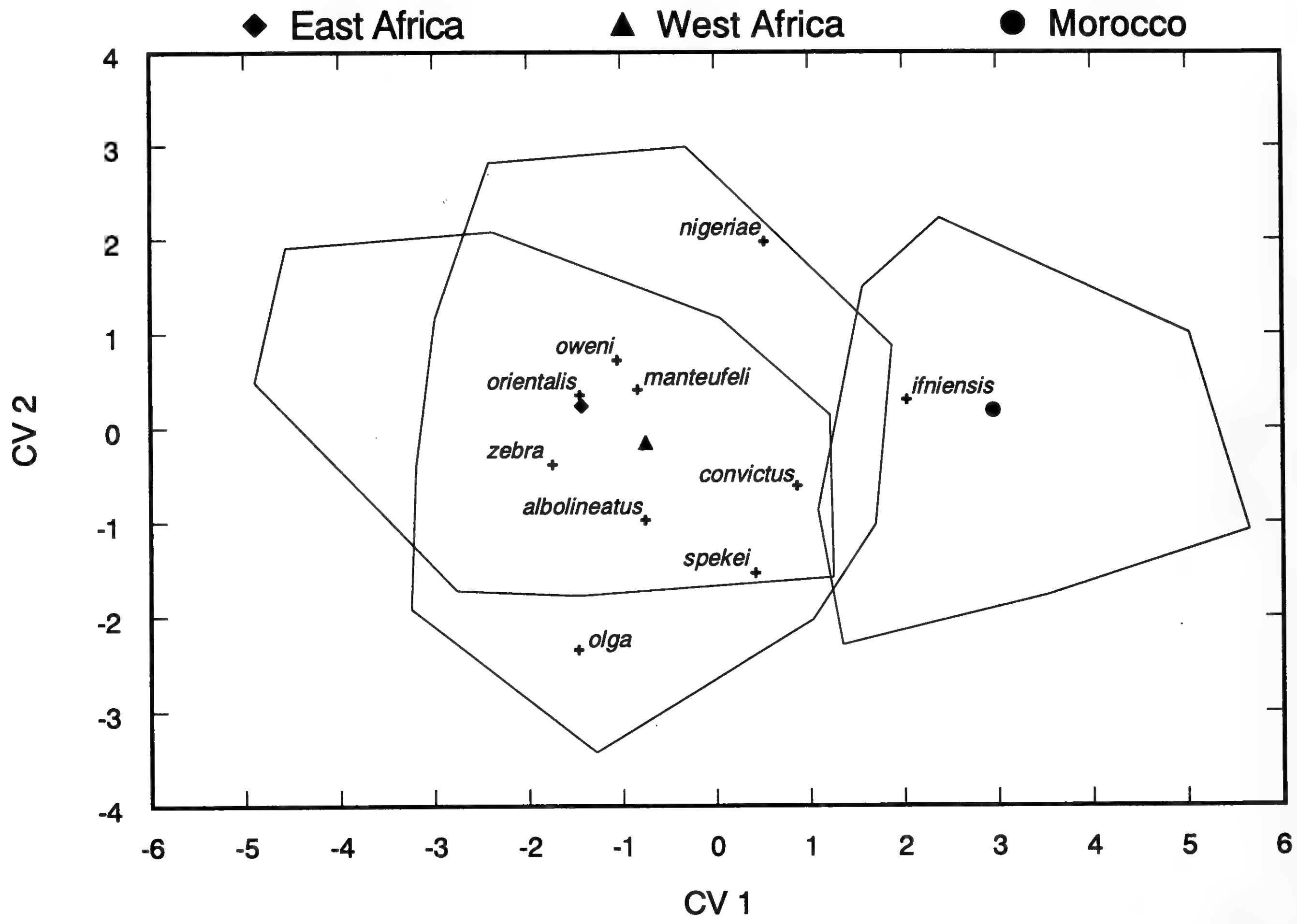

Fig. 7. Results of discriminant function analysis presented in Fig. 5, with a posteriori classification of type specimens representing ten species-group taxa of the *Lemniscomys barbarus* complex. Polygons enclose maximal dispersion of individual scores around group centroids for each geographic region.

and unique as exemplified by the holotypes and small hypodigms for the various epithets created in the late 1800s and early 1900s. However, as more specimens, larger locality series, and broader geographic representation have become available, the individuality of these color morphs is observed to break down and merge imperceptibly. By 1969, Rosevear concluded that even subspecific separation of West African *nigeriae* from *oweni*, originally assigned to separate species on the basis of having white versus buffy light stripes as purported by Thomas (1911b, 1912), was indefensible. We agree with Rosevear's assessment and further note that the occurrence of boldly marked striping versus more muted dorsal patterns–such as advanced to discriminate *albolineatus* versus *convictus* (Osgood 1910) or *nubalis* versus *dunni* (Thomas 1903, Thomas & Hinton 1923)—can be duplicated by extreme individual patterns just within USNM Nigerian series. Hatt (1935) identified the absence of facial stripes as a useful feature for sorting specimens of *nubalis* from those of *orientalis* and *zebra.* Nevertheless, we have found the continuation of trunk markings (the fourth lateral pair of light and dark stripes) onto the cheeks as highly variable within Subsaharan locality samples and doubt the trait's utility as a diagnostic tool at the level intended by Hatt (and see Discussion below). The hispid or spiny quality of the dorsal fur has been also mentioned in some descriptions of striped mice, but such textural differences are difficult to objectively convey and practically apply. And so forth for many of the pelage traits given as diagnostic criteria.

Certain geographic trends in pelage color and pattern do emerge with the better series

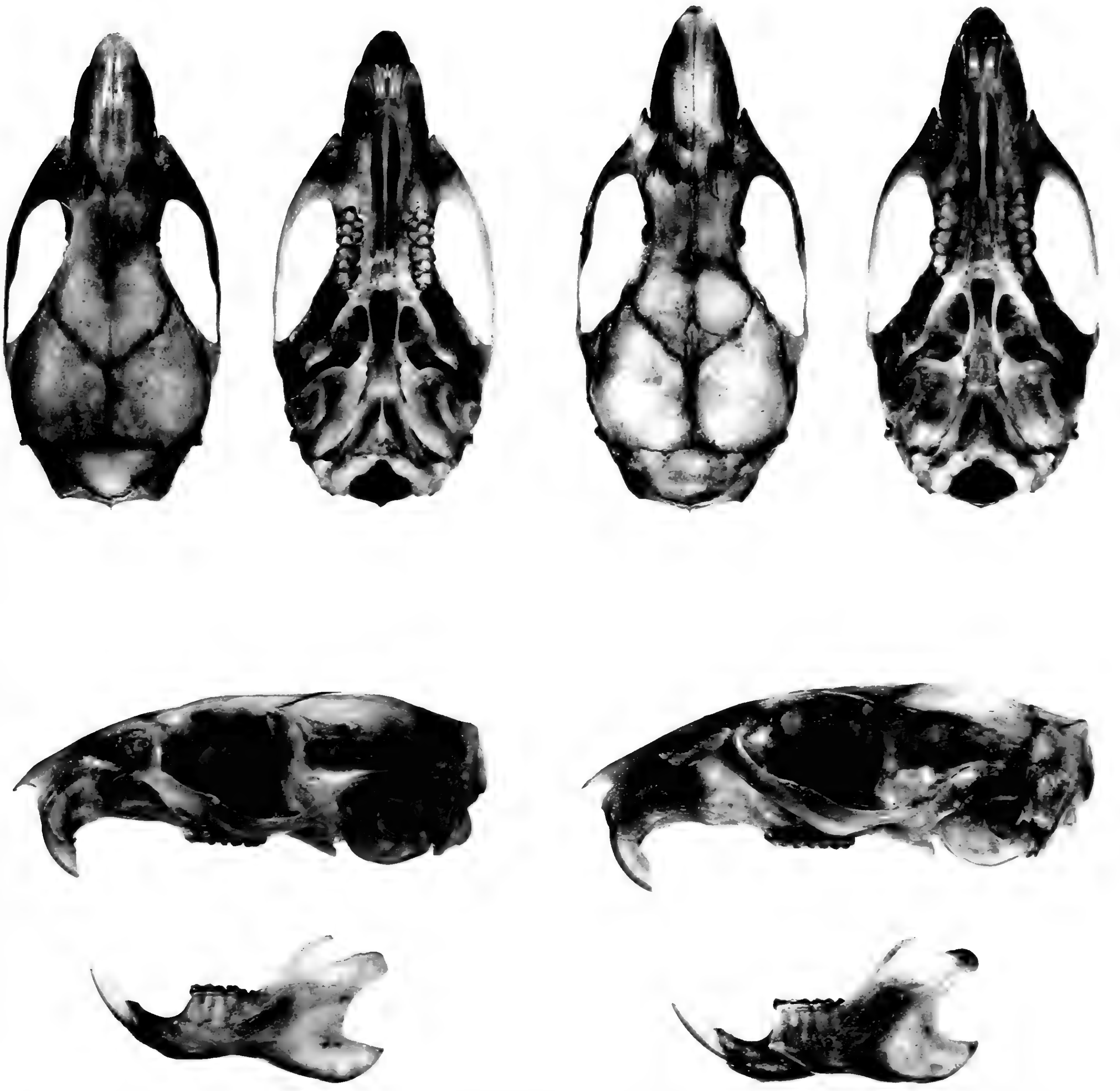

Fig. 8. Dorsal, ventral, and lateral views of crania and mandibles of young adult *Lemniscomys* (both Age Class 2): left, *L. zebra* (USNM 465402), a female from Burkina Faso, 6 mi SE Seguenega; and right, *L. barbarus* (USNM 475145), a male from from Morocco, 15 km E Agadir.

now at hand, but these are presented only as average differences or general impressions. Higher numbers of dorsal stripes appear more common within Subsaharan populations, which usually exhibit five, occasionally six, pairs of primary dark and light bands on either side of the mediodorsal line; in contrast, specimens from Northwest Africa possess four or five countable pairs of primary dark and light stripes. The impression of more dorsal stripes among Subsaharan series is visually accentuated by the development of secondary light lines, which usually subdivide the first as well as the second primary dark stripes (Figs. 9B, D); within samples from northwestern Africa, secondary light lines are typically evident only within the first primary dark stripes, obscurely defined in the second and those more laterad (Fig. 9A). A pattern consisting of a broad, black vertebral line, bordered by more consolidated dark stripes and irregularly defined secondary light stripes (Fig. 9C), occurs more often among population samples from East Africa (the source of taxa such as *zebra*, *spekei*, and *nubalis*);

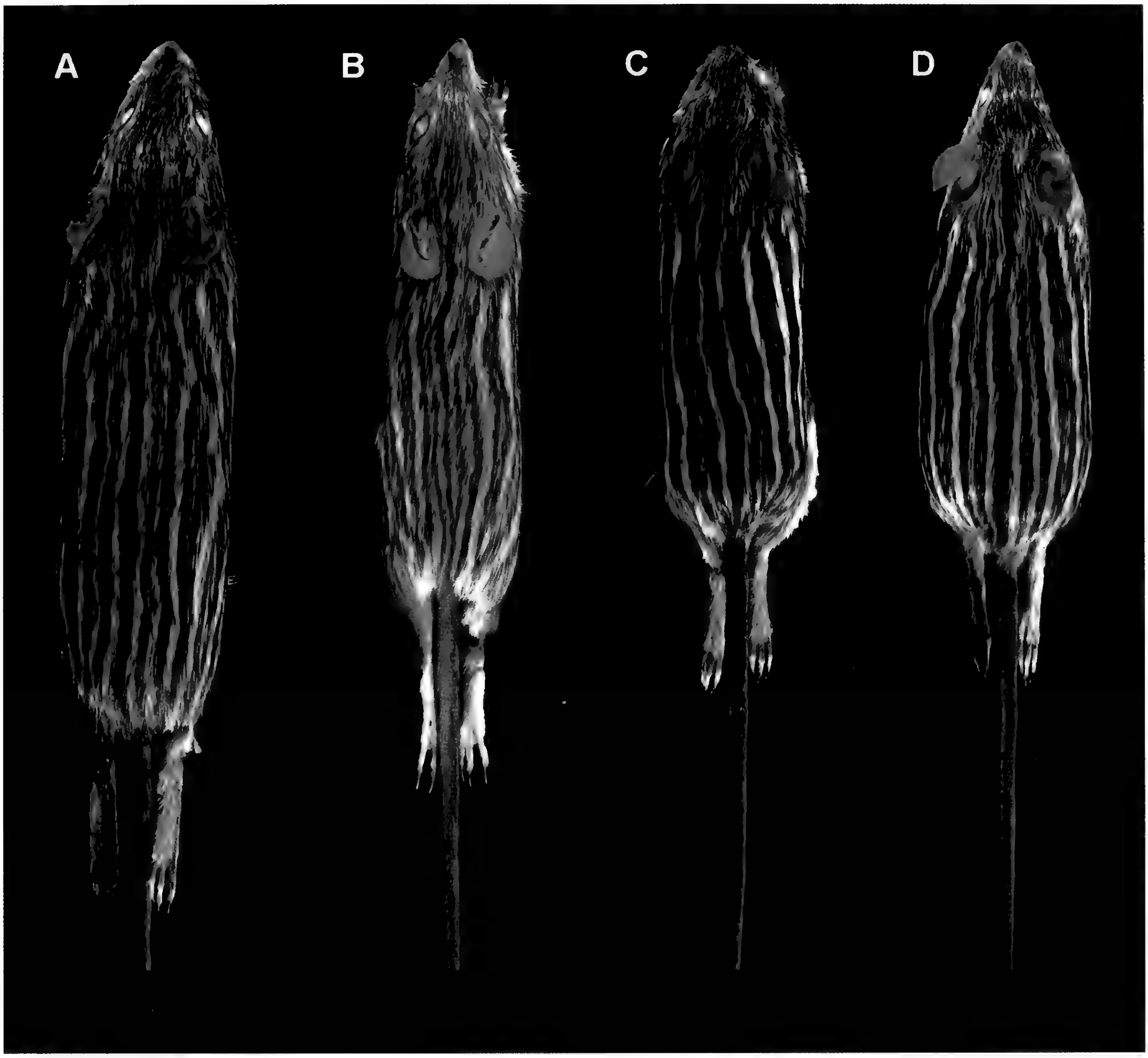

Fig. 9. Variation in dorsal pelage pattern of four specimens of striped grass mice, the *Lemniscomys barbarus* species group. A. *L. barbarus* (USNM 475121, LHB = 108 mm), a male from Morocco, 17 km SW Rabat. B. *L. zebra* (BMNH 23.5.12.81, LHB = 86 mm), a female from Niger, Farak (region of *olga* Thomas & Hinton 1921). C. *L. zebra* (USNM 165191, LHB = 89 mm), a female from Uganda, Rhino Camp (region of nominate *zebra* Heuglin 1864). D. *L. zebra* (USNM 376535, LHB = 88 mm), a male from Senegal, Kotiare Naoudé (region of *oweni* Thomas 1911).

a finely streaked dorsum (vertebral stripe narrower and secondary light stripes well delineated within the first and second primary dark bands) is typical of West African populations (taxa such as *nigeriae* and *oweni*—Fig. 9D).

With regard to the degree of pelage saturation, we observe a subtle trend toward paler, diluted upperparts in examples from more xeric vegetation zones. This association is best evidenced by the many USNM examples from West Africa, wherein a darker pelage tone characterizes those specimens obtained from localities within Guinea savanna compared to the slightly paler aspect of series collected within Sudan savanna. At the darker extreme, somewhat muted colors and subdued contrast mark the dorsum of Moroccan populations (Fig. 9A) that occupy the relatively mesic Mediterranean region of Northwest Africa; at the pallid end of this spectrum are the few specimens (Fig. 9B), including the holotype of *olga*, that originate from the Sahel zone in West Africa.

As a generality, specimens of the *L. barbarus* group possess moderately hispid dorsal fur, especially over the rump, compared to those of the *L. striatus* complex. Within the *L. barbarus* group, most taxa, as represented by their type specimens, generally conform in this trait with the exception of the more hispid condition characteristic of *olga*.

Discussion

Taxonomic conclusions.—The major pattern of craniodental variation uncovered here provides evidence for the specific divergence of the Moroccan samples from those representing populations that occur to the south of the Sahara Desert. The former correspond to *Lemniscomys barbarus* s.s. (Linnaeus 1766), and the oldest name applicable to the latter is *L. zebra* (Heuglin 1864), whose type locality lies in southern Sudan. Seven of our 11 OTUs were regrettably coarsely defined in geographic coverage, an analytical approach dictated by the generally small sample sizes available from the majority of collecting localities. Notwithstanding the composite nature of most OTUs, we believe that the regions thus broadly sampled are sufficient to sustain the principal taxonomic conclusion recommended here—the recognition of northwest African populations (*L. barbarus*) as a species distinct from those occupying savanna biomes in West and East Africa (*L. zebra*).

Infraspecific taxonomic uncertainties persist, however, within the Subsaharan moeity we identify as *L. zebra*, as intimated by the appreciable size and chromatic variation observed among those samples. The earlier conclusions of Robert T. Hatt of the American Museum illustrate the biological problems inherent in understanding that variation. In his reports (Hatt 1935, 1940) on the rodents collected by the AMNH Congo Expedition (1909–1915), Hatt provided diagnostic criteria for three "natural groups" of the *L. barbarus* group that originated from a single locality, Faradje. Hatt identified the three as separate species—*L. zebra*, *L. dunni nubalis*, and *L. oweni orientalis*, the last newly described as a "dwarf" subspecies of West African *oweni*. For us, unambiguous, repeatable separation of East African specimens into discrete species using Hatt's identification criteria remains elusive. The mensural diagnostic values (means?) listed by Hatt for each "species"—for instance, foot length, 25 versus 25 versus 23 mm; greatest skull length, 27.5 versus 27.2 versus 26.7 mm; length upper molar row, 4.8 versus 5.1 versus 4.6 mm—span the normal variational spectrum that we find within population and regional samples (Appendix 2). Unfortunately, Hatt provided no measures of sample dispersion nor gave any attention to potential age effects for the numerical contrasts offered, statistical precautions now standardly addressed when evaluating intersample mean differences. The pelage attributes given (general color, spininess, and facial stripes) are subjective to apply precisely and suggest no variation between individuals from large series, which contradicts our experience. Within the Faradje material, it is notable that Hatt allocated the two "pallid, very hispid" individuals to *L. dunni nubalis* (named from central Sudan) and the remainder of the "dark, hispid" specimens, totaling 17, to either *L. zebra* or *L. oweni orientalis*, the latter two separable by average size. Darker versus paler pelage hues and hispid versus very hispid fur are traits whose expression appears subject to slight variation within locality series and to clinal trends over broad regions, for example, Guinea through Sahel savannas in West Africa. In view of the geographic location of Faradje near the southern limit of Guinea savanna in eastcentral Africa, one might anticipate that the majority of specimens would appear relatively dark and moderately hispid.

In summary, we interpret the differences tabulated by Hatt (1935, 1940) as examples of intraspecific variation of the one species, *L. zebra*, not sympatry of three members of the *L. barbarus* group. In the same papers, Hatt (1935:1–2) previewed this possibility:

> "That a more conservative person or one with a greater series of specimens than have been available to me might lump all three as fortuitous variations of a single subspecies, I readily admit, but such a procedure would, . . . with the present evidence, but mask the simple assortment of characters as they have presented themselves and tend to smother rather than encourage further investigation of the problem of speciation or, it may be ecologic differentiation, in this region."

His was a reasoned and reasonable taxonomic viewpoint, given the state of knowledge about African striped mice in the 1930s. From our vantage point of the late 20th century, and hoping to "encourage further investigation," we draw attention to three alpha-systematic problems not yet adequately resolved by the Subsaharan material at out disposal.

For one, the nature of morphological differentiation between East (*zebra*) and West African (*oweni*) populations should be further appraised drawing upon other kinds of data and improved geographic sampling (Chad and the Central African Republic are apparently unrepresented in museum collections). For example, another sibling species pair of *Lemniscomys*, *L. macculus* and *L. bellieri* of the *striatus* group, is distributed as East and West African counterparts (Van der Straeten 1975, Van der Straeten & Verheyen 1979, 1980). Some geographic integrity of East versus West African examples of striped grass mice is suggested by the phenetic clusters generated from craniodental similarity, but the segregation is not complete: one West African sample (Senegal, OTU 3) groups among East African OTUs, and another from East Africa (Kenya, OTU 11) aligns with those from West Africa (Fig. 6). In light of such ambiguous results, set against the inadequacy of geographic coverage and the apparent want of other diagnostic traits, we prefer at this investigatory stage to retain all Subsaharan populations, except *L. hoogstraali* (see below), under the one species *L. zebra* (Heuglin 1864) without formal delineation of geographic races.

For another, the taxonomic status of Thomas & Hinton's (1921) *olga* merits reexamination. The form, described from a few specimens and fewer localities in Sahel Savanna in southcentral Niger, is characterized by small size, pale color, finely delineated striping pattern (Fig. 9B), and slightly more hispid pelage texture. The three specimens from Timbuktu, Mali, another locality in the Sahel, also recall this morphology. In view of the type specimen's morphometric association with other West African populations (Fig. 7), and while acknowledging the distinctiveness of the form's pelage and habitat, retention of *olga* as a junior synonym of *L. zebra* seems prudent as a provisional arrangement. Careful geographic transects across Sudan and Sahel woodlands, both in West and East Africa, are required to illuminate the nature of morphological variation in characters attributed to *olga* and critically judge its taxonomic status.

The third species of the *Lemniscomys barbarus* complex herein recognized, *L. hoogstraali*, was described by Dieterlen (1991) from the Upper Nile Province of southern Sudan (Figs. 1, 12). As noted by Dieterlen, the form contrasts with neighboring Sudanese examples of *L. barbarus* (=*L. zebra* as here understood) by its larger external and cranial size and by the dorsal striping pattern (see additional commentary under Taxonomic Accounts). The dark stripes of the upperparts are exceptionally black and broad, which, together with the purity of the primary white stripes and indistinct secondary white stripes, heightens the alternating, zebra-like effect of the holotype (and only known specimen). Such an appearance is suggested, as an extreme of pelage variation, by some individuals from East Africa (see Fig. 9C), but their cranial measurements otherwise fit those recorded

Table 4.—Selected cranial dimensions (as measured by Van der Straeten) of thirteen type specimens of species-group taxa assigned to the *Lemniscomys barbarus* group. All taxa listed are viewed as junior synonyms of *L. zebra,* except *ifniensis,* allocated to *L. barbarus* (Linnaeus 1766), and *hoogstraali,* retained as a third species of the group.

Taxon & authorship (type)	Age class	Variables									
		ONL	ZB	BBC	IOB	LN	LIF	LD	BM1s	BZP	ALM
zebra Heuglin, 1864 (SMNS 1100a/5422)	1–2	26.7	12.8	11.7	4.5	10.0	5.0	6.0	5.3	3.5	5.30
spekei De Winton, 1897 (BMNH 63.7.7.23)	3	29.3	13.6	12.3	4.5	11.1	5.5	6.7	6.4	3.9	5.75
dunni Thomas, 1903 (BMNH 3.2.8.15)	5	27.8	—	12.0	4.3	10.4	5.7	6.3	5.7	3.7	5.70
albolineatus Osgood, 1910 (FMNH 17194)	3	27.5	13.0	12.5	4.3	10.4	5.7	6.3	5.8	3.3	5.45
convictus Osgood, 1910 (FMNH 17206)	4–5	29.9	13.8	12.1	4.5	11.5	5.9	6.7	5.9	3.7	5.35
oweni Thomas, 1911 (BMNH 11.6.10.61)	2–3	27.0	12.5	11.4	4.3	10.3	5.5	6.3	—	3.2	5.25
manteufeli Matschie, 1911 (BZM 16025)	1	26.7	13.0	11.9	4.3	9.1	5.2	5.9	5.2	2.9	5.10
nigeriae Thomas, 1912 (BMNH 12.1.16.45)	5	29.1	13.1	11.7	4.9	11.1	5.7	6.9	6.0	3.7	5.55
olga Thomas & Hinton, 1921 (BMNH 21.2.11.128)	2	27.1	12.8	11.7	4.3	10.5	5.1	6.1	5.8	3.5	5.50
nubalis Thomas & Hinton, 1923 (BMNH 18.7.2.14)	4	29.2	—	12.1	4.5	11.5	6.0	6.9	6.1	4.0	5.60
orientalis Hatt, 1935 (AMNH 49626)	5	26.8	12.5	11.4	4.1	10.1	5.7	6.3	5.5	3.2	5.00
ifniensis Morales A., 1935 (MNCN 9638)	6	31.3	14.3	13.0	4.9	12.5	6.4	7.4	6.3	3.9	5.35
hoogstraali Dieterlen, 1991 (USNM 342078)	5–6	32.0	—	12.8	5.0	12.5	6.1	7.5	6.5	4.0	5.75

for eastern series of *L. zebra* and are clearly smaller than the holotype of *L. hoogstraali* (Table 4). In dimensions of the skull and molars alone, the type of *L. hoogstraali* instead agrees with those of *L. barbarus* proper from Morocco (Table 4, Appendix 2). Although based on a single specimen, the combination of large size and dramatically striped dorsum, considered with the form's geographic occurrence approximate to typical examples of *L. zebra*, leads us to accept Dieterlen's (1991) judgement of *hoogstraali* as a species. Additional samples should be sought in order to enhance appreciation of its variation, phyletic relationships, and level of differentiation from *L. barbarus* and *L. zebra.*

With revision of the striped grass mice, there now exists a basic framework of species definitions and their distributional limits within *Lemniscomys*, a moderately diverse genus embracing at least 11 species associated in three groups: namely, *barbarus* (*barbarus*, *hoogstraali*, and *zebra*), *griselda* (*griselda*, *linulus*, *rosalia*, and *roseveari*), and *striatus* (*bellieri*, *macculus*, *middendorfi*, and *striatus*). Future systematic attention should focus on phylogenetic relationships among the species and the evidence for accepting these nominal groupings as monophyletic. While visually obvious and thus advantageous for employment in taxonomic keys, the dorsal pelage patterns that have traditionally afforded definition of the species groups of *Lemniscomys* may not necessarily convey phyletic affinity. Although readily distinctive as represented by the typical species of each group, these basic striping configurations are not necessarily so well defined among all of a group's members. Some individuals of West African *L. linulus*, for instance, exhibit indistinct lateral spotting in addition to the pronounced middorsal stripe, a pattern remniscent of the upperparts of some *L. bellieri*. For another example, the Nigerian form *fasciatus*, now synonymized under *L. striatus* (see Van der Straeten & Verheyen 1980), was long confused with *L. barbarus* (now = *L. zebra*) as a result of the nearly continuous union of its lateral spots.

In contrast to their external dissimilarity, one is impressed by the fundamental craniodental resemblance among the species of *Lemniscomys*. Certain morphological traits may further characterize these groups, at least as exemplified by their typical species. Examples of *L. barbarus* possess well inflated ectotympanic bullae relative to those of *L. griselda* (intermediate) and *L. striatus* (smallest); the degree of inflation may correspond to the openness of the habitats occupied by each species. The molars of *L. griselda* are broad and robust compared to those of *L. barbarus* and especially *L. striatus*. Along with its heavier, more rounded cusps, the t3 of M1 in *L. griselda* is weakly defined and the t9 appears as a short spur off t8; the t3 of M2 is minute and irregularly formed. The cheekteeth of *L. striatus* seem more cuspidate, with the t3 of M1 separated from t2 by a distinct cleft and the t9 formed as a small albeit discrete cusp apart from t8; the t3 of M2 is small but consistently formed. In general, the molars of *L. barbarus* more closely resemble those of *L. griselda*. Such observations should be extended to the other species of *Lemniscomys* and additional morphological characters sought in order to test the monophyly of the currently defined species groups.

Investigation of chromosomal homologies promises to shed light on kinship groups within *Lemniscomys*, as suggested by the karyotypic differences so far reported. Based on a single specimen from Algeria, Filippucci et al. (1987) reported the diploid number (2N) of *L. barbarus* as 54 and the number of autosomal arms (AN) as 58, dominated by a graded series of 23 small to large acrocentric pairs, along with two pairs of small metacentrics and one large submetacentric pair. This diploid count agrees with those reported for *L. zebra* from Burkina Faso (Gautun et al. 1986, as *L. barbarus*), Ivory Coast (Matthey 1954, also as *L. barbarus*), and from Cameroun (Van der Straeten, pers. com.); the Cameroun animals even display the same fundamental number (AN = 58), although having three pairs of small metacentrics and apparently lacking the large submetacentric pair. These chromosomal traits appreciably differ from karyotypes that Van der Straeten & Verheyen (1978) documented for Ivory Coast samples of *L. bellieri* (2N = 56) and of *L. striatus* (2N = 44). Such preliminary results should be reconfirmed and extended to include other species, and their differences and mechanism of karyotypic change explored with the banding techniques now available.

Distributions and zoogeographic implications.—Museum specimens of *L. barbarus* and *L. zebra* have originated from habitats that can be loosely categorized as savanna, woodland, or scrubland. All such places, in general, have ample grass and-or herbaceous ground cover intermingled with bushes to small trees, but never close-canopied, high forest. Nonetheless, the vegetational character where each species occurs can be broadly contrasted.

On skin tags and in field catalogs, collectors in West Africa have recorded the vegetation of almost all trapping sites of *L. zebra* as either Guinea or Sudan savanna (or woodland), following Rosevear's (1953, 1965) terminology. To date, only a handful of specimens come from the Sahel, but few collections have been made in this very arid zone. These vegetational associations differ in their dominant plant species, physiognomy of the low-canopied woods, and density of ground cover, features which in turn correspond to amount of annual rainfall, length of dry season, and prevailing lowest relative humidity (Guinea savanna, more mesic, to Sahel savanna, more arid). To the east, areas where striped grass mice live have been characterized as grass and scrub (Uganda—Delany 1975), drier savannas and steppes (East Africa—Kingdom 1974), or simply as savanna (annotations on USNM skin tags of Sudanese specimens collected by H. W. Setzer). Our localities from Sudan, Zaire, and Uganda also lie within vegetation zones mapped by Rosevear (1953, 1965) as Guinea, Sudan, or Sahel savanna.

At Zizonkame, about 8° north latitude in Benin (Fig. 10, Top), degraded Guinea savanna contained prolific grasses three to four feet high, periodically burned, as well as some cultivated plots (cassava) and oil palms (field notes of J. W. LeDuc and C. B. Robbins, USNM Mammal Division archives). Here, individuals of *L. zebra* were obtained with a variety of small mammals, including: *Atelerix albiventris*, *Galago senegalensis*, *Xerus erythropus*, *Thryonomys swinderianus*, *Tatera* sp., *Taterillus gracilis*, *Cricetomys gambianus*, *Arvicanthis niloticus*, *Dasymys rufulus*, *Lemniscomys striatus*, *Mastomys natalensis*, *Myomys daltoni*, *Mus musculoides*, and *Uranomys ruddi*. In the vicinity of Cella, about 11°30′ north latitude in Burkina Faso (Fig. 10, Bottom), examples of *L. zebra* were trapped amongst dry grasses that formed a uniform ground cover, interspersed with shrubs and low-canopied trees, which together composed a plant community typical of Sudan savanna. The less diverse set of small mammals collected at this site included: *Atelerix albiventris*, *Galago senegalensis*, *Tatera* sp., *Taterillus gracilis*, *Steatomys pratensis*, *Arvicanthis niloticus*, and *Mastomys natalensis*. Populations of *L. zebra* and *L. striatus* were found to co-occur at the locality within Guinea savanna, but only examples of *L. zebra* were collected in the drier Sudan savanna.

Populations of *L. barbarus* also inhabit various nonforested, relatively dry habitats, but along the coastal region and contiguous low plateaus of Northwest Africa, where the severity of drought is moderated by the Atlantic Ocean and Mediterranean Sea. In Morocco, notations on specimen tags identify collecting places as "rocky outcrop in vegetated coastal dunes," "coastal scrub," "sandy hummocks with dense vegetation," "juniper scrub," "argon-sage-grassland," and "argon savanna." Such Moroccan locales denote a spectrum of climatic domains classified as arid, semiarid, or even humid (see fig. 6 in Saint Girons & Petter 1965: 18).

At two places along the valley of the Souss River in Agadir Province, Morocco (about 30°30′ north latitude), specimens of *L. barbarus* were obtained with those of *Atelerix algirus*, *Gerbillus* sp., *Gerbillus hoogstraali*, *Meriones shawi*, *Mastomys erythroleucus*, and *Mus spretus*. The collector, R. E. Vaden, described the site at 16 km W Aoulouz (Fig. 11, Top) as "more coastal type of vegetation . . . predominantly argon trees and grass . . . clumps of assorted shrubs, from sage through thorn-bushes (acacia?) up to small argons, maximum of about 6 feet in height . . . in between [shrubby clumps], it's grassy." The locality at 5 km S Taroudannt (Fig. 11, Bottom), he characterized as "heavily-vegetated sandy dune area . . . dominant shrubs are the same thorny bushes seen all along . . . some sage, but not like the last camp [16 km W Aoulouz]—relatively smaller . . . plenty of grass both under the shrubs and in the open areas" (R. E. Vaden field notes, USNM Mammal Division). At the latter site, samples of *L. barbarus* were captured in the grassy areas.

The regional distributions of *L. zebra* and *L. barbarus* do concord with previously recognized biogeographic subregions of Africa, as distilled from both plant and animal studies (Chapin 1932; Moreau 1952, 1966; Rosevear 1953, 1965; Davis 1962; Brenan 1978; Quézal 1978; Rautenbach 1978; Crowe & Crowe 1982; see Skinner & Smithers 1990:xxii, for their helpful map

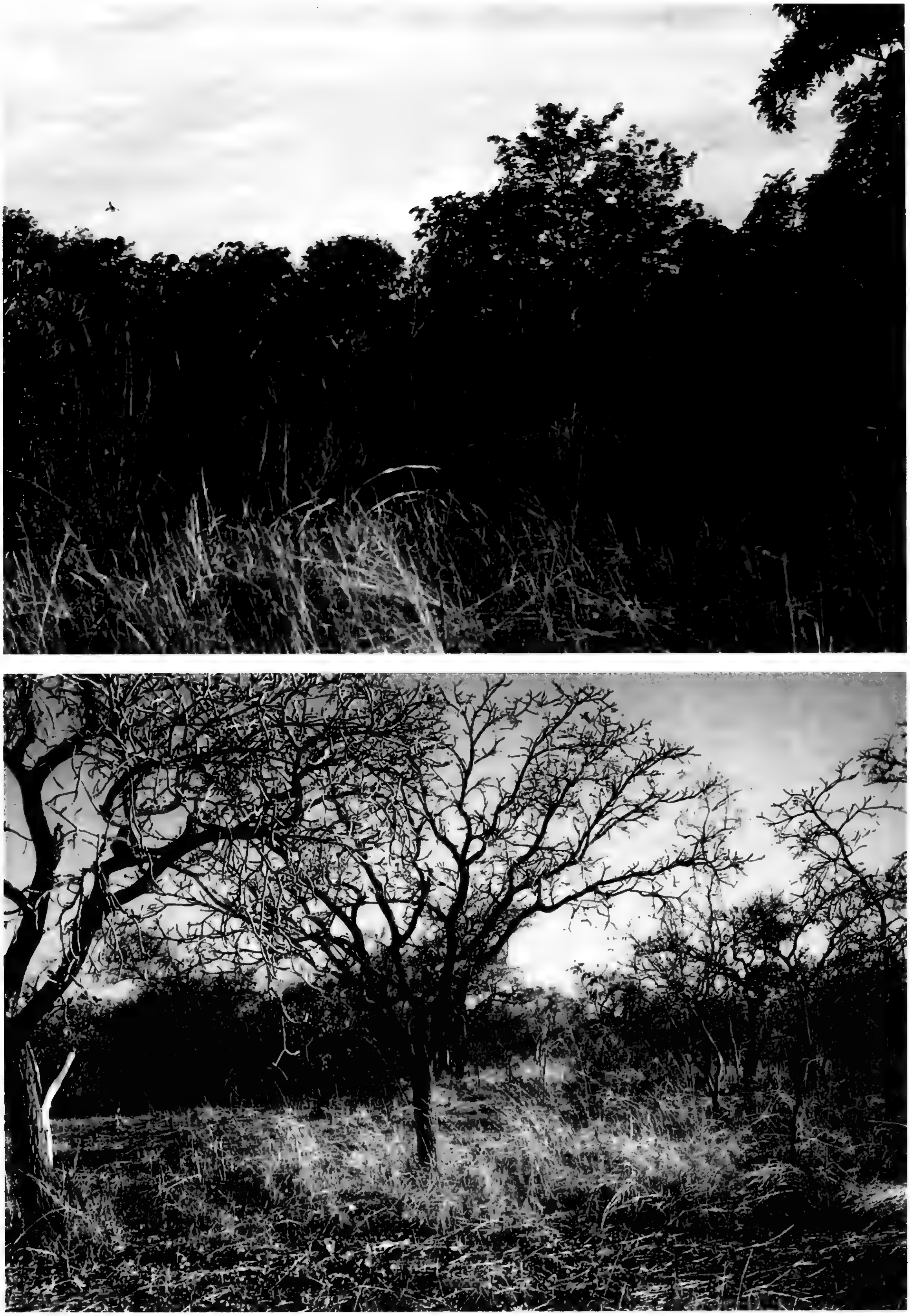

Fig. 10. Two examples of West African vegetation inhabited by populations of *Lemniscomys zebra*. Top, degraded Guinea Savanna in the vicinity of Zizonkame (07°55′N, 02°01′E), Benin, in the early rainy season (middle April); examples of both *L. striatus* and *L. zebra* were captured here. Photograph by James W. LeDuc. Bottom, Sudan Savanna in the vicinity of Cella (11°38′N, 00°22′W), Burkina Faso, in the late dry season (middle March); only specimens of *L. zebra* were trapped here. Photograph by Robert E. Vaden.

Fig. 11. Two examples of Moroccan coastal vegetation inhabited by populations of *Lemniscomys barbarus*. Top, mixed argon-sage-grassland at 16 km W Aoulouz (30°42′N, 08°18′W), Agadir Province; snow covered peaks of the High Atlas Mountains are visible in the left background. Bottom, heavily vegetated dunes with thorny shrubs, dense brush, and grasses at 5 km S Taroudannt (30°26′N, 08°54′W), Agadir Province; samples of *L. barbarus* were mainly collected in the grassy areas. Photographs by Robert E. Vaden.

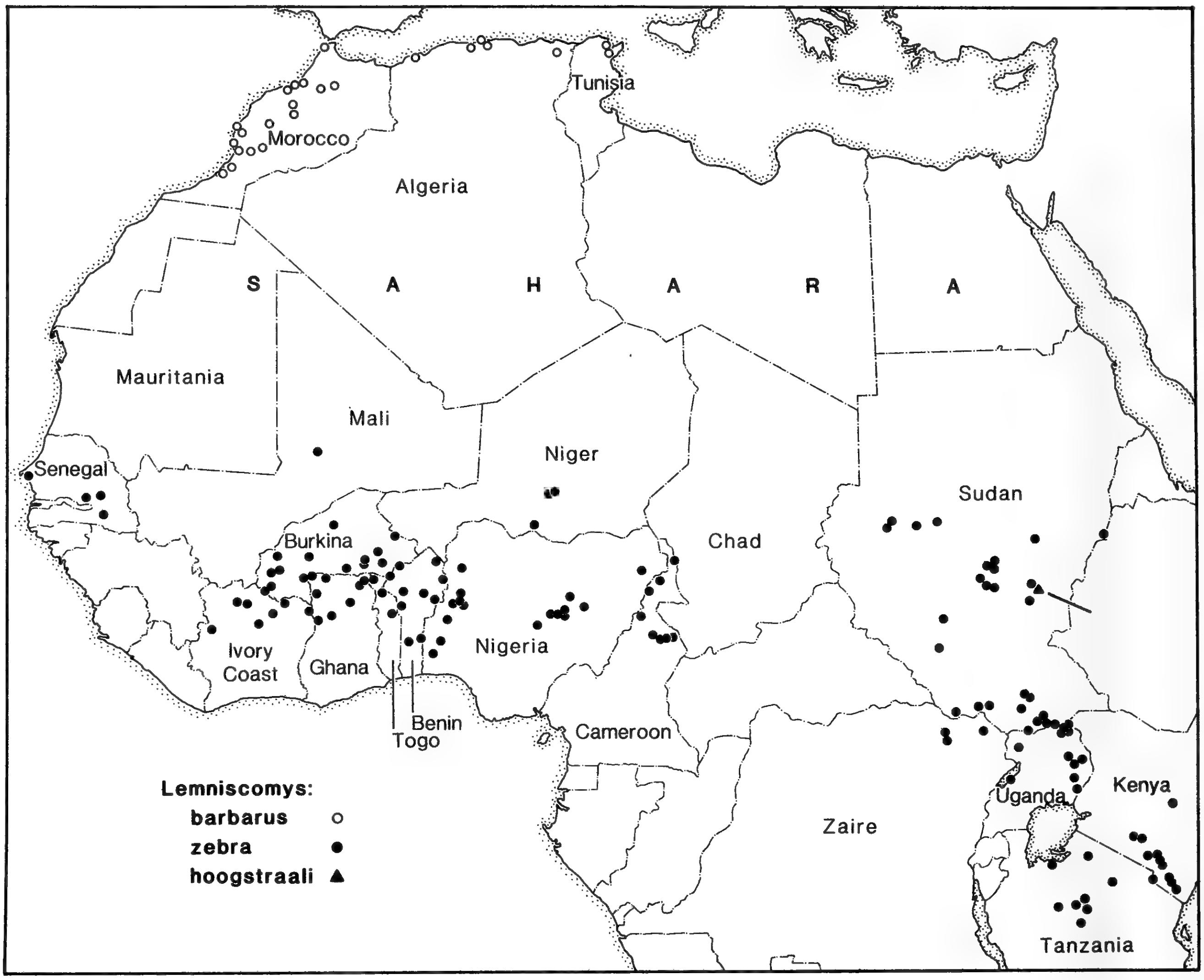

Fig. 12. Distribution map of African striped mice of the *Lemniscomys barbarus* species group, based on 649 specimens examined by the authors (see Taxonomic Accounts) from 177 principal collecting localities (see Appendix 1).

and tabular comparison of biotic classifications). Although the formal names adopted for ecophysical subdivisions may differ, particularly between plant and animal investigations, the principal areas (whether called subregions, zones, districts, domains, etc.) are remarkably complementary across these several works on African biogeography. For the present discussion, we employ the terminology formulated by Davis (1962) for Ethiopian Africa, as modeled after the earlier avifaunal studies of Chapin (1932) and Moreau (1952), with the addition of a Barbarian province as delineated by Heim de Balsac (1936), Moreau (1952), and Quézal (1978, called Mediterranean-Northern African Domain).

Museum specimens of *L. zebra* vouch its occurrence across a swath of savanna biotopes to the south of the Sahara Desert, from Senegal to central Sudan and southwards to southern Kenya and northcentral Tanzania (Fig. 12). These localities are virtually coterminous with three biotic zones within tropical Africa that have been designated as Sudanese Arid (Sahel and Sudan Savannas of Rosevear 1953), Northern Savanna (Guinea Savanna of Rosevear 1953), and Somali Arid. At the western terminus of its distribution in Senegal, *L. zebra* does not enter the Sahara Desert proper (not present in USNM series from Mauritania). The abrupt southward projection of its range in Benin and western Nigeria (The Dahomey Gap), almost to the Gulf of Guinea, conforms to the anthropogenic proliferation of invasive Guinea savanna (Booth 1958, Robbins 1978). At its eastern limits, the extension of *L. zebra* into Kenya and Tanzania follows an arid tract of acacia steppe called the Somali Arid Zone. Although this eastern African region of relatively high endemism shares species also native to either northern or southern savanna biomes (Moreau 1966, Brenan 1978, Coe & Skinner 1993), it displays a slightly stronger biogeographic affinity with the Southern Savanna Zone based on nonforest bird distributions (Crowe & Crowe 1982). However, as so far known, populations of *L. zebra* do not inhabit any part of the Southern Savanna Zone (Davis 1962, Rautenbach 1978—including both his Southern Savanna Woodland and Southern Savanna Grassland), whose northernmost extent reaches western Tanzania (see map in Skinner & Smithers 1990:xxii).

Locality records of *L. barbarus* outline a comparatively restricted distribution that adheres to the coastal sectors of Morocco, Algeria, and Tunisia and is bounded by the upper elevations of the Atlas Mountains (Fig. 12). In Morocco, its distribution covers the coastal lowlands and the contiguous Central Plateau, extending inland only to the northern and northwestern foothills of the Anti Atlas, High Atlas, and Middle Atlas Mountains (also see Aulagnier & Thevenot 1986:80). USNM locality records for Morocco document an altitudinal range from sea level to about 750 m, as interpolated from topographic maps. In Algeria and Tunisia, the species occurs mainly along the narrow Mediterranean coastal strip but also among the folded ridges of the Tell Atlas, low mountains which closely approach the seacoast (and see Bernard 1969:109, and Kowalski & Rzebik-Kowalska 1991:257).

Biogeographers have previously recognized the area inhabited by *Lemniscomys barbarus* as the Barbarian Zone (Heim de Balsac 1936, Moreau 1952), a biological island isolated on the north and west by the Atlantic Ocean and Mediterranean Sea and on the south and east by the Sahara Desert, which reaches the coastline in Mauritania and in Libya. The northwest rim of the African continent, by virtue of its maritime geological setting coupled with climatic oscillations of the Plio-Pleistocene and accompanying vegetational shifts, has formed a mixing bowl for species spreading from Afrotropical, European, and Asian landscapes. Indeed, the high diversity and striking endemism recorded for plants and animals of the area bear testimony to its refugial character and recurring opportunity for taxonomic differentiation (Heim de Balsac 1936, Moreau 1966, Quézal 1978, Cheylan 1990).

Although the Barbarian Zone today harbors a predominance of temperately adapted species of Palearctic affinities, Heim de Balsac (1936) had regarded the majority of mammals living there as having Ethiopian origins. Such an interpretation contrasted to the large Palearctic contingent observed among the avifauna, an apparent zoogeographic anomaly expanded by Moreau (1966). However, Heim de Balsac had conflated under his "Indo-Ethiopian" category not only broadly distributed paleotropical mammals (many carnivores) but also xeric-adapted species occurring across the deserts of the Sahara, Arabian Peninsula, and Middle East. The many gerbilline rodents numbering among the latter prejudice the interpretation of Moroccan mammals as predominantly "Ethiopian" sensu Heim de Balsac. Subsequent biogeographic studies of Barbarian mammals have supported their substantial Palearctic pedigree (Saint Girons & Petter 1965, Agustí 1989, Aulagnier 1990, Cheylan 1990, Kowalski & Rzebik-Kowalska 1991), a finding concordant with the broad picture of Northwest African biodiversity as disclosed by other organisms (Moreau 1966, Quézal 1978). Still, the mosaic of tropical and temperate habitats long offered within the Barbarian region has fostered some isolation and differentiation of Subsaharan groups, and Linnaeus' Barbary Mouse, *Lemniscomys barbarus*, represents

Table 5.—Rodent species[a] indigenous to the Barbarian Zone[b] of Northwest Africa, with indication of their biogeographic affinity or probable origin.

Taxon (* = endemic)	Ethiopian	Palearctic	
		European	Saharo-Sindean
Sciuridae			
*Atlantoxerus getulus**	X		
Xerus erythropus	X		
Muridae: Gerbillinae			
Gerbillus campestris			X
*Gerbillus hesperinus**			X
*Gerbillus hoogstraali**			X
*Gerbillus jamesi**			X
*Gerbillus maghrebi**			X
*Gerbillus occiduus**			X
Meriones shawi			X
Muridae: Murinae			
Apodemus sylvaticus		X	
*Lemniscomys barbarus**	X		
Mastomys erythroleucus	X		
Mus spretus		X	
Myoxidae			
Eliomys melanurus		X	
Dipodidae			
Jaculus orientalis			X
Hystricidae			
Hystrix cristata	X?		
Totals	5	3	8

[a] Species compiled from systematic reviews of mammals for Morocco (Aulagnier & Thevenot 1986; Saint Girons & Petter 1965), Algeria (Kowalski & Rzebik-Kowalska 1991), and Tunisia (Bernard 1969), with the taxonomy updated to accord with Wilson & Reeder (1993).

[b] The limits of the Barbarian Zone have been variously defined, but are here understood to include the coastal lowlands of Morocco, Algeria, and Tunisia, the inland high plateaus, and the Atlas Mountains (for example, per Quézal 1978). Such a regional definition thus excludes typical desertic formations of the Sahara and, correspondingly, many rodents, especially gerbillines.

another of these endemics, one of the few rodent species plausibly derived from Afrotropical (Ethiopian) relatives (Table 5). Other rodent species with satellite populations in Northwest Africa similarly merit renewed study of their differentiation and taxonomic status (for example, *Apodemus sylvaticus*, *Mastomys erythroleucus*, many species of *Gerbillus*, *Meriones shawi*, and *Eliomys melanurus*).

The historical biogeography of Africa's savanna landscapes has received less attention in contrast to that devoted to forest-dwelling vertebrates and their patterns of distribution, species diversity, and endemism (for example: Moreau 1966, Crowe & Crowe 1982, Carleton & Robbins 1985, Grubb 1990, and references cited by each). Nevertheless, biotic affinities among savanna biomes, as currently delimited and understood, provide sufficient insight to frame a series of hypotheses to explore the evolutionary diversification of species of *Lemniscomys.*

1.—Are single-striped mice (*griselda-rosalia-roseveari*), largely confined to the Southern Savanna Zone, the sister group to the *striatus* and *barbarus* complexes of northern savannas and woodlands? That is, does possession of multiple stripes, arranged either in continuous (*barbarus* group) or in punctulated lateral lines (*striatus* group), form a synapomorphy for those more northern mice? Is *L. linulus*, a single-striped form isolated in far West Africa (Van der Straeten 1980a), the vicariant sister species to *L. griselda* and its kin in the Southern Savanna Zone, or does the former represent an instance of evolutionary convergence, having been derived from a *striatus*-like ancestor through suppression of lateral striping?

2.—If the *striatus* group (distribution centered in Guinea savanna) and *barbarus* group (more common in Sudan vegetation) are so closely related, how can one explain their divergence? Other studies have divulged little support for the latitudinally graded, contiguous savanna bands found south of the Sahara Desert as refugia or centers of endemism (Moreau 1966, Brenan 1978). Evidence from ornithological diversity and centers of endemism (Crowe & Crowe 1982), however, provides some support for a nonforest refugium in eastern equatorial Africa (within the contemporary Somali Arid Zone), where the progenitor of one complex (*striatus*?) may have differentiated in isolation from the other (*barbarus*?) in arid habitats fringing the Sahara, before secondary contact and distributional overlap.

3.—The autochthonous origin of *L. barbarus* in the Barbarian Zone is parsimoniously explained as allopatric speciation after final severance (late Pliocene–early Pleistocene?) from Subsaharan populations (ancestral to *L. zebra*) along the West African coast. The ranges of other Afrotropical species with apparently conspecific segments in southern Morocco similarly intimate former connection (*Xerus erythropus*) or document present continuity (*Acomys cahirhinus*, *Mastomys erythroleucus*) of populations across this westernmost region. Although reasonable as a first explanation, caution is advised, for yet other corridors of contact with Subsaharan Africa may have existed during pluvial intervals of the Pleistocene: for example, via the highlands that occur through the middle of the Saharan Desert or along the eastern Mediterranean coast (Quézal 1978). In either case, determining the nearest kinship of *L. hoogstraali* (eastcentral Sudan) and the status of East versus West African moieties of *L. zebra* will assume importance in understanding the evolutionary derivation of *L. barbarus*.

Such phylogenetic questions and their geographic scale elegantly lend themselves to investigation using genetic sequencing and phylographic reconstruction (for example, see Matthee & Robinson 1997, on the springhare, *Pedetes*).

Taxonomic Accounts

Lemniscomys barbarus (Linnaeus 1766)

Mus barbarus Linnaeus, 1766: unpaginated addenda at end of volume (type locality, "Barbaria" = Morocco).—Trouessart, 1881:124.

Arvicanthis barbarus, Trouessart, 1897: 498.—Trouessart, 1904:388.

Lemniscomys barbarus, Thomas, 1916:68 (subsequent designation as type species).—Cabrera, 1921:58.—Misonne, 1974: 20 (part).—Honacki et al., 1982:520 (part).—Aulagnier & Thevenot, 1986:80 (part).—Le Berre, 1990:276 (part).—Corbet & Hill, 1991:180 (part).—Musser & Carleton, 1993:601 (part).

Lemniscomys barbarus barbarus, Cabrera: 1932:272.—Allen, 1939:391.—Ellerman, 1941:131.—Saint Girons & Petter, 1965: 37.—Kowalski & Rzebik-Kowalska, 1991:259.

Lemniscomys barbarus ifniensis Morales Agacino, 1935:390 (type locality, Spanish Morocco [Morocco], Sidi Ifni, Ifni; holotype–MNCN 9638).—Allen, 1939: 391.—Ellerman, 1941:131.—Saint Girons & Petter, 1965:37.—Misonne, 1974: 20 (listed in synonymy without indication of rank).—Aulagnier & Thevenot, 1986: 80 (listed in synonymy without indication of rank).—Le Berre, 1990:276 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Emended diagnosis.—A species of *Lemniscomys* characterized by longitudinally continuous dorsal stripes; upperparts generally more muted in tone, alternating dark and light stripes less sharply contrasting due to suffusion of ochraceous over middle dorsum; primary dark stripes on either side of mediodorsal line typically four in number, fifth stripe absent or indistinct; secondary light line usually present and continuous within first lateral dark stripe, incomplete or poorly defined in second lateral dark stripe; size relatively large and skull robustly developed, as observed in adult dimensions of both the body (total length > 235 mm) and cranium (occipitonasal length > 29.0 mm; zygomatic breadth > 13.5 mm).

Distribution.—Coastal region of Morocco, Algeria, and Tunisia, northwest and north of the Atlas Mountains (Fig. 12). Other locality records based on owl-pellet recoveries or reliable sightings of *L. barbarus* have been reported for Morocco (Aulagnier & Thevenot 1986), Algeria (Kowalski & Rzebik-Kowalska 1991), and Tunisia (Bernard 1969), but these sites do not alter the general picture of distribution as documented by the specimens we examined and enumerate below.

Remarks.—Although some specimens used by Linnaeus in his Systema Naturae still exist and may be regarded as types (see Addendum on *L. striatus*), Van der Straeten has searched unsuccessfully for a likely type of *Mus barbarus* in the Naturhistoriska Riksmuseet, Stockholm, and the museum of the University of Uppsala, Sweden. Since *L. barbarus* is the only species of *Lemniscomys* isolated in northwest Africa, wholly allopatric to other congenors, identification poses no problems and restriction of the type locality to some place other than "Barbaria," regarded as equivalent to Morocco (Allen 1939, Ellerman 1941), is unwarranted at this time.

Specimens examined.—124, as follows.

Algeria: Alger (BMNH 12.3.12.144–12.3.12.151, 19.7.7.1952; BZM 1664; MNHN 1975.117); Hammam Meskoutine (BMNH 20.7.19.51); Hammam Rirha (BMNH 12.6.12.152–12.6.12.155); Oran (ZMA 8653, 8654; MNHN 1953.830–1953.832, 1955.618, 1955.619, 1961.894, 1961.1063); Reghaia (MAKB 54.111, 54.112). Algeria, locality unknown (BMNH 44.50, 44.51, 19.7.7.1952, MNHN 1956.616).

Morocco: Enzel (BMNH 98.7.4.29); Forêt de Néfifik (MNHN 1957.499, 1958.248); 31.5 km on road from Marrakesh to Casablanca (MNCN 9657-9659); 15 km WNW Marrakesh (SMF 47.781); Meknès (MNHN 1964.377); Oued Sebo (BMNH 76.1077); Oued Cherrat (ZMA 4834). Agadir Province, 8 km S Tiznit (USNM 475125); 15 km E Agadir (USNM 475126–475148); 16 km W Aoulouz (USNM 475150–475164); 5 km S Taroudannt (USNM 475165–475168); 8 km N Tamri (USNM 475169). Khouribga Province, 5 km S Oued Zem (CM 45286; USNM 475170–475182). Rabat Province, 17 km SW Rabat (USNM 475121, 475122). Safi Province, 13 km E Essaouira (USNM 475123, 475124); 15 km SW Rabat (USNM 475149); 5 km NE Essaouira (USNM 482104, 483092–483094). Sidi Ifni Province, Ifni (MNCN 9638). Tanger Province, 3 km S Cap Spartel (USNM 475183); Tanger (MNCN 9654). Morocco, locality unknown (MNCN 9655, 9660, 9661; MNHN 1950.405, 1950.407, 1950.872).

Tunisia: Algeriet (NHRS M810); Cédria (Potinville) (MAKB 71.210–71.214); La Marsa (MAKB 71.215).

Lemniscomys hoogstraali Dieterlen, 1991

Lemniscomys hoogstraali Dieterlen, 1991: 11 (type locality, Sudan, Upper Nile Province, 12 miles N Niayok, Paloich, about 10°22′N–32°33′E; holotype, USNM 342078).—Musser & Carleton, 1993: 601.

Emended diagnosis.—Linear markings of upperparts sharply contrasted, the primary dark stripes wide and black, offset by narrower, almost white primary light stripes; secondary light stripes weakly expressed and incomplete, hence primary dark stripes undivided; size of skull closely similar to *L. barbarus*, notably larger relative to *L. zebra*.

Distribution.—Known only from the type locality in eastern Sudan (Figs. 1, 12).

Remarks.—Dieterlen (1991:11) diagnosed this new form as a "Large species of the *Lemniscomys barbarus* group. Tail length small (101% of head and body length); dorsal coloration rich in contrast and with broad blackish stripes; skull relatively large; incisive foramina ending anterior to M^1; zygomatic plate indented below." However, the discriminatory value of several of these traits is unhelpful when compared to large series of *L. barbarus* and *L. zebra*. Many specimens of the latter two species have the forward edge of their zygomatic plate undercut ventrally. In fact, the protuberance of the anterodorsal edge of the plate typically becomes accentuated in older specimens, and, as noted by Dieterlen, the holotype of *L. hoogstraali* is an old individual (age class 5–6). Similarly, the absolute and relative length of the incisive foramina is foreshortened in older individuals of *L. barbarus*, just meeting the anterior roots of the first molar instead of extending conspicuously between them. Contrary to Dieterlen's assertion that *L. hoogstraali* exceeds even *L. barbarus* sensu stricto in cranial size, the measurements of the holotype are typical of old adult specimens of *L. barbarus* and fall within the variational limits recorded for our Moroccan samples (Table 4, Appendix 2). Finally, the terminal caudal segment of the holotype's skin appears missing, which may partially account for the exceptional shortness (101%) of its relative tail length (proportion of TL/HBL ranges from 115 to 123% in samples of *L. barbarus* and *L. zebra*—Appendix 2).

Notwithstanding the caveats attached to certain diagnostic features advanced by Dieterlen, we concur with his naming of the specimen as a new species. Although similar to *L. hoogstraali* in cranial size, no specimen of true *L. barbarus* exhibits such strongly delineated upperparts and broad, richly black stripes. Furthermore, the robust size of *L. hoogstraali*, as judged by both hindfoot length (28 mm) and most cranial dimensions (Table 4), is certainly greater than any surrounding Sudanese examples of *L. zebra*. And while some skins of East African *L. zebra* may approach the consolidated striping evident in *L. hoogstraali*, none that we have seen quite matches it. More and larger series must be assembled to rigorously evaluate the characters and status of Dieterlen's new form, so far known only by the holotype, its condition imperfect (tail tip missing; skull with both zygoma incomplete, right bulla crushed, and pterygoid processes broken off).

Specimens examined.—1, the holotype. Sudan: Upper Nile Province, 12 miles N Niayok, Paloich (USNM 342078).

Lemniscomys zebra (Heuglin 1864)

Mus zebra Heuglin, 1864:10 (type locality, Bahr el Ghazal [Sudan], "Lande der Req-Neger, Djur und Bongo;" lectotype, SMNS 1100a).—Trouessart, 1881:124.

Arvicanthis zebra, Trouessart, 1897:499.—Trouessart, 1904:388.

Arvicanthis barbarus zebra, Osgood, 1910: 10.

Lemniscomys barbarus zebra, Hollister, 1919:144.—Allen, 1939:392.—Hatt, 1940: 511.—Ellerman, 1941:131.—Setzer, 1956:511.—Kingdon, 1974:620.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Lemniscomys zebra, Kershaw, 1924b:25.

Arvicanthis spekei De Winton, 1897:318 (type locality, Tanganyika Territory [Tanzania], Unyamuezi; holotype, BMNH 63.7.7.23).—Trouessart, 1904:388.

Arvicanthis barbarus spekei, Osgood, 1910: 10.

Lemniscomys barbarus spekei, Matschie, 1911:338.—Allen, 1939:391.—Ellerman, 1941:131.—Kingdon, 1974:620.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Arvicanthis dunni Thomas, 1903:297 (type locality, Western Kordofan [Sudan], Kaga Hills, about 120 mi [193 km] W El Obeid; holotype, BMNH 3.2.8.15).—Trouessart, 1904:388.

Lemniscomys dunni dunni, Allen, 1939: 392.—Setzer, 1956:512.

Lemniscomys barbarus dunni, Ellerman, 1941:131.—Dekeyser, 1955:204.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Arvicanthis barbarus convictus Osgood, 1910:10 (type locality, British East Africa [Kenya], Voi; holotype, FMNH 17206).

Lemniscomys barbarus convictus, Hollister, 1919:146.—Allen, 1939:391.—Ellerman, 1941:131.—Kingdon, 1974:620.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Arvicanthis barbarus albolineatus Osgood, 1910:11 (type locality, British East Africa [Kenya], Ulukenia Hills, Lukenya Mountain; holotype, FMNH 17194).

Lemniscomys barbarus albolineatus, Hollister, 1919:144.—Allen: 1939:391.—Ellerman, 1941:131.—Kingdon, 1974:620.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Lemniscomys albolineatus, Kershaw, 1924a: 536.

Arvicanthis oweni Thomas, 1911b:120 (type locality–French Gambia [Senegal], upper Gambia River, Gemenjulla, 50 ft [15 m]; holotype, BMNH 11.6.10.61).

Lemniscomys oweni oweni, Allen, 1939: 394.

Lemniscomys barbarus oweni, Ellerman, 1941:131.—Dekeyser, 1955:204.—Rosevear, 1969:336.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Lemniscomys barbarus manteufeli Matschie, 1911:338 (type locality, Tanganyika Territory [Tanzania], south coast of Lake Victoria, Mwanza; holotype, BZM 16025).—Allen, 1939:391.—Ellerman, 1941:131.—Kingdon, 1974:620.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Arvicanthis barbarus nigeriae Thomas, 1912:272 (Nigeria, Panyam, 4000 ft [1220 m]; holotype, BMNH 12.1.16.45).

Lemniscomys barbarus nigeriae, Allen, 1939:391.—Ellerman, 1941:131.—Rosevear, 1953:102.—Dekeyser, 1955: 204.—Rosevear, 1969:336.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Lemniscomys olga Thomas & Hinton, 1921:9 (type locality, Damergou [Niger], Takoukout, 1550 ft [472 m], about 15°N and 09°E; holotype, BMNH 21.2.11.128).—Ellerman, 1941:131.—Dekeyser, 1955:204.

Lemniscomys dunni olga, Allen, 1939:392.

Lemniscomys barbarus olga, Rosevear, 1969:335.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Lemniscomys dunni nubalis Thomas & Hinton, 1923:267 (type locality, Southern Kordofan [Sudan], Nuba Country, Talodi, 1300 ft [396 m]; holotype, BMNH 18.7.2.14).—Allen, 1939: 392.—Hatt, 1935:1; 1940:513.—Setzer, 1956:512.

Lemniscomys barbarus nubalis, Ellerman, 1941:131.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Lemniscomys oweni orientalis Hatt, 1935:2 (type locality, Belgian Congo [Zaire], Faradje; holotype, AMNH 49626).—Allen, 1939:391.—Hatt, 1940:513.

Lemniscomys barbarus orientalis, Ellerman, 1941:131.—Misonne, 1974:20 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:601 (listed in synonymy without indication of rank).

Emended diagnosis.—A species of *Lemniscomys* characterized by longitudinally continuous dorsal stripes; upperparts generally brighter, alternation of dark and light stripes better defined compared to *L. barbarus*; primary dark stripes on either side of mediodorsal line typically five in number, with secondary light lines usually present and continuous within first and second dark laterals; external and cranial size medium and skull moderate in build (total length < 230 mm; occipitonasal length < 29.0 mm; zygomatic breadth < 13.5 mm).

Distribution.—Grassy woodlands and savannas south of the Sahara Desert, from Senegal in the west to southern Sudan in the east, southwards through northeasternmost Zaire, northern Uganda and western Kenya, to northcentral Tanzania (Fig. 12); altitudinal range from near sea level to 1220 m in West Africa (Panyam, Nigeria) and to 1065 m in East Africa (north of Dodoma, Tanzania).

Remarks.—Heuglin (1864) did not indicate a type specimen for *Mus zebra*, a common omission for the period, nor is his text clear about the number of specimens available when he described the new species. During his visits (in 1979, 1983, and 1989) to the Staatliches Museum für Naturkunde, Stuttgart (SMNS), Van der Straeten located two specimens of *Lemniscomys* that bear evidence of association with Heuglin's original description, a mounted skin and skull (SMNS 1100a) and a complete specimen in alcohol (SMNS 1100b). Labels attached to the mounted skin and fluid specimen each contain the information "Bongo; Von Heuglin, 1865," and the notation as type, the last datum obviously appended more recently. Heuglin's original characterization of the new form provides little help, for it only mentions coloration, pattern of stripes, and external measurements, all of which could have been plausibly derived from either a whole mount or a fluid-preserved carcass, or from both. He did note that he was not yet able to examine the molars, which admission suggests that the skull had not been cleaned (Heuglin provided cranial measurements for other species described in the same paper). Both Stuttgart specimens are currently listed as a "Holotypus" of *Lemniscomys barbarus zebra* in the SMNS card catalog (Fritz Dieterlen, personal communication), but they should be properly regarded as syntypes of Heuglin's (1864) *Mus zebra*.

The fully mounted skin with cleaned skull, however, is more useful for ascertaining diagnostic traits of the form, and we designate this specimen (SMNS 1100a) as lectotype of *Mus zebra* Heuglin (1864). The fluid specimen (SMNS 1100b) becomes the de facto paralectotype of the binomen (see Recommendation 73F, International Code of Zoological Nomenclature, Third Edition, 1985). The skin is mounted in a more or less realistic posture, and its label indicates male, but the sex cannot be confirmed by inspection of the skin. Although faded, presumably from years of museum exhibit, the mounted skin clearly displays the alternating dark and light (six to seven) dorsal stripes typical of the dorsal pelage of the *barbarus* group. Associated with the skull is an older but now invalid museum number, "Skelett-Katalog 5422," an extraneous number dating from the outmoded practice of assigning separate registrations to osteological and skin preparations, even for the same individual. The light molar wear (age class 1-2) suggests a young, perhaps immature, animal. Except for slight breakage of the pterygoid processes and mandibular rami, the skull of the lectotype is otherwise intact and in good condition. According to a posteriori probabilities of membership derived from discriminant function analysis, specimen number SMNS 1100a predictably intermingles with other Subsaharan samples that we identify as *L. zebra* (Fig. 7); in particular, the lectotype was marginally classified ($P = 0.45$) with specimens from Zaire (OTU 8), a group assignment likely due to its young age and correspondingly smaller size as compared to most Sudanese examples used in our analyses.

The form *Arvicanthis fasciatus* Wroughton (1906), named from southern Nigeria and occasionally listed as a subspecies of *L. barbarus* (Allen 1939, Rosevear 1969), was reidentified as a synonym of *L. striatus* by Van der Straeten & Verheyen (1980).

Rosevear (1969:333) erred in listing the type locality of *L. olga* Thomas & Hinton (1921) as Farniso, Nigeria, and citing the type specimen as BMNH 21.2.11.87. Van der Straeten has not been able to locate this specimen in the BMNH; the type locality (Niger, Takoukout) and registration number (BMNH 21.2.11.128) given in our synonymy agree both with the authors' original publication and with the provenience as written on the skin tag of the holotype.

Although *L. zebra* probably occurs in westernmost Ethiopia, Yalden's et al. (1996) report of its presence (as *L. barbarus*) at Arba Minch is questionable. Rupp (1980) had allocated these specimens (SMNS 16751, 16754), both young individuals, to *L. striatus* but also confided his difficulty in discerning the striping configuration as typical of that of *striatus* or of *barbarus*. The damaged condition of their skins and skulls precludes exact determination, but Van der Straeten tentatively refers the two specimens to *L. macculus* based on their smaller auditory bullae as determined from his subsequent examination in 1983.

Specimens examined.—524, as follows.

Benin: Atacora Region, Kouande (USNM 439584, 439585); Porga (USNM 439586); Soubroukou (USNM 439582, 439583). Borgou Region, Bimbereke (USNM 422058–422060); Guene (USNM 422061, 422062); Nikki (USNM 422081–422084); Segbana (USNM 422063–422080). Central Region, Diho (USNM 422057); Zizonkame (USNM 439580, 439581). Benin, locality unknown (MNHN 1913.13).

Burkina Faso: Arly (USNM 450853, 450854); 5 mi N Boussouma (USNM 465401); 6 mi S Cella (USNM 465404, 465405); 1 km N Cella (USNM 465406–465410); Djipologo (USNM 466682–466684); Fo (USNM 466674–466679); 5 km SW Koutoura (USNM 466681); Nasso (RUCA 1278, 1281–1283, 1289, 1345–1347, 1349–1356, 1370–1380, 1393–1398, 1414–1416, 1459, 1470, A.1–A.9, A.12–A.15); Natiaboani (USNM 450855); 3 km SE Nayoure (USNM 465411); Niangoloko (BEL 13243); 9 mi S Nobere (USNM 450852); 27 km ENE Orodara (USNM 466680); Ougarou (USNM 465412); Oulo (USNM 465413, 465414); 6 mi SE Seguenega (USNM 465402, 465403).

Cameroun: Boukma (RUCA 2.134); Fort Foureau (MNHN 1956.678); 35 km S Garoua (AMNH 241233); 35 km S and 10 km E Garoua (CM 58903, 58905, 58909); Isiri (RUCA 1087); Kali (RUCA 1098, 1099, 1114); Koum (RUCA 1018, 1066, 1095, 1122); Maroua, 20 km NW Dogba (CM 14975, 14978); Mora (MAKB 73.393–73.395, 73.397, 73.398); Sir (RUCA 1.479, 1.482, 1.492, 1.549, 1.591, 1.592, 1.595).

Ghana: Damango (USNM 466694–466697). Eastern Region, Legon, Accra Plains (USNM 412745–412747). Northern Region, Gambaga (USNM 435405); Nabogo (USNM 435400–435402); Sakpa (USNM 420577–420585). Upper Region, Bangwon (USNM 420573–420576); Pirisi (USNM 420570); Pulima (USNM 420571, 420572); Shishe (USNM 435403, 435404).

Ivory Coast: Bambela (BEL 13177, 13178); Bandama, near Tiebila (FMNH 105180); Bouna (BEL 3798; MNHN 1971.757, 1971.758); Kafiné (BEL 13695); Kong (USNM 465398–465400); Ouango Fitini (BEL 3802, 3932, 13902, 13903, 13931, 13945, 13949, 13984, 23354, 23368, 23373, 23375, 23377, 23379–23382); Tyenko (USNM 466685–466687); Yama (USNM 466688–466693).

Kenya: Garissa District, Galma Galla, 270 ft (AMNH 187678, 187679); Machakos District, Kathekani, 760 m (CM 102462, 102463); Kilabasi (AMNH 114445); Voi District, Kenya Karanzi (AMNH 114446); Machakos District, Kiboko, 3100 ft (USNM 437394); Machakos District, 11 km N and 17 km E Kibwezi (CM 98258); Machakos (BMNH 34.10.26.11, 34.10.26.12); Maungu (CM 57977); Masi, Sand River (AMNH 114449); 50 mi S Moctow (AMNH 114447, 114448); Mtoto Andei (USNM 181737–181740); near Tana River (MCZ

16222); Taveta (BMNH 10.7.2.115); Ulukenia Hills, Athi Plains (USNM 162884); Ulukenia Hills, Lukenya Mountain (FMNH 17194); Voi (BMNH 10.6.2.125, 29.3.17.167; FMNH 17206).

Mali: Timbuktu (FMNH 44713; ZMK 3885, 3886).

Niger: Farak, 1475 ft (BMNH 25.5.12.80, 25.5.12.81, 39.2083, 39.2084); Gerari (Tessawa) (BMNH 25.5.12.83); Takoukout (BMNH 21.2.11.128).

Nigeria: Bauchi (BMNH 68.491); Borgu (HAP 1318, 1322); Dada (USNM 404085–404087); Igbo Ora (USNM 404041); Kabwir (BMNH 12.9.10.3, 13.5.2.3, 13.5.2.4, 14.11.8.3); 1 mi S Kabwir (USNM 375975); Kishi (HAP 1026); Mada River, 3 mi E Gudi (USNM 404043); 22 mi S Maiduguri, Bornu Ranch (USNM 379011-6); New Bussa (HAP 1068, 1069, 1073); Panyam, 4000 ft (BMNH 12.1.16.42–12.1.16.47, 12.4.3.34, 12.4.3.36); Panyam Fish Farm, 2 mi N Panyam, Jos Plateau (USNM 404020–404040, 404044–404084); Shangunu (USNM 379647); Upper Ogun Ranch, 12 mi N Iseyin (USNM 404042); Wawa (HAP 901, 938, 943, 1778, 1779); Yankari (HAP 1106); Zaria (HAP 585).

Senegal: Bandia (MAKB 76.269); Gemenjulla (BMNH 11.6.10.61, 11.6.10.63–11.6.10.67); Kotiare Naoude, 27 km NE Tambacounda (USNM 376533–376536); Koussanar (USNM 376529–376532).

Sudan: Agur (BMNH 28.3.11.51, 28.3.11.52); Badigeru Swamp, 20 mi E Mongalla (BMNH 20.4.26.22); Bahr el Zeraf (MAKB 27–30); Bahr al Ghazal (BMNH 17.10.4.18); Bongo (SMNS 1100a, 1100b); Delami (BMNH 29.5.19.26); Duk Majok (BMNH 8.4.2.41, 8.4.2.42); El Fasher (BMNH 23.1.1.302, 23.1.1.303, 23.1.1.305); Fashoda (BMNH 1.8.8.26); Gallabat (BMNH 28.1.11.151); Gondokoro (USNM 165192); Ikoto, 2500 ft (USNM 299764; ZMK 11942, 11944, 11947); Imurok (ZMK 11934–11937); Juga Juga (BMNH 20.7.30.18); Kadugli (SMF 33.218); Kaga Hills, about 120 mi W El Obeid (BMNH 3.2.8.15); Nuba Mountains, G. Koalib, Kudring (BMNH 29.5.19.27; FMNH 35313, 35314); Kuna (BMNH 23.1.1.308); Li Rangu (USNM 318003); Loa (ZMK 14084); Maridi (SMNS 27396); Molongori (ZMK 14096); Nimule, 1800 ft (FMNH 67293; USNM 299771); Nile-Congo watershed (BMNH 21.1.8.7); Nuba Mountains (BMNH 18.7.2.16); Tadoro (SMF 33.217); Talodi, 1300 ft (BMNH 18.7.2.13, 18.7.2.14); Terrakekka (BMNH 28.3.11.53); Torit, 2000 ft (FMNH 66853, 66854, 66857, 66859, 66860, 67171, 67172, 67175, 79500–79502; USNM 299765–299770; ZMK 14081–14083, 14088, 14092, 14100, 14104); 30 km W Torit (SMNS 27398, 27399, 27401, 27402); 80 km E Juba-Torit (SMNS 27397); Umm Keddada (BMNH 23.1.1.309, 23.1.1.311, 23.1.1.312). Southern Sudan, locality unknown (SMNS 27405, 27406).

Tanzania: Banagi (KBIN 15575); 50 mi N Dodoma, 3500 ft (CM 57782); Jumbe Kadala, Ussnoro (AMNH 55533; BMNH 24.1.1.180); Manyara Lake (BMNH 71.1246, 71.1247, 71.1249); Mawere (AMNH 83916–83920); Mdjengo's (BMNH 24.1.1.178, 24.1.1.179); Mtali's (MCZ 22958); Mwanza, south coast of Lake Victoria (BZM 16025); Ndogowe (BMNH 24.1.1.181); Pooma (MCZ 22957); Unyamuezi (BMNH 63.7.7.23).

Togo: Dapango (USNM 438311–438313); Paio (RUCA 551); Pewa (USNM 438314).

Uganda: Apeluk (BMNH 46.757–46.760); Apoka, Kidepo Valley National Park, Karamoja (BMNH 71.274); near Kaiso Valley, Bunyono (BMNH 71.277); west of road to Kananarock, Karamoja (BMNH 71.272); Karamoja (BMNH 71.273); Kidepo Valley National Park (BMNH 70.1065, 70.1066); near Loi Jome (AMNH 180121); Lorengikipi (AMNH 119166, 119169, 119170); south of Lorupei River crossing and post 18, Karamoja (BMNH 71.275, 71.276); Malera (BMNH 46.761); Nabilatuk (BMNH 63.928, 63.929); Nabumali (BMNH 67.900, 67.901); Rhino Camp, Lado Enclave (CM 850; USNM 165191, 165193, 165194, 165197, 165198, 165200–165205, 165422).

Zaire: Faradje (AMNH 49610–49615, 49617–49619, 49621–49633; KMMA 9040, 9191, 13015, 13016); Niangara (AMNH 49608, 49609); Tingasi (AMNH 2150).

Addendum on the Type of *Mus striatus* Linnaeus

Among the types housed by the Naturhistoriska Riksmuseet, Stockholm (NHRS), is a specimen of *Lemniscomys* that probably served as the basis of Linnaeus' (1758) description of *Mus striatus*, its habitat of origin then given as "India." In correcting the type locality of *striatus* to Sierra Leone, Thomas (1911a) did not remark on the existence of any original specimen, and as of 1969, Rosevear wrote that no type is known to exist. The preparation located by Van der Straeten in 1982 is a whole carcass (with skull still inside) preserved in alcohol. No formal registration number was associated with the fluid specimen, nor did Linnaeus mention any catalog number, per the nonstandardized descriptive conventions of the earliest taxonomy. In a paper bag affixed to the bottle is an old label, upon which occurs the handwritten scientific name, "*Mus Striatus*," both in cursive and in printed letters; the number 48 appears on the outside of this bag. A newer label (one copy on the bottle and one inside with the specimen) contains the information: "*Mus striatus* Linne Typ. f.beshr.i.Mus. Ad Sp I.10 Syst Nat 10.62 Gamla saml. 48." This line provides the bibliographic essentials for the name: the reference to Linnaeus' original description that appeared in a publication (1754) of the Museum Regis Adophi Frederici, Volume I, page 10; and the Systema Naturae, 10th edition (1758), page 62, which references the former. Dr. Bo Fernholm, Department of Vertebrate Zoology, Naturhistoriska Riksmuseet, informed us that "Gamla saml. is short for gamla samlingen and means Old Collection and refers to the fact that this specimen was # 48 of the old collection (i.e., before 1839) of the Royal Academy of Science, which was our mother institution until 1965 when the museum was separated as an independent government institution."

The small size and proportions of the specimen clearly indicate a juvenile animal. The sex of the immature individual appears to be male, although gender is not indicated on any tag. The pelage color seems diluted, perhaps from decades of leaching in old alcohol, and the stripes of the specimen immersed in fluid appear continuous. Nevertheless, seven pairs of dark and light punctulated stripes, distributed in the manner of *striatus*, are discernable on either side of the now brown (once black?) mediodorsal stripe when the specimen was removed from the jar and partially dried. The first through third light stripes exhibit distinctly separated spots, but the light markings of the fourth through seventh lines are set close together, suggesting an almost continuous effect. The belly is wholly white, like most *Lemniscomys*. Measurements obtained from the fluid specimen, as taken by Van der Straeten in 1982, include: length of head and body, 49.1 mm; tail length, 34.5 mm; hindfoot length, without claw, 13.4 mm. Its immaturity is underscored by comparison to these same dimensions in adult *L. s. striatus* from Ivory Coast, West Africa: length of head and body, 118.1 mm; tail length, 114.1 mm; hindfoot length, 26.0 mm (Van der Straeten & Verheyen 1978).

Troussart's (1881, 1898) early listings of *Mus striatus* supply circumstantial evidence that the Stockholm specimen is the one actually viewed by Linnaeus. That author indicated "*Mus striatus* L. (juv.)" as a synonym of *M. barbarus*, an interpretation consistent with the age and condition of the fluid specimen examined a century later by Van der Straeten. In the absence of any contrary evidence, this individual (NHRS A53.2048) in the Naturhistoriska Riksmuseet, Stockholm, should be considered the holotype of *Mus striatus* Linnaeus (1758) by reason of monotypy (see Article 73, International Code of Zoological Nomenclature, Third Edition, 1985).

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Literature Cited

Aggundey, I. R., & D. A. Schlitter. 1984. Annotated checklist of the mammals of Kenya. I. Chiroptera.—Annals of Carnegie Museum 53:119–161.

Agustí, J. 1989. On the peculiar distribution of some muroid taxa in the western Mediterranean.—Bollettino della Società Paleontologica Italiana 28:147–154.

Allen, G. M. 1939. A checklist of African Mammals.—Bulletin of the Museum of Comparative Zoology, Harvard 83:1–763.

Aulagnier, S. 1990. Zoogéographie et statut des carnivores sauvages du Maroc.—Vie et Milieu 40: 150–155.

———, & M. Thevenot. 1986. Catalogue des mammiferes sauvages du Maroc.—Travaux de l'Institut Scientifique Cherifien, Série Zoologique 41:163 pp.

Bernard, J. 1969. Les mammifères de Tunisie et des regions voisines.—Bulletin de la Faculté d'Agronomie 24–25:41–172.

Booth, A. M. 1958. The Niger, the Volta, and the Dahomey Gap as geographic barriers.—Evolution 12:48–62.

Brenan, J. P. M. 1978. Some aspects of the phytogeography of tropical Africa.—Annals of the Missouri Botanical Gardens 65:437–478.

Cabrera, A. 1921. Los Murinae de Marruecos.—Boletin Real Sociedad Española de Historia Natural, special 50th Anniversary Volume, pp. 42–58.

———. 1932. Los Mamíferos de Marruecos. Trabajos del Museo Nacional de Ciencias Naturales, Madrid, Serie Zoológica 57:361 pp.

Carleton, M. D., & C. B. Robbins. 1985. On the status and affinities of *Hybomys planifrons* (Miller 1900) (Rodentia:Muridae).—Proceedings of the Biological Society of Washington 98:956–1003.

———, & C. Martinez. 1991. Morphometric differentiation among West African populations of the rodent genus *Dasymys* (Muroidea: Murinae), and its taxonomic implications.—Proceedings of the Biological Society of Washington 104:419–435.

Chapin, J. P. 1932. The birds of the Belgian Congo. Part 1.—Bulletin of the American Museum of Natural History 65:756 pp.

Cheylan, G. 1990. Endémisme et spéciation chez les Mammifères Méditerranéens.—Vie et Milieu 40:137–143.

Coe, M. J., & J. D. Skinner. 1993. Connections, disjunctions, and endemism in the eastern and southern African mammal faunas.—Transactions of the Royal Society of South Africa 48: 233–255.

Corbet, G. B., & J. E. Hill. 1991. A world list of mammalian species, 3rd edition. Natural History Museum Publication, London, 243 pp.

Crowe, T. M., & A. A. Crowe. 1982. Patterns of distribution, diversity, and endemism in Afrotropical birds.—Journal of Zoology 198:417–442.

Davis, D. H. S. 1962. Distribution patterns of South African Muridae, with notes on some of their fossil antecedants.—Annals of the Cape Provincial Museums 2:56–76.

———, & X. Misonne. 1964. Gazetteer of collecting localities of African rodents.—Koninklijk Museum voor Midden-Afrika, Tervuren, Zoologische Documentatie 7:1–100.

Dekeyser, P. L. 1955. Les mammiféres de l'Afrique Noire Française.—Initiations Africaines, Institut Français d'Afrique Noire, Dakar 1:426 pp.

Delany, M. J. 1975. The Rodents of Uganda. British Museum (Natural History), London, 165 pp.

De Winton, W. E. 1987. On a collection of small mammals from Uganda.—Annals & Magazine of Natural History, London, series 6, 20:316–320.

Dieterlen, F. 1991. *Lemniscomys hoogstraali*, an new murid species from Sudan.—Bonner Zoologische Beiträge 42:11–15.

Ellerman, J. R. 1941. The families and genera of living rodents. Volume 2, Family Muridae. London: British Museum (Natural History), 690 pp.

Filippucci, M. G., M. V. Civitelli, & E. Capanna. 1987. The chromosomes of *Lemniscomys barbarus* (Rodentia, Muridae).—Bollettino di Zoologia 53:355–358.

Gautun, J.-C., M. Tranier, & B. Sicard. 1986. Liste preliminaire des rongeurs du Burkina Faso (ex Haute-Volta).—Mammalia 49:537–542.

Grubb, P. 1990. Primate geography in the Afro-tropical forest biome. Pp. 187–214 *in* G. Peters and R. Hutterer, eds., Vertebrates in the Tropics. Museum Alexander Koenig, Bonn, 424 pp.

Happold, D. C. D. 1987. The mammals of Nigeria. Oxford University Press, New York, 402 pp.

Hatt, R. T. 1935. Taxonomic notes concerning arvicanthine rodents.—American Museum Novitates 790:4 pp.

———. 1940. Lagomorpha and Rodentia other than Sciuridae, Anomaluridae, and Idiuridae, collected by the American Museum Congo Expedition.—Bulletin of the American Museum of Natural History 76:457–604.

Heim de Balsac, H. 1936. Biogéographie des mammifères et des oiseaux de l'Afrique du Nord.—Bulletin Biologique de France et de Belgique, Supplément XXI, 447 pp.

Heuglin, Th. von. 1864. Beiträge zur Zoologie Central—Afrika's Leopoldina 31, Abhandlungen 7: 1–15.

Hollister, N. 1919. East African mammals in the United States National Museum. Part II. Rodentia, Lagomorpha, and Tubulidentata.—Bulletin of the United States National Museum 99:184 pp.

Honacki, J. H., K. E. Kinman, & J. W. Koeppl. 1982. Mammalian species of the world. Association for Systematic Collections, Kansas, 641 pp.

Kershaw, P. S. 1924a. On some small mammals from Tanganyika Territory.—Annals & Magazine of Natural History, series 9, 12:534–536.

———. 1924b. On two collections of mammals: (1) from Mongalla and Bahr-el-Ghazal, (2) from Lake Tsana, Abyssinia.—Annals & Magazine of Natural History, series 9, 13:19–29.

Kingdon, J. 1974. East African Mammals. Volume II, Part B (Hares and Rodents): pp. 343–704. The University of Chicago Press, Chicago.

Kowalski, K., & B. Rzebik-Kowalska. 1991. Mammals of Algeria. Ossolineum Publishing House, Wroclaw, Poland, 370 pp.

Lamine Cheniti, T., & K. Sami. 1989. *Lemniscomys barbarus* (Rongeurs, Muridae), donnees biosystematiques et ecologiques.—Revue de la Faculté des Sciences Tunis, Série D, 4:89–102.

Le Berre, M. 1990. Faunes du Sahara. Volume 2. Mammiferes. Lechevalier-R. Chabaud, Paris, 360 pp.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. 10th Edition. Volume 1. Laurentii Salvii, Stockholm, 824 pp.

———. 1766. Systema naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. 12th Edition. Volume 1. Regnum Animale, part 1, pp. 1–532. Laurentii Salvii, Stockholm.

Matschie, P. 1911. Über einige Säugetiere aus Muansa am Victoria-Nyansa.—Sitzungs-Berichte der Gesellschaft naturforschender Freunde, Berlin 8:333–343.

Matthee, C. A., & T. J. Robinson. 1997. Mitochondrial DNA phylogeography and comparative cytogenetics of the springhare, *Pedetes capensis* (Mammalia: Rodentia).—Journal of Mammalian Evolution 4:53–73.

Matthey, R. 1954. Nouvelles recherches sur les chromosomes des Muridae.—Caryologia 6:1–44.

Misonne, X. 1974. Rodentia, main text. *in* J. Meester & H. W. Setzer, eds., The mammals of Africa, an identification manual, Part 6. Smithsonian Institution Press, Washington, D. C., 39 pp.

Morales Agacino, E. 1935. Mamiferos de Ifni.—Boletin Sociedad Española de Historia Natural, Madrid 35:381–393.

Moreau, R. E. 1952. Africa since the Mesozoic: with particular reference to certain biological problems.—Proceedings of the Zoological Society of London 121:869–913.

———. 1966. The bird faunas of Africa and its islands. Academic Press, New York, 424 pp.

Musser, G. G., & M. D. Carleton. 1993. Family Muridae. Pp 501–755 *in* D. E. Wilson & D. M.

Reeder, eds., Mammal species of the World, a taxonomic and geographic reference, Second Edition. Smithsonian Institution Press, Washington D. C., 1206 pp.

Osgood, W. H. 1909. Revision of the mice of the American genus *Peromyscus*.—North American Fauna 28:1–285.

———. 1910. Diagnoses of new East African mammals, including a new genus of Muridae.—Field Museum of Natural History, Zoological Series, 10(2):5–13.

Quézal, P. 1978. Analysis of the flora of Mediterranean and Saharan Africa.—Annals of the Missouri Botanical Gardens 65:479–534.

Rautenbach, I. L. 1978. A numerical re-appraisal of the southern African biotic zones.—Bulletin of Carnegie Museum of Natural History 6:175–187.

Robbins, C. B. 1978. The Dahomey Gap—a reevaluation of its significance as a faunal barrier to West African high forest mammals.—Bulletin of Carnegie Museum of Natural History 6:168–174.

Rosevear, D. R. 1953. Checklist and atlas of Nigerian mammals, with a foreword on vegetation. The Government Printer, Lagos, Nigeria, 131 pp.

———. 1965. The bats of West Africa. British Museum (Natural History), London, 418 pp.

———. 1969. The rodents of West Africa. British Museum (Natural History), London, 604 pp.

Rupp, H. 1980. Beiträge zur Systematik, Verbreitung und Ökologie äthiopischer Nagetiere. Ergebnisse mehrerer Forschungsreisen.—Säugetierkundliche Mitteilungen 28:81–123.

Saint Girons, M.-C., & F. Petter. 1965. Les rongeurs du Maroc.—Travaux de l'Institut Scientifique Cherifien, Série Zoologique 31:1–58.

Setzer, H. W. 1956. Mammals of the Anglo-Egyptian Sudan.—Proceedings of the United States National Museum 106:447–587.

Skinner, J. D., & R. H. N. Smithers. 1990. The mammals of the southern African Subregion, Second Edition. University of Pretoria, South Africa, xxxii + 771 pp.

Swynnerton, G. H., & R. W. Hayman. 1951. A checklist of the land mammals of the Tanganyika Territory and the Zanzibar Protectorate.—Journal of the East Africa Natural History Society 20: 274–392.

Thomas, M. R. O. 1903. On some mammals collected by Capt. H. N. Dunn, R. A. M. C., in the Soudan.—Proceedings of the Zoological Society of London 1903:294–301.

———. 1911a. The mammals of the Tenth Edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species.—Proceedings of the Zoological Society of London 1911:120–158.

———. 1911b. List of small mammals obtained by Mr. G. Fenwick Owen on the Upper Gambia and in Fouta Djallon.—Annals and Magazine of Natural History, London, series 8, 8:117–124.

———. 1912. Mammals of the Panyam Plateau, northern Nigeria. II.—Annals and Magazine of Natural History, London, series 8, 9:269–274.

———. 1916. On the rats usually included in the genus *Arvicanthis*.—Annals and Magazine of Natural History, London, series 8, 18:67–70.

———, & M. A. C. Hinton. 1921. Captain Angus Buchanan's Aïr Expedition. II. On the mammals (other than ruminants) obtained during the expedition to Aïr (Asben).—Novitates Zoologicae 28:1–13.

———, & ———. 1923. On the mammals obtained in Darfur by the Lynes-Lowe Expedition.—Proceedings of the Zoological Society of London 1923:247–271.

Trouessart, E.-L. 1881. Catalogue des mammifères vivants et fossiles. Ordre des Rongeurs.—Bulletin de la Société d'Études Scientifiques d'Angers 10:58–212.

———. 1898–1899. Catalogus mammalium tam viventium quam fossilium. Volume 1. R. Friedländer & Sohn, Berlin, 664 pp.

———. 1904–1905. Catalogus mammalium tam viventium quam fossilium. R. Friedländer & Sohn, Berlin, 929 pp.

Van der Straeten, E. 1975. *Lemniscomys bellieri*, a new species of Muridae from the Ivory Coast (Mammalia, Muridae).—Revue de Zoologie Africaine 89:906–908.

———. 1976. *Lemniscomys striatus dieterleni*, a new subspecies of Muridae from Zaïre (Mammalia, Muridae).—Revue de Zoologie Africaine 90: 431–434.

———. 1980a. Etude biométrique de *Lemniscomys linulus* (Afrique Occidentale) (Mammalia, Muridae).—Revue de Zoologie Africaine 94:185–201.

———. 1980b. A new species of *Lemniscomys* (Muridae) from Zambia.—Annals of the Cape Provincial Museums, Natural History, 13:55–62.

———. 1981. Note sur *Lemniscomys striatus venustus* (Thomas, 1911).—Mammalia 45:125–128.

———, & B. Van der Straeten-Harrie. 1977. Étude de la biométrie crânienne et répartition d'*Apodemus sylvaticus* et d'*A. flavicollis* en Belgique.—Acta Zoologica et Pathologica Antwerpiensia 69:169–182.

———, & W. N. Verheyen. 1978. Karyological and morphological comparisons of *Lemniscomys striatus* (Linnaeus, 1758) and *Lemniscomys bellieri* Van der Straeten, 1975, from Ivory Coast (Mammalia:Muridae).—Bulletin of Carnegie Museum of Natural History 6:41–47.

———, & ———. 1979. Note sur la position systématique de *Lemniscomys macculus* (Thomas et Wroughton 1910) (Mammalia, Muridae).—Mammalia 43:377–389.

———, & ———. 1980. Relations biométriques dans le groupe spécifique *Lemniscomys striatus* (Mammalia, Muridae).—Mammalia 44:73–82.

Voss, R. S., & L. F. Marcus. 1992. Morphological evolution in muroid rodents II. Craniometric factor divergence in seven Neotropical genera, with experimental results from *Zygodontomys*.—Evolution 46:1918–1934.

Wilson, D. E., & D. M. Reeder (eds.). 1993. Mammal species of the World, a taxonomic and geographic reference, Second Edition. Smithsonian Institution Press, Washington D. C., 1206 pp.

Wroughton, R. C. 1906. On some mammals collected by Mr. Robin Kemp in S. Nigeria.—Annals and Magazine of Natural History, London, series 7, 17:375–379.

Yalden, D. W., M. J. Largen, D. Kock, & J. C. Hillman. 1996. Catalogue of the mammals of Ethiopia and Eritrea. 7. Revised checklist, zoogeography and conservation.—Tropical Zoology 9:73–164.

Appendix 1.—Geographic coordinates of principal collecting localities mapped in Figure 12. Coordinates are presented either as extracted from the country gazetteers published by the United States Board on Geographic Names (= *G*) or as they appear on original specimen tags and in field catalogs, as designated by the collector (= *C*). To verify the equivalence of older placenames and currently recognized coordinates, we generally cross-referenced the cartographic information provided by Aggundey & Schlitter (1984), Davis & Misonne (1964), Delany (1975), Happold (1987), Rosevear (1965), Setzer (1956), and Swynnerton & Hayman (1951) with that contained in the USBGN gazetteers. Where directional and distance modifiers are given following a comma, the collector's coordinates apply specifically to that point from the named village or town.

Algeria	
Alger	36°47′N, 03°03′E *G*
Hammam Meskoutine	36°27′N, 07°16′E *G*
Hammam Rirha	36°23′N, 02°24′E *G*
Oran	35°42′N, 00°38′E *G*
Reghaia	36°44′N, 03°21′E *G*
Benin	
Bimbereke	10°14′N, 02°40′E *C*
Diho	08°05′N, 02°31′E *C*
Guene	11°44′N, 03°13′E *C*
Kouande	10°20′N, 01°41′E *C*
Nikki	09°56′N, 03°13′E *C*
Porga	11°02′N, 00°58′E *C*
Segbana	10°56′N, 03°42′E *C*
Soubroukou	09°41′N, 01°38′E *C*
Zizonkame	07°55′N, 02°01′E *C*
Burkina Faso	
Arly	11°34′N, 01°26′E *C*
Boussouma, 5 mi N	12°57′N, 01°05′W *C*
Cella, 1 km N	11°38′N, 00°22′W *C*
Cella, 6 mi S	11°32′N, 00°22′W *C*
Djipologo	10°56′N, 03°07′W *C*
Fo	11°53′N, 04°31′W *C*
Koutoura, 5 km SW	10°19′N, 04°53′W *C*
Nasso	11°13′N, 04°26′W *G*
Natiaboani	11°42′N, 00°30′E *C*
Nayoure, 3 km SE	12°15′N, 00°16′E *C*
Niangoloko	10°17′N, 04°55′W *G*
Nobere, 9 mi S	11°26′N, 01°10′W *C*
Orodara, 27 km ENE	11°04′N, 04°41′W *C*
Ougarou	12°10′N, 00°56′E *C*
Oulo	11°54′N, 02°58′W *C*
Seguenega, 6 mi SE	13°24′N, 01°55′W *C*
Cameroun	
Boukma	08°32′N, 13°55′E *G*
Fort Foureau	12°05′N, 14°56′E *G*

Appendix 1.—Continued.

Garoua, 35 km S & 10 km E	09°06′N, 13°29′E *C*
Isiri	08°24′N, 14°36′E *G*
Kali	08°23′N, 14°21′E *G*
Koum	08°23′N, 14°31′E *G*
Maroua	10°35′N, 14°20′E *G*
Mora	11°03′N, 14°09′E *G*
Sir	10°36′N, 13°41′E *G*
Ghana	
Bangwon	10°58′N, 02°41′W *C*
Damango	09°04′N, 01°45′W *C*
Gambaga	10°31′N, 00°28′W *C*
Legon	05°40′N, 00°12′W *C*
Nabogo	09°45′N, 00°49′W *C*
Pirisi	10°07′N, 02°27′W *C*
Pulima	10°51′N, 02°03′W *C*
Sakpa	08°52′N, 02°21′W *C*
Shishe	10°42′N, 00°13′W *C*
Ivory Coast	
Bambela	09°37′N, 03°54′W *G*
Bouna	09°19′N, 02°53′W *G*
Kafiné	08°31′N, 05°19′W *G*
Kong	09°09′N, 04°37′W *C*
Ouangofetini	09°34′N, 04°03′W *G*
Tiebila (Tyébila)	09°45′N, 05°50′W *G*
Tyenko	08°14′N, 07°24′W *C*
Yama	09°36′N, 06°18′W *C*
Kenya	
Galma Galla	01°11′S, 40°47′E *G*
Kathekani	02°37′S, 38°09′E *C*
Kenya Karanzi	Not located
Kiboko	02°12′S, 37°42′E *C*
Kibwezi, 11 km N & 17 km E	02°19′S, 38°07′E *C*
Kilabasi	03°58′S, 38°57′E *G*
Lukenya Mountain	01°28′S, 37°03′E *G*
Machakos	01°31′S, 37°16′E *G*
Maktau (50 mi S)	03°24′S, 38°08′E *G*
Masi, Sand River	Not located
Maungu	03°33′S, 38°45′E *G*
Mtito Andei	02°41′S, 38°10′E *G*
Taveta	03°25′S, 37°42′E *G*
Voi	03°23′S, 38°34′E *G*
Mali	
Timbuktu (Timbouctou)	16°49′N, 02°59′W *G*
Morocco	
Agadir, 15 km E	30°24′N, 09°28′W *C*
Aoulouz, 16 km W	30°42′N, 08°18′W *C*
Cap Spartel, 3 km S	35°46′N, 05°55′W *C*
Enzel (Anzel)	33°13′N, 05°58′W *G*
Essaouira, 5 km NE	31°31′N, 09°46′W *C*

Appendix 1.—Continued.

Essaouira, 13 km E	31°30′N, 09°40′W *C*
Ifni	29°23′N, 10°10′W *G*
Marrakesh, 15 km WNW	31°53′N, 08°07′W ?
Meknès	33°54′N, 05°33′W *G*
Néfifik	33°43′N, 07°21′W *G*
Oued Cherrat	33°50′N, 07°07′W *G*
Oued Sebo	34°04′N, 04°56′W *C*
Oued Zem, 5 km S	32°49′N, 06°35′W *C*
Rabat, 15 km SW	33°57′N, 06°57′W *C*
Rabat, 17 km SW	33°55′N, 06°59′W *C*
Tamri, 8 km N	30°20′N, 09°50′W *C*
Taroudannt, 5 km S	30°26′N, 08°54′W *C*
Tiznit, 8 km S	29°38′N, 09°43′W *C*
Niger	
Farak	15°18′N, 08°55′E *G*
Gerari	13°46′N, 07°55′E *G*
Takoukout	15°07′N, 08°30′E *G*
Nigeria	
Bauchi	10°16′N, 09°50′E *G*
Borgu	09°52′N, 04°04′E *G*
Dada	11°34′N, 04°29′E *C*
Igbo Ora	07°26′N, 03°17′E *G*
Kabwir	09°24′N, 09°34′E *G*
Kishi	09°05′N, 03°51′E *G*
Mada River	08°54′N, 08°17′E *C*
Maiduguri, 22 mi S	11°33′N, 13°16′E *C*
New Bussa	09°53′N, 04°31′E *G*
Panyam	09°27′N, 09°09′E *G*
Panyam Fish Farm	09°27′N, 09°12′E *C*
Shagunu	10°21′N, 04°28′E *C*
Upper Ogun Ranch	08°09′N, 03°30′E *C*
Wawa	09°55′N, 04°27′E *G*
Yankari	09°45′N, 10°30′E *G*
Zaria	11°04′N, 07°42′E *G*
Senegal	
Bandia	14°37′N, 17°02′W *G*
Gemenjulla (Diénoundialla)	13°13′N, 13°07′W *G*
Kotiari Naoudé	13°54′N, 13°27′W *G*
Koussanar	13°52′N, 14°05′W *G*
Sudan	
Agur	11°35′N, 30°28′E *G*
Badigeru Swamp	05°20′N, 32°02 E *G*
Bahr el Derof	Not located
Bahr al Ghazal	07°46′N, 27°40′E *G*
Delami (Dalami)	11°52′N, 30°28′E *G*
Duk Majak	09°05′N, 27°51′E *G*
El Fasher (Al Fashir)	13°38′N, 25°21′E *G*
Fashoda	09°53′N, 32°07′E *G*
Gallabat (Qallabat)	12°58′N, 36°09′E *G*
Gondokoro	04°54′N, 31°40′E *G*

Appendix 1.—Continued.

Ikoto	04°06'N, 33°06'E *G*
Imurok	04°19'N, 32°24'E *G*
Juga Juga	13°48'N, 25°25'E *G*
Kadugli	11°00'N, 29°44'E *G*
Kaga Hills	13°50'N, 27°45'E *G*
Kudring	11°30'N, 30°06'E ?
Kuna	12°54'N, 32°31'E *G*
Li Rangu	04°43'N, 28°22'E *G*
Loa	03°48'N, 31°57'E *G*
Maridi	04°55'N, 29°28'E *G*
Molongori	04°10'N, 32°52'E *G*
Nimule	03°36'N, 32'03 E *G*
Nuba Mountains	10°40'N, 32°11'E *G*
Paloich	10°28'N, 32°32'E ?
Tadoro	10°41'N, 30°01'E *G*
Talodi (Talawdī)	10°38'N, 30°23'E *G*
Terrakekka (Terakeka)	05°26'N, 31°45'E *G*
Torit	04°24'N, 32°34'E *G*
Torit, 30 km W	Not plotted
Juba-Torit, 80 km E	Not plotted
Umm Kaddadah	13°36'N, 26°42'E *G*
Tanzania	
Banagi	02°16'S, 34°51'E *G*
Dodoma, 50 mi N	Not located
Jumbe Kadala (Ndala)	04°46'S, 33°16'E *G*
Manyara Lake	03°30'S, 35°50'E *G*
Mawere	Not located
Mdjengo's (Misinko)	04°45'S, 34°40'E *G*
Mtali's	04°22'S, 34°36'E *G*
Mwanza	02°31'S, 32°54'E *G*
Ndogowe	05°28'S, 34°22'E *G*
Pooma	04°59'S, 34°44'E *G*
Unyamwezi	04°–06°20'S, 32°–33°40'E *G*
Togo	
Dapango	10°52'N, 00°13'E *C*
Paio (Payo)	10°14'N, 00°41'E *C*
Pewa	09°17'N, 01°14'E *C*
Tunisia	
Algeriet	Not located
Cédria (Potinville)	36°42'N, 10°23'E *G*
La Marsa (Al Marsá)	36°53'N, 10°20'E *M*
Uganda	
Apeluk (Ajeluk)	01°30'N, 33°50'E *G*
Apoka	03°44'N, 33°43'E *C*
Kaiso Valley	01°31'N, 30°58'E *C*
Kananarock	03°58'N, 33°45'E *C*
Karamoja	03°43'N, 33°36'E *C*
Kidepo Valley Natl. Park	03°56'N, 33°42'E *G*
Loi Jome (Lotome)	02°24'N, 34°31'E *G*

Appendix 1.—Continued.

Lorengikipi	02°24'N, 33°54'E *G*
Lorupei	03°48'N, 33°40'E *C*
Malera	01°27'N, 34°03'E *G*
Nabilatuk	02°03'N, 34°35'E *G*
Nabumali	00°59'N, 34°13'E *G*
Rhino Camp	02°58'N, 31°24'E *G*
Tana River, near	00°08'N, 38°50'E *C*
Zaire	
Faradje	03°44'N, 29°43'E *G*
Niangara	03°42'N, 27°52'E *G*
Tingasi	03°24'N, 27°55'E *G*

Appendix 2.—Descriptive statistics for selected external and cranial variables and OTUs of the *Lemniscomys barbarus* group.

Species and OTU	*n*	Mean	Range	*SD*
Total length				
Lemniscomys barbarus				
OTU 1	37	238.2	211–266	12.6
OTU 2	15	251.8	193–273	19.4
Lemniscomys zebra				
OTU 4	23	218.2	196–236	10.9
OTU 5	27	211.6	192–232	9.5
OTU 7	47	204.8	172–230	13.7
OTU 10	17	203.3	170–231	14.5
OTU 11	12	212.3	196–230	9.3
Tail length				
Lemniscomys barbarus				
OTU 1	37	127.0	110–145	10.5
OTU 2	14	139.7	130–148	6.0
Lemniscomys zebra				
OTU 4	23	120.4	105–134	8.0
OTU 5	27	114.7	105–130	6.8
OTU 7	47	112.2	91–130	8.7
OTU 10	17	112.1	98–162	14.5
OTU 11	12	113.9	109–120	2.7
Hindfoot length				
Lemniscomys barbarus				
OTU 1	44	27.1	24–29	1.0
OTU 2	15	28.7	27–30	0.9
Lemniscomys zebra				
OTU 4	25	25.2	24–27	1.0
OTU 5	32	25.3	23–27	1.0
OTU 7	51	25.5	23–27	0.9
OTU 10	21	24.4	23–25	0.7
OTU 11	12	24.3	22–27	1.6
Weight				
Lemniscomys barbarus				
OTU 1	44	45.8	28–56	5.9
OTU 2	15	55.5	38–69	8.9
Lemniscomys zebra				
OTU 4	23	26.3	18–31	3.4
OTU 5	32	25.9	18–34	4.2
OTU 7	51	25.6	20–34	3.5
Occipitonasal length				
Lemniscomys barbarus				
OTU 1	44	30.1	28.3–32.3	0.9
OTU 2	14	31.2	30.0–31.2	0.6
Lemniscomys zebra				
OTU 4	22	27.8	26.1–29.1	0.8
OTU 5	25	27.7	26.1–29.3	0.9
OTU 7	51	27.2	25.9–29.1	0.8
OTU 10	12	27.1	25.7–28.6	1.1
OTU 11	12	27.9	26.4–29.1	0.8
Zygomatic breadth				
Lemniscomys barbarus				
OTU 1	43	14.2	13.6–15.1	0.4
OTU 2	14	14.7	13.7–15.7	0.5
Lemniscomys zebra				
OTU 4	22	12.7	11.9–13.4	0.4
OTU 5	25	12.7	11.8–13.9	0.4
OTU 7	51	13.0	12.2–13.8	0.4
OTU 10	12	12.6	11.7–13.3	0.5
OTU 11	12	13.3	12.6–14.1	0.5
Breadth of braincase				
Lemniscomys barbarus				
OTU 1	44	12.4	11.8–13.1	0.3
OTU 2	14	12.5	12.1–12.9	0.2
Lemniscomys zebra				
OTU 4	22	11.8	11.1–12.5	0.3
OTU 5	25	11.8	11.2–12.3	0.3
OTU 7	51	11.8	11.2–12.4	0.3
OTU 10	12	11.8	11.5–12.1	0.2
OTU 11	12	12.0	11.5–12.5	0.3
Interorbital breadth				
Lemniscomys barbarus				
OTU 1	44	4.7	4.4–5.1	0.2
OTU 2	14	4.9	4.5–5.3	0.2
Lemniscomys zebra				
OTU 4	22	4.5	4.0–4.9	0.2
OTU 5	25	4.5	4.1–4.8	0.2
OTU 7	51	4.3	4.0–4.8	0.2
OTU 10	12	4.3	4.1–4.6	0.2
OTU 11	12	4.3	3.9–4.5	0.2
Length of nasals				
Lemniscomys barbarus				
OTU 1	44	11.5	10.1–12.6	0.5
OTU 2	14	12.2	11.6–13.2	0.4
Lemniscomys zebra				
OTU 4	22	10.6	9.7–11.3	0.4
OTU 5	25	10.6	9.6–11.7	0.5
OTU 7	51	10.3	9.3–11.4	0.5
OTU 10	12	10.0	9.1–10.9	0.6
OTU 11	12	10.5	9.9–11.0	0.4
Postpalatal length				
Lemniscomys barbarus				
OTU 1	44	10.5	9.6–11.5	0.5
OTU 2	13	10.7	10.4–10.9	0.2

Appendix 2.—Continued.

Species and OTU	*n*	Mean	Range	SD
Lemniscomys zebra				
OTU 4	22	9.4	8.5–10.3	0.4
OTU 5	23	9.4	8.8–10.3	0.4
OTU 7	51	9.1	7.6–10.0	0.4
OTU 10	12	9.3	8.5–10.1	0.6
OTU 11	12	9.8	9.3–10.7	0.5
Length of incisive foramen				
Lemniscomys barbarus				
OTU 1	44	5.9	5.4–6.6	0.2
OTU 2	14	6.2	5.7–6.5	0.2
Lemniscomys zebra				
OTU 4	22	5.4	4.7–6.0	0.3
OTU 5	25	5.5	4.9–5.9	0.3
OTU 7	51	5.2	4.5–5.9	0.3
OTU 10	12	5.2	4.5–5.6	0.3
OTU 11	12	5.4	5.0–5.8	0.3
Length of diastema				
Lemniscomys barbarus				
OTU 1	44	7.4	6.7–8.2	0.3
OTU 2	14	7.8	7.3–8.3	0.3
Lemniscomys zebra				
OTU 4	22	6.5	6.0–7.2	0.3
OTU 5	25	6.6	6.0–7.4	0.3
OTU 7	51	6.3	5.8–7.0	0.3
OTU 10	12	6.4	5.8–6.9	0.3
OTU 11	12	6.6	5.9–7.1	0.4
Palatal breadth across M1s				
Lemniscomys barbarus				
OTU 1	44	6.2	5.9–6.6	0.2
OTU 2	15	6.2	5.9–6.5	0.2
Lemniscomys zebra				
OTU 4	22	5.8	5.5–6.3	0.2
OTU 5	25	5.8	5.5–6.3	0.2
OTU 7	51	5.8	5.3–6.2	0.2
OTU 10	12	5.6	5.2–5.9	0.2
OTU 11	12	5.7	5.3–5.9	0.2
Breadth of zygomatic plate				
Lemniscomys barbarus				
OTU 1	44	3.8	3.4–4.3	0.2
OTU 2	14	3.9	3.4–4.3	0.2
Lemniscomys zebra				
OTU 4	22	3.4	3.0–3.9	0.2
OTU 5	25	3.4	3.1–3.8	0.2
OTU 7	51	3.4	3.0–3.8	0.2
OTU 10	12	3.3	3.1–3.7	0.2
OTU 11	12	3.5	3.3–3.8	0.1

Appendix 2.—Continued.

Species and OTU	*n*	Mean	Range	*SD*
Alveolar length of maxillary toothrow				
Lemniscomys barbarus				
OTU 1	44	5.59	5.22–5.98	0.18
OTU 2	15	5.60	5.37–5.83	0.15
Lemniscomys zebra				
OTU 4	24	5.31	4.95–5.81	0.23
OTU 5	32	5.25	5.02–5.59	0.14
OTU 7	51	5.31	4.95–5.74	0.19
OTU 10	22	5.09	4.89–5.26	0.11
OTU 11	15	5.33	5.07–5.62	0.17
Width of first upper molar				
Lemniscomys barbarus				
OTU 1	44	1.73	1.61–1.86	0.06
OTU 2	15	1.74	1.68–1.83	0.05
Lemniscomys zebra				
OTU 4	25	1.66	1.54–1.82	0.07
OTU 5	32	1.68	1.57–1.82	0.07
OTU 7	51	1.71	1.54–1.84	0.07
OTU 10	22	1.61	1.48–1.73	0.06
OTU 11	15	1.68	1.56–1.80	0.05

OTU codes: 1, Morocco, Agadir Province; 2, Morocco, Khouribga and Rabat provinces; 4, northern Ivory Coast and western Burkina Faso; 5, Ghana and Togo; 7, Nigeria, Northern Region, Jos Plateau; 10, Sudan, Equatorial Province; 11, Kenya.

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A phylogenetic analysis of the southern pines (*Pinus* subsect. *Australes* Loudon): biogeographical and ecological implications

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Abstract.—A parsimony analysis on morphological characters was performed to estimate the phylogenetic relationships of the taxa of *Pinus* subsect. *Australes*. The Adams consensus tree placed the Caribbean species as a monophyletic clade with *P. rigida–P. serotina* as its sister taxon. Based on this phylogeny, area cladograms were constructed and compared to geologic cladograms constructed from plate-tectonic evidence. This comparison and an ancestral area analysis indicate that colonization of the tropics most likely occurred from Florida to Hispaniola, rather than by the circumferential-Gulf route. Subsequent dispersal events to Central America, Cuba, and the Bahamas are proposed to explain the geographic distribution of *P. caribaea*. Ecological comparisons within subsect. *Australes* found that sister species are not syntopic and that syntopic species are not sister species. Although some North American sister species are ecologically quite different, there is low ecological diversity among the Caribbean species.

Pinus is one of the most widespread genera of plants in the northern hemisphere (Mirov 1967:307–308; Strauss & Doerksen 1990). Its species are found from Central America and Sumatra to the Arctic circle (Little & Critchfield 1969, Strauss & Doerksen 1990, Farjon 1996), occupy xeric to mesic habitats, and comprise one of the dominant vegetation types on the earth. They are important economically, being used for fuel and lumber, and are frequently planted for commercial purposes in parts of the world where they do not naturally occur (Mirov 1967:451). While often considered early successional species well-adapted to poor soils (Govindaraju 1984), pines are actually ecologically diverse and are found from sea level to the timberline, from seasonally wet savannas to deserts, and from monotypic stands to multispecies climax forests where there is co-occurrence with hardwoods. McCune (1988) characterized the ecological diversity for North American pines and defined five ecological groups: (1) fire-resistant species, (2) mesophytic shade-tolerant species, (3) stress-tolerant species, (4) fire-resilient species, and (5) southern mesic species.

Other studies provide a more quantitative assessment of the interaction between pines and their environment. In particular, studies of bark ontogeny and fire have shown most pines to be particularly well adapted to surviving surface fires (Harmon 1984, D. C. Adams 1994). Recent work by Jackson and Adams demonstrates the evolution of negative bark allometry (D. C. Adams & Jackson 1995) in species whose habitats are characterized by frequent surface fires. This finding is consistent with models of defensive structure evolution, where resources are allocated earlier to defense as the likelihood of a mortality factor increases.

Although the ecological roles of pines are relatively well defined, aspects of the classification and systematics of the genus *Pinus* have been uncertain (Mirov 1967: 540, Strauss & Doerksen 1990). Shaw (1914) published the first major taxonomic work on pines, where he recognized two subgenera, *Strobus* and *Pinus*. Pilger (1926) presented a second classification of the pines, classifying many of Shaw's (1914) varieties as species and further dividing the subgenera into eleven sections. Because of his heavy reliance on needle number, however, Pilger's classification is considered to be a step backwards (Mirov 1967:526). Duffield (1952) revised the classification of the pines, using information from hybridization studies. He divided Shaw's "Group *Australes*" into two "Groups," the eastern species (XI) and the western species (XII). In Shaw's (1914) classification, most of the southern pines (*P. echinata*, *P. elliottii*, *P. glabra, P. palustris*, and *P. taeda*) as well as the Caribbean and many western species, were included in the "Group *Australes*". Duffield also added three species from Shaw's "Group *Insignes*" to his "Group XI": *P. rigida*, *P. serotina*, and *P. pungens*. Little & Critchfield (1969) reviewed the many classification schemes for *Pinus*. In particular, they restored the name *Australes*, at the subsectional rank, to Duffield's "Group XI," which now included the eight southern pines and three Caribbean species.

With the advent of phylogenetic methodology, many subsections of the genus *Pinus* have been reexamined in an evolutionary context, so that the relationships among many of the North American taxa are now better known (Wheeler et al. 1983, Strauss & Doerksen 1990, Malusa 1992, Govindaraju et al. 1992, Krupkin et al. 1996). The species comprising subsect. *Australes*, however, have not been examined in a phylogenetic context. In particular, it is of interest to determine whether the Caribbean taxa comprise a monophyletic clade and, if so, what its relationship is to the North American species. Mirov (1967:555) thought that insular varieties of *P. caribaea* originated from a Central American progenitor, but without a phylogenetic analysis he could not specify whether this was the original colonization of the Caribbean islands by subsect. *Australes* or was part of a subsequent radiation within the Caribbean region. Farjon (1996) on the other hand, suggested that the Caribbean taxa were of a North American origin, and that the Central American *P. caribaea* originated from Caribbean immigrants. Because of these outstanding questions, we felt that an examination of the relationships of the taxa in subsect. *Australes* was needed, and therefore performed a phylogenetic analysis of the southern pines using morphological characters. In addition, we generated an area cladogram for the geographic regions occupied by the taxa and compared this to geologic evidence in order to better understand the vicariance and dispersal of the taxa in the Caribbean.

Methods

Phylogenetic analysis.—The eight species of subsect. *Australes* in the eastern United States and certain geographically defined OTUs of the three Caribbean species were used in this study (Appendix I). *Pinus caribaea* from the Bahamas, Cuba, Belize, and Honduras-Nicaragua were treated as separate OTUs. Because *P. caribaea* in the uplands of Belize and Honduras may be subject to hybridization with *P. oocarpa* (Williams 1955) we used only specimens from lowland localities. *Pinus elliottii* var. *densa* was also treated as a separate OTU. The subsection *Australes* is included within the hard pines (subg. *Pinus*) as classified by Little & Critchfield (1969). While the relationships among the hard pines are still somewhat controversial (see Strauss & Doerksen 1990, Govindaraju et al. 1992), we chose to use two taxa (*P. virginiana* and *P. clausa*) from subsect. *Contortae* as out-

Table 1.—Data matrix for the taxa of *Pinus* used in this study. Descriptions of characters and character codes are found in Appendix II.

Species	Character states
P. caribaea—Bahamas	0000101011 1101311112 7
P. caribaea—Belize	0001111011 1101411111 8
P. caribaea—Cuba	0000111001 1100511111 9
P. caribaea—Honduras—Nicaragua	0001111011 1101411112 6
P. clausa	0010101110 3100100000 2
P. cubensis	0000111011 1111211014 7
P. echinata	0000011111 1100200000 2
P. elliottii var. *elliottii*	1000110011 1100211012 2
P. elliottii var. *densa*	1000111011 1100211013 3
P. glabra	0000011111 1100100000 2
P. occidentalis	0000101011 1101611113 3
P. palustris	1001100000 2000401113 0
P. pungens	1101100000 3100201005 0
P. rigida	0000111011 3100411102 1
P. serotina	0000111011 2101511102 0
P. taeda	1101100000 3100301100 4
P. virginiana	0010101110 3100101000 5

groups, based on the phylogenies of Govindaraju et al. (1992) and Farjon (1996).

Twenty one morphological characters were scored from herbarium specimens (LAF, MO, NY), with supplementary information from North American specimens collected by us and from literature sources (Farjon & Styles 1997, Radford et al. 1964); species were assigned values based on an average of several specimens. Fourteen characters were based on cone morphology and seven on needle morphology (Appendix II). Four of these characters were coded as ordered, multi-state characters (Table 1; Appendix II). Binary scoring was employed for the remainder. While recognizing that some of the characters are quantitative (Stevens 1996), we believe binary scoring adequately approximates character states among taxa where we have used it. We generated a phylogenetic hypothesis through Wagner parsimony using the branch and bound algorithm in PAUP version 3.1 (Swofford 1991). Wagner parsimony attempts to reconstruct an evolutionary tree by minimizing the number of changes of the character states along the tree (Kluge & Farris 1969, Strauss & Doerksen 1990). If one assumes that a species from a closely related group reflects previous character states, it can be used as an outgroup to root the tree and to polarize the character states as well (Wiley 1981).

Biogeographic analysis.—Comparing the current distributions of taxa with their phylogenetic history to elucidate patterns, as well as to evaluate the relative plausibilities of vicariance and dispersal, is the purpose of cladistic biogeography (Nelson & Platnick 1981, Wiley 1988, Morrone & Crisi 1995). To examine the biogeography of subsect. *Australes* in a phylogenetic context, we used the method outlined by Brooks & McLennan (1991). After the phylogenetic relationships were estimated, the geographic areas containing the taxa were defined: eastern North America (NA), the Bahamas (B), Cuba (Cb), Hispaniola (H), the Yucatan peninsula (Y), and Honduras-Nicaragua (Ch). The relationships of these geographic areas were then determined by representing the relationships of the taxa by a matrix containing additive binary codes, replacing the species with their respective geographic areas, and performing a parsimony analysis. Brooks Parsimony Analysis (BPA) has been criticized for its treatment of widespread taxa as synapomorphous for areas (Kluge 1988) and as a method for generating general area cladograms (Nelson & Ladiges 1991). Our goal was to evaluate alternative historical biogeographies rather than to produce a general area cladogram. Having treated the species population of each major Caribbean locale as an OTU, our data set did not, by definition, have widespread taxa, but there was a redundant distribution with two OTUs in Cuba. We chose to derive area cladograms by BPA with (inclusive ORing: Cressey et al. 1983) and without redundant distributions in order to evaluate the redundancy (Brooks 1990). The ancestral area of the Caribbean taxa was estimated by the technique of Bremer (1992). This involves comparing areas in regard to the numbers of necessary gains and losses in the area cladogram by Camin-Sokal parsimony and under the assumption that each area is ancestral. The putative ancestral area best supported by the biogeographic evidence is that having the highest ratio of gains to losses.

Phylogenetically-based cladograms are intended for comparison with geological area cladograms. Much work has been done on the biogeography of the Caribbean flora and fauna (e.g., Rosen 1976, 1978, 1985; Guyer & Savage 1986; Page & Lydeard 1994; Hedges et al. 1994). However, due to the complex geologic history of the region (see Pindell & Barrett 1990), many of the interpretations of biogeography are highly controversial and out of date. In light of the increased knowledge of Caribbean geology (Burke 1988, Pindell & Barrett 1990), we felt that using geologic cladograms from previous biogeographic work might be unwise. We therefore compared the area cladograms for subsect. *Australes* to geologic cladograms generated from recent tectonic evidence on the relationships of the geologic regions of the Caribbean.

Results

Phylogenetic analysis.—We found three most parsimonious trees from our cladistic analysis, each containing 81 steps and a consistency index (CI) of 0.469 (Fig. 1). When uninformative characters were excluded, the consistency index was reduced by only 0.010 to CI = 0.459, implying that most characters were phylogenetically informative. From these three most parsimonious trees we generated a consensus tree, using the procedure described by E. N. Adams (1972, 1986). This tree contains only that information present in all rival tree topologies, and is thus a conservative estimate of the true topology.

Based on this phylogeny, subsect. *Australes* is divided into several distinct subclades. The smaller subclade is a polytomy containing *P. taeda*, *P. pungens*, and *P. palustris*. A second polytomy is located deeper in the phylogeny and contains the smaller subclade, the larger subclade, and *P. echinata* and *P. glabra* as single taxa. The remaining taxa are all found within the larger subclade. That the phylogeny locates *P. rigida* and *P. serotina* as sister taxa accords with the proposal by Smouse and Saylor (1973), who consider them conspecific. The most significant aspect of this phylogeny is that the Caribbean species are monophyletic within the larger subclade.

Within the larger subclade, it is noteworthy that *P. elliottii* var. *densa* is the sister taxon to *P. elliottii* var. *elliottii*. Based on the chemical composition of its turpentine, Mirov et al. (1965) and Mirov (1967:555) proposed that *P. elliottii* var. *densa* was more closely related to the Caribbean species, and was a recent arrival to Florida. Our findings suggest that it is in fact more closely related to the mainland slash pine than to any Caribbean taxon. In addition, our phylogeny suggests that *P. cubensis* is more closely related to *P. caribaea* than to *P. occidentalis*, in contradiction to the proposal by Mirov (1967:232). Our findings place *P. occidentalis* basal to the Caribbean subclade.

Biogeographic analysis.—Much of the history of the Caribbean region is still unknown, as is evident from the numerous tectonic models of the region (Perfit & Williams 1989). However, the present study focuses on taxa in the Greater Antilles, the Bahamas, the Yucatan peninsula, and Honduras-Nicaragua, where there seems to be a general consensus of opinion concerning the geologic history. We therefore present a brief account of the geologic history of the region (summarized in Fig. 2) and use this to generate geologic cladograms for the taxa.

Mexico collided with the North American plate during the Jurassic (Burke 1988, Pindell & Barrett 1990). The Greater Antilles were part of a larger body called the Great Arc, which originated in the Pacific during the late Cretaceous and migrated northeast into the Atlantic in the Paleocene

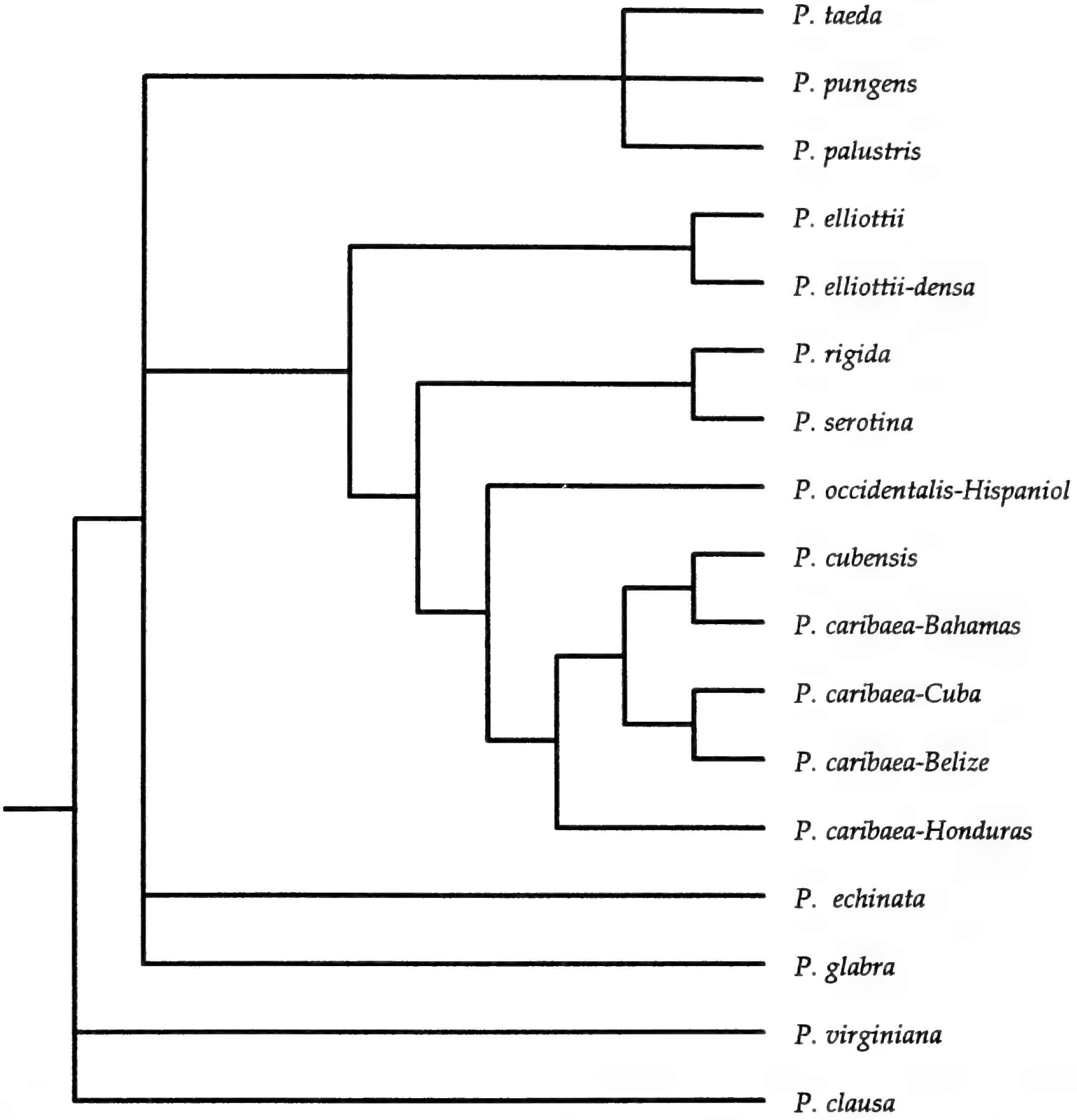

Fig. 1. Adams consensus tree found from three most parsimonious trees based on twenty-one morphological characters of *Pinus* spp.

(Burke 1988, Pindell & Barrett 1990). The Great Arc broke into three segments sometime in the late Cretaceous to early Paleocene (Burke 1988). The northern segment became the Greater Antilles, the central became the Lesser Antilles, and the southern segment is presumed to have collided with the South American continent.

During the late Paleocene, the Greater Antilles began to collide with the Bahaman plate (Pindell & Dewey 1982, Burke 1988, Pindell & Barrett 1990). However, Burke (1988) claims that prior to this, the Greater Antilles collided with the Yucatan. Others (Pindell & Barrett 1990) claim that although there is geologic evidence for such a collision, it cannot be determined whether it was the Greater Antilles or some other geologic body that collided with the Yucatan. Strike-slip faults began to separate Cuba and Hispaniola in the mid-Eocene (Pindell & Barrett 1990), and the Honduras-Nicaraguan block (called Chortis) began to collide with the Yucatan shortly after in the Miocene (Perfit & Williams 1989). Though Pindell and Barrett place this collision slightly earlier in the Oligocene, this does not affect our geologic cladograms. Based

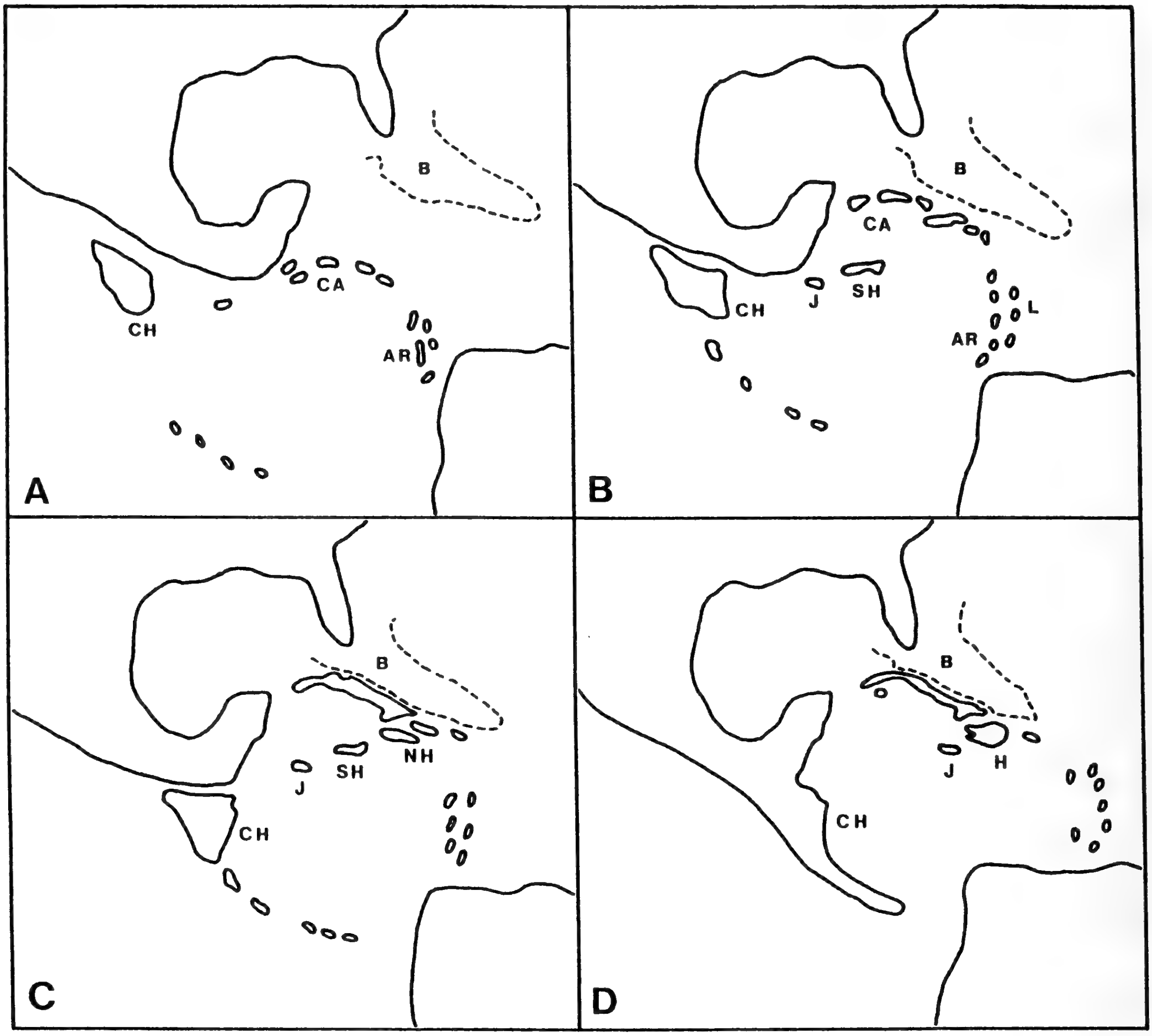

Fig. 2. Tertiary paleogeography of the Caribbean (redrawn from Perfit and Williams 1989). A. Late Cretaceous. B. Paleocene. C. Mid-Eocene. D. Late Miocene-Pliocene. AR = Aves Ridge, B = Bahaman Platform, CA = Cuban Arc, CH = Chortis, H = Hispaniola, J = Jamaica, L = Lesser Antilles Arc, NH = North Island of Hispaniola, SH = South Island of Hispaniola.

on this geologic information, we have constructed two area cladograms (Figs. 3a, b). The first (Fig. 3a) represents the relationships of the areas if the Yucatan had not collided with the Greater Antilles (*sensu* Pindell & Barrett 1990), and the second (Fig. 3b) if it had (*sensu* Burke 1988).

The taxon-based area cladogram derived with inclusive ORing has Hispaniola as the sister area to the other Caribbean areas and situates Cuba as the sister area to the Yucatan, in a derived position (Fig. 4a). The taxon-based area cladogram that treated Cuba as two separate areas historically (exclusive ORing) has a pattern of branching identical to that of the taxon cladogram, but with Cuba as a sister area to both the Yucatan and the Bahamas (Fig. 4b). The ancestral area analysis (AAA) of Bremer (1992) was carried out in two ways: on an area cladogram with terminal sister taxa not grouped, which corresponds to Fig. 4b; and on an area cladogram that considered there to be no node separating the two OTUs of *P. caribaea* of Cuba and Belize. The logic of combining the areas of the terminal sister

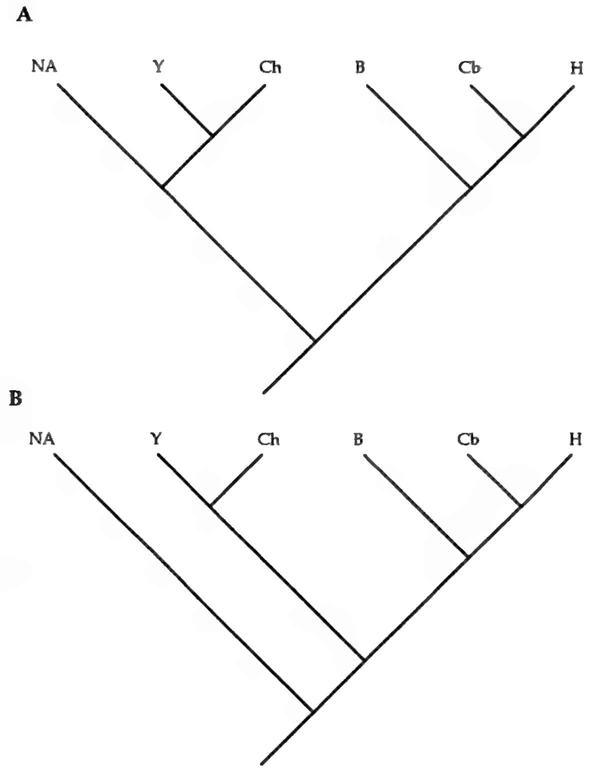

Fig. 3. Geologic cladograms based on tectonic evolution in the Caribbean. (A) corresponds to hypothesis of Pindell and Barrett (1990), where the Yucatan did not collide with the Greater Antilles; (B) corresponds to Burke's (1988) hypothesis, which includes this collision.

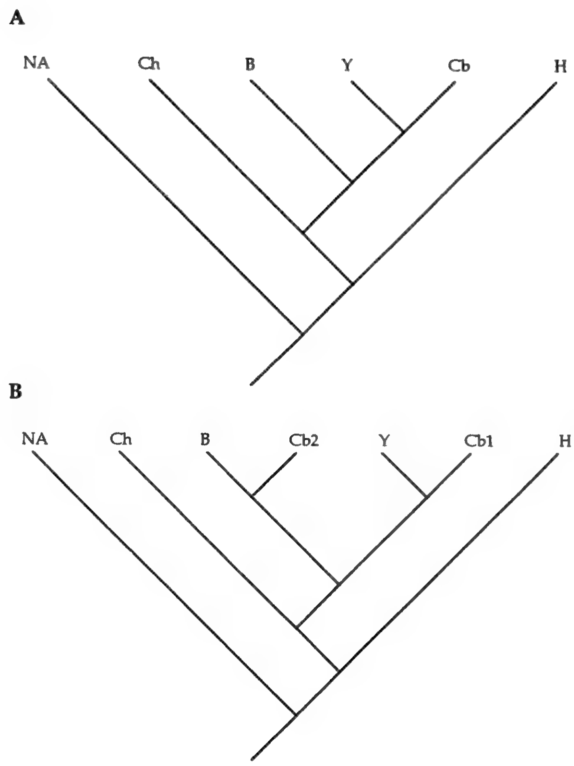

Fig. 4. Area cladograms of six geographic localities based on the phylogeny for *Pinus* subsect. *Australes* using: (A) inclusive ORing, and (B) exclusive ORing. Letters correspond to the different geographic regions: NA = southern United States, Ch = Chortis, B = Bahamas, Y = Yucatan, Cb = Cuba, H = Hispaniola.

taxa from this node is that the taxa are conspecific. For both approaches to AAA, Hispaniola is the most probable ancestral area, and Cuba is the next most probable (Table 2).

The positions of Yucatan-Chortis and Hispaniola differ between the geological and taxon-based area cladograms (Figs. 3 and 4). In the geological area cladograms, Yucatan-Chortis is either the sister area to North America or the basal area in the Caribbean, whereas the taxon-based area cladograms have Yucatan-Chortis separated and both in more derived positions. Hispaniola is placed near the origin of the Caribbean subclade by the taxon-based area cladogram, but in a derived position by the geological data. We conclude that the cladogram based on geological contact and separation corresponds poorly to the sequence of areas colonized by the Caribbean taxa of subsect. *Australes*.

The derived placement of Cuba in the taxon-based area cladogram calculated by inclusive ORing is due to there being two derived taxa (*P. cubensis* and *P. caribaea*) on Cuba that determine the location of Cuba on the area cladogram (Brooks &

Table 2.—Estimation of ancestral area for the Caribbean subclade of the subsection *Australes*. Values not in parentheses are for cladogram that reduces conspecific sister taxa. Values in parentheses are for cladogram without reduction of conspecific sister taxa. G = number of necessary gains under forward Camin-Sokal parsimony. L = number of necessary losses under reverse Camin-Sokal parsimony. AA = G/L rescaled by division by the largest G/L. $\overline{AA}$ = mean of AA's calculated by the two reduction alternatives.

Area	G	L	G/L	AA	$\overline{AA}$
Hispaniola	1 (1)	1 (1)	1.00 (1.00)	1.00 (1.00)	1.00
Cuba	2 (2)	3 (4)	0.67 (0.50)	0.67 (0.50)	0.59
Chortis	1 (1)	2 (2)	0.50 (0.50)	0.50 (0.50)	0.50
Yucatan	1 (1)	3 (4)	0.33 (0.25)	0.33 (0.25)	0.29
Bahamas	1 (1)	4 (4)	0.25 (0.25)	0.25 (0.25)	0.25

McLennan 1991:212). The presence of derived taxa and the lack of ancestral taxa on Cuba can be explained through intra-Cuban differentiation combined with colonization of other Caribbean areas from Cuba. The AAA clearly supports this explanation.

Discussion

Based on our phylogenetic hypothesis of the southern pines, several ecoevolutionary trends can be recognized. First, sister species are not syntopic. For example, the sister clades of *P. rigida* and *P. serotina* as well as *P. cubensis* and *P. caribaea* represent taxa that are allopatric. *Pinus pungens* and *P. palustris* are allopatric as well and occupy different habitats. Second, species that are syntopic are not sister species. Examples of this are *P. palustris* and *P. elliottii* in the eastern Gulf coastal plain flatwoods, *P. palustris* and *P. echinata* in the uplands of the western Gulf coastal plain, and *P. taeda* and *P. echinata* in the southern Piedmont.

Major ecological divergence is found between some sister species. For example, *P. pungens* grows in dense monospecific stands in xeric montane locations and maintains dominance by mass recruitment after stand-replacing crown fires; its bark grows with positive allometry (Adams 1994). In comparison, *P. palustris* grows as widely spaced individuals in parkland vegetation subject to frequent surface fires, and early life history stages of this species are fire-resistant (McCune 1988), as typified by its "grass" stage and negative allometry of bark. Curiously, there is a general lack of ecological divergence in the Caribbean subclade of subsect. *Australes* (Smith 1954). This subclade is less diverse in that there are no mountain ridge specialists like *P. pungens*, there are no shade-tolerant species like *P. glabra*, and there are no species with a fire-resistant seedling stage like *P. palustris* or *P. elliottii* var. *densa*.

The purpose of cladistic biogeography is to attempt to discern whether current distribution patterns are the result of vicariance or dispersal. In subsect. *Australes* this issue is related to whether the initial colonization of Caribbean islands was from eastern North America or from Central America. Both the ancestral area analysis and the fact that neither Yucatan nor Chortis branch low on the area cladogram suggest that the Greater Antilles were the first sites of colonization in the Caribbean. This could have occurred by dispersal from North America in the late-Tertiary or Quaternary, or by vicariance from Central America if a component of Hispaniola collided with, and then separated from, Yucatan during the Paleocene (Burke 1988). The issue is one of timing and therefore cannot be decided conclusively without molecular data on the divergence time between North American and Caribbean taxa. However, several facts argue in favor of dispersal to Hispaniola. For example, there is no evidence in Central America of a Caribbean ancestor; *P. caribaea* cannot play this role given its derived status. The Caribbean subclade was derived from an ancestor that shared many traits, particularly of cones, with *P. serotina.* Currently *P. serotina* has an Atlantic-East Gulf Coastal Plain distribution, not being found west of Mobile Bay. This puts *P. serotina* geographically closer to the late-Tertiary Greater Antilles than to the putative contact between the Yucatan and the proto-Greater Antilles. In addition, the lack of ecological diversification in the Caribbean clade could suggest an occupation of the region too recent to have occurred via Paleocene vicariance. Farjon (1996) found that *P. occidentalis* and *P. caribaea* var. *hondurensis* formed a sister group to all the other neotropical pines he considered, a result consistent with derivation from a southeastern North American ancestor.

Dispersal of *Australes* to the Greater Antilles may have been part of a pattern of colonization by xeric-adapted biota. R. P. Adams (1989) presented evidence from leaf morphology and volatile leaf oils that strongly indicates an origin of West Indian

Juniperus species from eastern North America, rather than from Mexico. Buck (1990) suggested that several xeric bryophyte species found in North America and upland Hispaniola colonized the island via dispersal during glacial episodes of the Pleistocene when over-water distances were less due to lower sea levels (Gascoyne et al. 1979) and when savanna habitats were more widespread than at present because of a more xeric climate (Pregill & Olson 1981). Such a scenario could apply to colonization of the Greater Antilles by subsect. *Australes* as well as to inter-island movement and colonization of Central America.

Mirov (1967:555) hypothesized that *P. caribaea* colonized the Caribbean islands from Central America. The area cladogram, with Chortis as the sister area to all other areas occupied by *P. caribaea*, supports this direction of colonization in the species. Dispersal is implicated because no connection is known to have existed between Chortis and the Greater Antilles. The only possibility of vicariance within the *P. caribaea* clade would be between the taxonomic subunits in Cuba and Yucatan. However, any such vicariance would date from early Tertiary (Burke 1988), and this appears too longstanding for the small level of differentiation between the taxa. It is difficult to ascribe any of the divergences within the Caribbean subclade to vicariance.

It was believed by Mirov et al. (1965) that *P. elliottii* var. *densa* was a recent immigrant to Florida from the Caribbean and that it was therefore more closely related to the Caribbean species. Our results place *P. elliottii* var. *densa* as the sister taxon to *P. elliottii* var. *elliottii*, suggesting that it is more closely related to the mainland species. Squillace (1966) demonstrated multicharacter clinal variation between *P. elliottii* var. *elliottii* and *P. elliottii* var. *densa* in central Florida. We also found that *P. cubensis* is more closely related to *P. caribaea* than to *P. occidentalis*. Mirov (1967:232) had proposed that *P. cubensis* and *P. occidentalis* were closely related taxa. Clearly more work is needed to determine their relationship.

Klaus (1980) suggested that, for comparisons through nodes deep within the phylogeny of *Pinus*, cones display primitive character states at the apex and derived states at the base. Consideration of intracone character variation in the context of the subsect. *Australes* cladogram provides evidence of this phenomenon at a finer phylogenetic scale. *Pinus glabra*, *P. elliottii*, and *P. rigida* often have flattened, distally-pointed umbos at the cone base and more erect umbos at the apex. Within the cladogram, erect umbos characterize the outgroup and the *P. taeda*-*P. pungens*-*P. palustris* subclade, whereas flattened umbos are typical in *P. serotina* and the Caribbean subclade. In *P. caribaea* var. *hondurensis,* the umbo spine tends to be unconnected to the keel on basal scales, a character state more widespread in *P. cubensis* cones, but connected to the keel on apical scales, a state found throughout the cone in taxa derived from nodes below *P. caribaea* var. *hondurensis.* A counterexample, however, exists in the relatively erect umbos apically in some *P. caribaea* var. *hondurensis.* This character state is derived if the Caribbean clade arose through an ancestor like *P. occidentalis,* yet it appears at the apex.

Our phylogenetic hypothesis of subsect. *Australes* is a first step in understanding the history of the pines of the southern United States and the Caribbean. Based on this phylogeny, we have identified possible dispersal and vicariance events and have provided a framework on which future studies may be based. While it is appealing to interpret phylogenetic hypotheses as reconstructions of evolutionary history, it must be stressed that they are only estimations of the true topology based on the available data. Studies have shown that most phylogenetic methods can perform rather poorly in their estimation of true tree topology (Fiala & Sokal 1985; Rohlf et al. 1990). We therefore present this phylogenetic hypothesis as a tentative estimation of the relationships of the southern pines.

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Literature Cited

Adams, D. C. 1994. Defensive structures in the genus *Pinus*: heterochronic changes in bark ontogeny. Unpublished M.S. Thesis, University of Southwestern Louisiana, Lafayette, 83 pp.

———, & J. F. Jackson. 1995. Estimating the allometry of tree bark.—American Midland Naturalist 134:99–106.

Adams, E. N. III. 1972. Consensus techniques and the comparison of taxonomic trees.—Systematic Zoology 21:390–397.

———. 1986. N-trees as nestings: complexity, similarity, and consensus.—Journal of Classification 3:299–317.

Adams, R. P. 1989. Biogeography and evolution of the junipers of the West Indies. Pp. 167–190 *in* C. A. Woods, ed., Biogeography of the West Indies: past, present, and future. Sandhill Crane Press, Gainesville, Florida, 878 pp.

Bremer, K. 1992. Ancestral areas: a cladistic reinterpretation of the center of origin concept.—Systematic Biology 41:436–445.

Brooks, D. R. 1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update.—Systematic Zoology 39:14–30.

———, & D. A. McLennan. 1991. Phylogeny, ecology, and behavior. University of Chicago Press, Chicago, 434 pp.

Buck, W. R. 1990. Biogeography of the Greater Antillean mosses.—Tropical Bryology 2:35–48.

Burke, K. 1988. Tectonic evolution of the Caribbean.—Annual Review of Earth Planetary Sciences 16:201–230.

Cressey, R. F., B. Collette, & J. Russo. 1983. Copepods and scombrid fishes: a study in host-parasite relationships.—Fishery Bullettin 81:227–265.

Duffield, J. W. 1952. Relationships and species hybridization in the genus *Pinus*.—Silvae Genetica 1:93–97.

Farjon, A. 1996. Biodiversity of *Pinus* (Pinaceae) in Mexico: speciation and palaeo-endemism.—Botanical Journal of the Linnean Society 121: 365–384.

———, & B. T. Styles. 1997. *Pinus*. Flora Neotropica Monograph. New York Botanical Garden, New York. (in press).

Fiala, K. L., & R. R. Sokal. 1985. Factors determining the accuracy of cladogram estimation: evaluation using computer simulation.—Evolution 39: 609–622.

Gascoyne, M., G. J. Benjamin, & H. P. Schwarz. 1979. Sea-level lowering during the Illinoian glaciation: evidence from a Bahama "blue hole."—Science 205:806–808.

Govindaraju, D. R. 1984. Mode of colonization and patterns of life history in some North American conifers.—Oikos 43:271–276.

———, P. Lewis, & C. Cullis. 1992. Phylogenetic analysis of pines using ribosomal DNA restriction fragment length polymorphisms.—Plant Systematics and Evolution 179:141–153.

Guyer, C., & J. M. Savage. 1986. Cladistic relationships among anoles (*Sauria*: *Iguanidae*).—Systematic Zoology 35:509–531.

Harmon, M. E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park.—Ecology 65:796–802.

Hedges, S. B., C. A. Hass, & L. R. Maxson. 1994. Reply: towards a biogeography of the Caribbean.—Cladistics 10:43–55.

Klaus, W. 1980. Neue beobachtungen zur morphologe des Zapfens von Pinus.—Plant Systematics and Evolution 134:137–171.

Kluge, A. G. 1988. Parsimony in vicariance biogeography: a quantitative method and a Greater Antillean example.—Systematic Zoology 37: 315–328.

———, & J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans.—Systematic Zoology 18:1–32.

Krupkin, A. B., A. Liston, & S. H. Strauss. 1996. Phylogenetic analysis of the hard pines (*Pinus* subgenus *Pinus*, Pinaceae) from chloroplast DNA restriction site analysis.—American Journal of Botany 83:489–498.

Little, E. L., & W. B. Critchfield. 1969. Subdivisions of the genus *Pinus*. U.S. Department of Agriculture Miscellaneous Publication Number 1144, Washington, D. C., 51 pp.

McCune, B. 1988. Ecological diversity in North American pines.—American Journal of Botany 75:353–368.

Malusa, J. 1992. Phylogeny and biogeography of the pinyon pines (*Pinus* subsect. *Cembroides*).—Systematic Botany 17:42–66.

Mirov, N. T. 1967. The genus *Pinus*. Ronald Press, New York, 602 pp.

———, E. Frank, & E. Zavarin. 1965. Chemical composition of *P. elliottii* var. *elliottii* turpentine and its possible relation to taxonomy of several pine species.—Phytochemistry 4:563–568.

Morrone, J. J., & J. V. Crisci. 1995. Historical biogeography: introduction to methods.—Annual Review of Ecology and Systematics. 26:373–401.

Nelson, G., & N. I. Platnick. 1981. Systematics and biogeography; cladistics and vicariance. Columbia University Press, New York, 567 pp.

———, & P. Y. Ladiges. 1991. Three-area statements: standard assumptions for biogeographic analysis.—Systematic Zoology 40:470–485.

Page, R. D. M., & C. Lydeard. 1994. Towards a cladistic biogeography of the Caribbean.—Cladistics 10:21–41.

Perfit, M. R., & E. E. Williams. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean sea and its islands. Pp. 47–102 *in* C. A. Woods, ed., Biogeography of the West Indies: past, present, and future. Sandhill Crane Press, Gainesville, Florida, 878 pp.

Pilger, R. 1926. Genus *Pinus*. Pp. 271-342 *in* A. Engler & K. Prantl, eds., Die natürlichen Planzenfamilien. Vol. XIII. Gymnospermae, Wilhelm Engelmann, Leipzig.

Pindell, J., & S. F. Barrett. 1990. Geological evolution of the Caribbean region; a plate-tectonic perspective. Pp. 405–432 *in* G. Dengo & J. E. Case, eds., The geology of North America. Volume H, the Caribbean region. The Geological Society of America Press, Boulder, 528 pp.

———, & J. F. Dewey. 1982. Permo-Triassic reconstruction of western Pangea and the evolution of the gulf of Mexico/Caribbean region.—Tectonics 1:179–211.

Pregill, G. K., & S. L. Olson. 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles.—Annual Review of Ecology and Systematics. 12:75–98.

Radford, A. C., H. E. Ahles, & C. R. Bell. 1964. Manual of the vascular flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill, 1183 pp.

Rohlf, F. J., W. S. Chang, R. R. Sokal, & J. Kim. 1990. Accuracy of estimated phylogenies: effects of tree topology and evolutionary model.—Evolution 44:1671–1684.

Rosen, D. R. 1976. A vicariance model of Caribbean biogeography.—Systematic Zoology 24:431–464.

———. 1978. Vicariant patterns and historical explanation in biogeography.—Systematic Zoology 27:159–188.

———. 1985. Geological hierarchies and biogeographic congruence in the Caribbean.—Annals of the Missouri Botanical Garden 72:636–659.

Shaw, G. R. 1914. The genus *Pinus*.—Journal of the Arnold Arboretum 5:1–96.

Smith, E. E. 1954. The forests of Cuba. Maria Moors Cabot Foundation Publication No. 2, Cambridge, Mass.

Smouse, P. E., & L. C. Saylor. 1973. Studies of the *Pinus rigida-serotina* complex. I. A study of geographic variation.—Annals of the Missouri Botanical Garden 60:174–191.

Squillace, A. E. 1966. Geographic variation in slash pine.—Forest Science Monograph 10.

Stevens, P. F. 1996. On phylogenies and data bases—where are the data, or are there any?—Taxon 45:95–98.

Strauss, S. H., & A. H. Doerksen. 1990. Restriction fragment analysis of pine phylogeny.—Evolution 44:1081–1096.

Swofford, D. L. 1991. PAUP-Phylogenetic Analysis Using Parsimony. Version 3.0. Illinois Natural History Survey, Champaign.

Wheeler, N. C., R. P. Guries, & D. M. O'Malley. 1983. Biosystematics of the genus *Pinus*, subsection *Contortae*.—Biochemical Systematics and Ecology 11:333–340.

Wiley, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. Wiley, New York, 439 pp.

———. 1988. Vicariance biogeography.—Annual Review of Ecology and Systematics 19:513–542.

Williams, L. 1955. *Pinus caribaea*.—Ceiba 4:299–300.

Appendix I

Herbarium specimens from which characters were scored.

Pinus caribaea Morelet var. *bahamensis* Barrett and Golfari. BAHAMAS. Grand Caicos: Correll 49463 (NY). New Providence: Degener 18753 (NY). *P. caribaea* var. *caribaea* Barrett & Golfari. CUBA. Pinar del Rio: Jack 8673 (NY), Leon & Charles 4935 (NY). *P. caribaea* var. *hondurensis* B. & G. BELIZE. Belize: Croat 24005 (MO), Kluge s.n. (MO). Corozal: Crane 315 (MO). Orange Walk: Lundell 677 (MO). Stann Creek: Stevenson 1128 (MO). Toledo: Gentle 3690 (MO). HONDURAS. Gracias a Dios: Clewell 4511 (MO), Nelson & Hernandez 1004 (MO). NICARAGUA. Zelaya: Marshall & Neill 6559 (MO), Seymour 3650 (MO), Stevens 7638 (MO), Stevens 7753 (MO), Stevens 21679 (MO), Vincelli 625 (MO). *P. clausa* (Chapm.) Vasey. USA. Florida: Franklin Co., Godfrey 69282 (LAF); Polk Co., Shuey 2317 (LAF); Walton

Co., Smith 2071 (LAF). *P. cubensis* Griseb. CUBA. Oriente: Ekman 3829 (NY), Shafer 4174 (NY). *P. echinata* Mill. USA. Louisiana: Bienville Par., Thieret 16836 (LAF), Westling 141 (LAF); Evangeline Par., Reese & Reese 1537 (LAF), Thieret 22256 (LAF); St. Helena Par., Allen 1499 (LAF). *P. elliottii* Engelm. var. *densa* Little & Dorman. USA. Florida: Dade Co., Small & Carter 1249 (NY); Monroe Co., Brizicky & Stern 378 (NY). *P. elliottii* var. *elliottii* L. & D. USA. Louisiana: Lafayette Par., Thieret 17423 (LAF); St. Tammany Par., Thieret 16770 (LAF), Thieret 21879 (LAF); Tangipahoa Par., Thieret 16758 (LAF). *P. glabra* Walt. USA. Louisiana: Livingstone Par., Thieret 16743 (LAF); St. Helena Par., Allen 1500 (LAF), St. Tammany Par., Lynch 940 (LAF); Washington Par., Thieret 16782 (LAF). *P. occidentalis* Swartz. DOMINICAN REPUBLIC. Zanoni, Mejia, Pimentel & Garcia 32443 (NY). HAITI. Nash 825 (NY). *P. palustris* Mill. USA. Louisiana: Allen Par., Thieret 10389 (LAF);-Beauregard Par., Thieret 16968 (LAF); Nachitoches Par., Thieret 16811 (LAF), Thieret 17035 (LAF); St. Helena Par., Thieret 17298 (LAF); Tangipahoa Par., Thieret 16782 (LAF); Winn Par., Thieret 16817 (LAF). *P. pungens* Lamb. USA. Pennsylvania: Franklin Co., Adams s.n. (LAF), Adams 25 (LAF). *P. rigida* Mill. CANADA. Quebec: Lemieux 1281 (LAF). USA. Maryland: Frederick Co., Windler & Stastny 3900 (LAF). North Carolina: Buncombe Co., Dunton s.n. (LAF); Jackson Co., Duncan 22793 (LAF). Pennsylvania: Franklin Co., Adams s.n. (LAF). West Virginia: Hardy Co., Wratchford s.n. (LAF). *P. serotina* Michx. USA. Alabama: Geneva Co., Kral 33947 (LAF). Georgia: McIntosh Co., Duncan 20688 (LAF). South Carolina: Charleston Co., Ahles 53156 (LAF), *P. taeda* L. USA. Louisiana: Livingston Par., Thieret 16742 (LAF) Thieret 16753 (LAF), Thieret 16754 (LAF); St. Helena Par., Thieret 17300 (LAF); Tangipahoa Par., Thieret 16756 (LAF). *P. virginiana* Mill. USA. Alabama: DeKalb Co., Vincent 1281 (LAF). Georgia: Rabun Co., Reade s.n. (LAF). Maryland: Allegany Co., Duncan 22944 (LAF). North Carolina: Orange Co., Ahles 53117 (LAF). Tennessee: Cheatham Co., Demaree 49183 (LAF).

Appendix II

Twenty-one morphological characters used in this study. The first fourteen characters describe mature megasporangiate cone morphology and the last seven describe needle morphology.

(1) Sum of maximum cone length and maximum cone width: less than 20 cm = 0; greater than 20 cm = 1.
(2) Cones subsessile or stalked = 0; sessile = 1.
(3) Transverse keel or dorsal surface of cone scale between apophysis and umbo: depressed at junction = 0; continuous at junction = 1.
(4) Lateral portion of most umbos not strongly elevated above apophysis = 0; strongly elevated above apophysis = 1.
(5) Umbo: weakly keeled or unkeeled = 0; strongly keeled = 1.
(6) Umbo keel: straight or monotypically curved = 0; undulating = 1.
(7) Proximal portion of umbo slopes at: high angle or is perpendicular to apophysis surface = 0; low angle from spine to proximal edge of umbo = 1.
(8) Proximal portion of umbo: not concave = 0; concave = 1.
(9) Portion of umbo proximal to keel: not larger than distal portion = 0; much larger than distal portion = 1.
(10) Junction of distal margin of umbo and apophysis: grooved = 0; not grooved = 1.
(11) Spine on umbo: unkeeled on apical half = 1; keeled on part of apical half but unkeeled at apex = 2; keeled on all of apical half = 3.
(12) Spine on umbo: reflexed = 0; straight or curved outward = 1.
(13) Spine: connected to keel = 0; substantially distal to keel = 1.
(14) Most umbos erect such that apex of spine is not pointed distally near the level of the apophyseal keel = 0; most umbos flattened and turned distally such that apex of spine is pointed distally near the level of the apophyseal keel = 1.
(15) Needle number: 2 = 1; 2(−3) = 2; 3(−2) = 3; 3 = 4; 3(−4) = 5; 3−5 = 6.
(16) Hypodermal cells in leaf angles: absent = 0; present = 1.
(17) Hypodermis structure: uniform = 0; biform = 1.
(18) Endodermal cells: walls normal = 0; walls thickened = 1.
(19) Resin canals medial = 0; internal = 1.
(20) Number of resin canals: coded character.
(21) Number of stomata: coded character.

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