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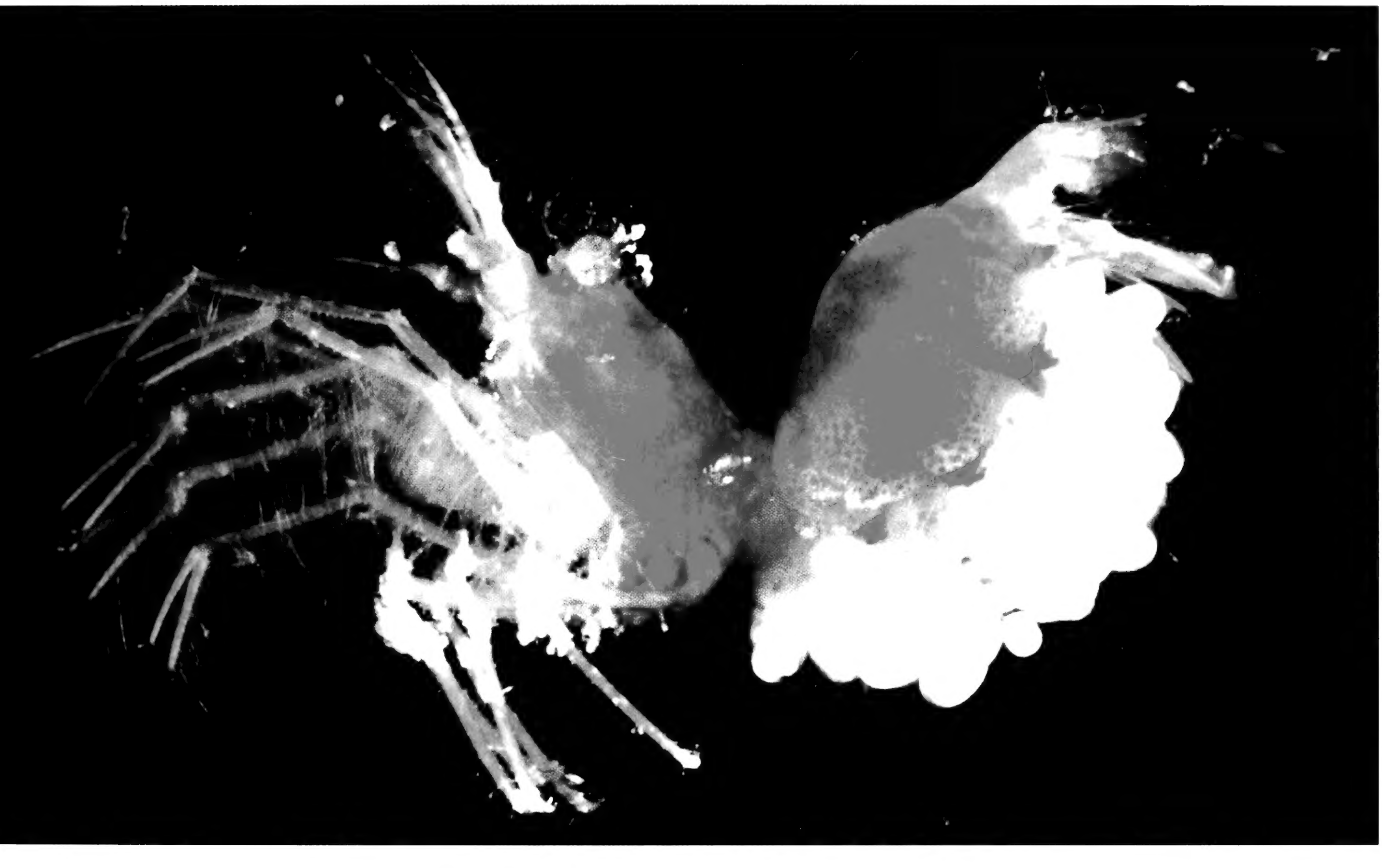

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Austin Beatty Williams (17 October 1919–27 October 1999). Biographical summary

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Abstract.—The professional career and aspects of the life of Austin Beatty Williams (17 October 1919–27 October 1999), Systematic Zoologist for the Systematics Laboratory of the U.S. National Marine Fisheries, are summarized. Included is a bibliography with the 118 papers published by Williams, and a list of all the new names he proposed along with the holotype repository and catalogue number of species and subspecies.

Austin B. Williams (Fig. 1) was Systematic Zoologist at the Systematics Laboratory, National Marine Fisheries Service (NMFS), based at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. After a valiant fight with cancer, Austin passed away at his home in Falls Church, Virginia. Shortly after his death, the Council of the *Biological Society of Washington* unanimously voted to dedicate this issue, the first of the new millenium, to his memory. This dedication is most fitting as Austin generously served the *Society* in many capacities during the last quarter of the 20th century, and gave luster to the *Proceedings* by using it to publish many of his important papers. He served the *Society* as a Editor of the *Proceedings* (1974–1977), Vice-president (1983–1986), President (1986–1988), Past-President (1989–1999), Custodian of Publications (1989–1995), and contributed significantly to its financial soundness as a member of the Finance Committee (1995–1999). He was editor of *Bulletin No. 3:* "Symposium on the Composition and Evolution of Crustaceans in the Cold and Temperate Waters of the World Oceans" (1979), based on the results of a U.S.-U.S.S.R. Cooperative Program. He also provided the summary chapter for *Bulletin No. 6:* "The hydrothermal vents of the eastern Pacific: An overview" (Williams 1985b).

Austin had a distinguished career spanning five decades during which he published 118 papers (see bibliography). Born in Plattsburg, Missouri in 1919, he was the first child of Oliver Perry Williams and Lucy Sell; his siblings are brothers Hillis and Oliver. He married Jean McNicol with whom he had their only child, David (married to Anita Kyle, with two children, Lauren and Kyle). His family had only modest means so he had to work to support his education, first at McPherson College (A.B. 1943), and then at the University of Kansas (Ph.D. 1951), where he studied Ozark crayfishes. His studies on these crayfishes remain among the key references to identify these decapods in the region. From 1951 to 1955 he was with the University of North Carolina Institute of Fisheries Research, studying the life history and ecology of penaeid shrimps. He then worked at the University of Illinois from 1956 to 1963, after which he returned to the North Carolina Institute of Fisheries Research to continue his studies on marine and estuarine decapods. In the mid 1960s, Donald F. Squires, Chairman of the Department of In-

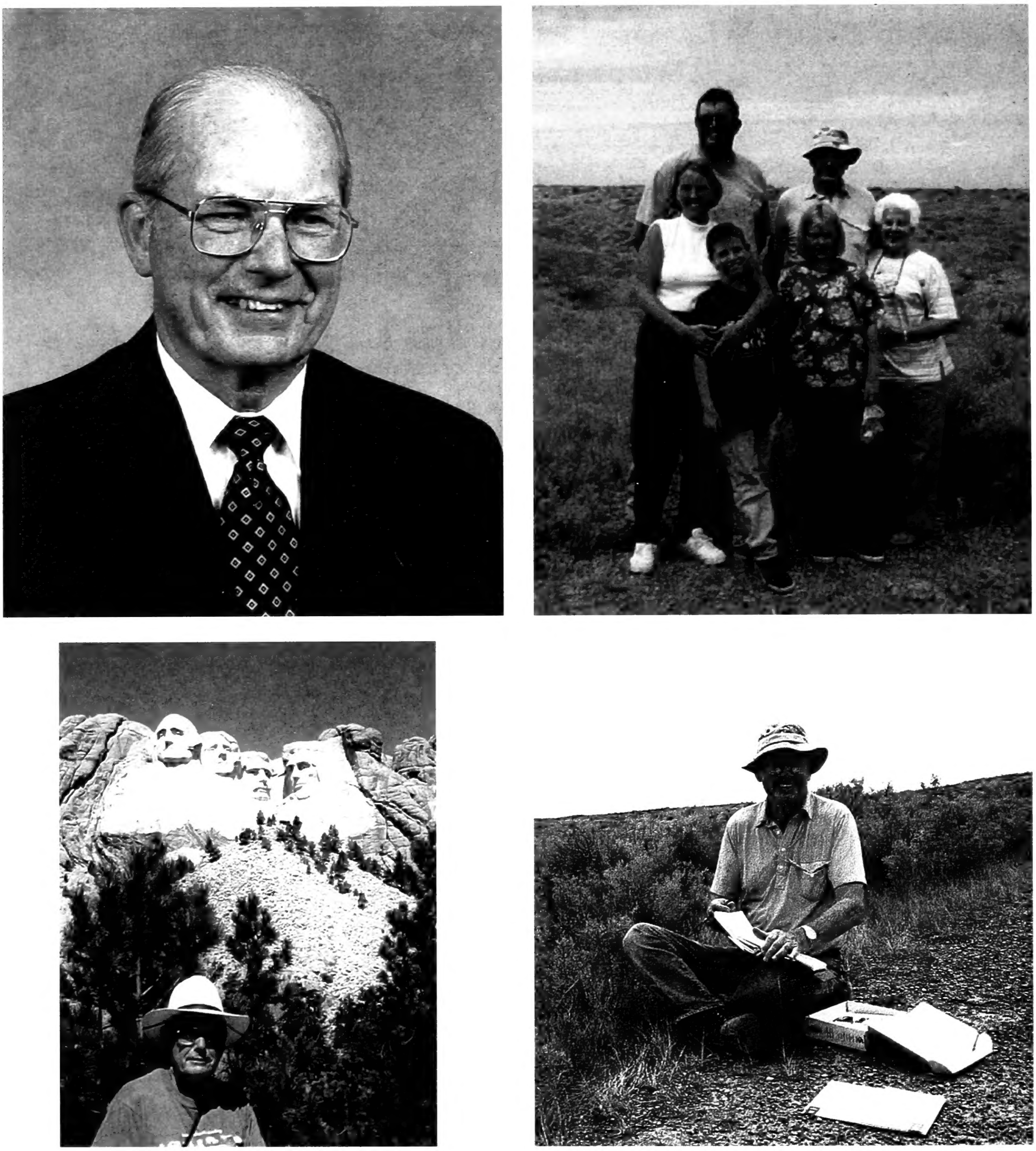

Fig. 1. Austin B. Williams. Clockwise from upper left: from church directory, 1995; with family and friends at Heart Tail Ranch, Butte County, South Dakota, one of his favorite fossil collecting sites, 31 July 1997, in back is son David, in front left to right are David's wife Anita with grandchildren Kyle and Lauren, and Norma Samuels (Norma Samuels); recording observations in his notebook on fossil Cretaceous decapods collected from the Pierre Shale at Heart Tail Ranch, Butte County, South Dakota, 6 August 1997 (Gale A. Bishop); at Mount Rushmore, South Dakota, August 1997 (Norma Samuels).

vertebrate Zoology and then Deputy Director of the National Museum of Natural History, Smithsonian Institution, considered him for a job; however, his interview with Secretary Dillon Ripley did not go well (most probably because of Austin's non-assuming personality), and he turned him down. This was a loss for the Museum but fortunately he was hired by the NMFS' Systematics Laboratory in 1971.

In addition to his crustacean work, Austin served NMFS and the Museum in a number of different ways. For example, he represented the Allied Agencies (NMFS, Agriculture, and what was then the Fish and Wildlife Service) on the Senate of Scientists in the Museum. During his tenure in this position, a question arose as to whether or not the administrative staff of the Museum had increased significantly in the several preceding years. Discussion went back and forth between the Senate and the Director of the Museum. Finally, Austin volunteered to get some real data on the issue. In a typical A. B. Williams way, he systematically went through the entire telephone directory and counted museum administrators at 5-year intervals, and demonstrated that the type of positions that the Senate considered as "administrative" had in fact increased significantly.

He was the acknowledged expert on and leader in studies of the systematics of eastern American decapod crustaceans. He is probably best known for his widely used monograph "Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States" published by the Smithsonian in 1984. His earlier study on the decapods of the Carolinas published in 1965, a precursor to his 1984 monograph, was selected as a Science Citation Classic in 1983, a rare honor for a systematist. His invaluable paper (Williams 1987a) on the identification of spiny lobsters by color patterns of the tails grew into a book co-authored with I. Dore, entitled "Lobsters of the world—an illustrated guide" (Williams & Dore 1988e); these two publications are indispensable for anybody interested in this group of economically significant decapods.

The primary focus of his research was the taxonomy, systematics, biogeography and evolution of various decapod groups, both fossil and Recent. He named 101 new decapod taxa (see list), including one superfamily, 2 families, 16 genera, 80 species, and 2 subspecies. Occasionally he also worked on other groups such as cirripeds, mysids, amphipods, and euphausiids, and even bird ecology. His publications provide us with a standard of excellence, and are well known for attention to detail, accuracy, and usefulness in the identification of specimens while at the same time giving insight into phylogenetic relationships. No major group of decapods escaped Austin's attention. He published important works on crayfishes, peneaeoids, carideans, thalassinideans, lobsters, anomurans, and brachyurans. His landmark studies on swimming crabs of the genus *Callinectes*, mud shrimps of the family Upogebiidae, commercial lobsters, xanthid crabs, and deep-sea hydrothermal vent decapods, among others, have earned him a place in the history of Zoology. His contributions to the systematics of hydrothermal vent decapods inspired other colleagues, and one genus and species of the crab family Bythograeidae Williams, 1980, was named after him (*Austinograea williamsi* Hessler & Martin, 1989, Journal of Crustacean Biology 9(4):645–661). In March of 1996 he traveled to Kumamoto, Japan, on a Japanese fellowship program to join Keiji Baba (Kumamoto University Faculty of Ecucation) in the study of galatheids and other vent decapods from hydrothermally active sites in the western Pacific. Although his work concentrated on aspects of systematics and evolution, he also published key studies on the biology of commercial penaeid shrimps, ecology of meroplankton, larval genetics, and crustacean fisheries and mariculture. At the time of his death he had completed work but unfortunately left unpublished, an important revision of the crab family Latreilliidae.

Austin's impact on carcinology is not limited to that derived from his publications. Throughout his exemplary career he actively participated in many professional societies in addition to the *Biological Society of Washington.* He was president of the *Atlantic Estuarine Research Society* (1960–1961); co-founder, secretary (1971–1973), and president (1983–1985) of the *Estuarine Research Federation*; secretary (1985-1988) for the *Society of Systematic Biology*; associate editor for *The Crustacean Society* (1986–1991); and vice-president (1990–1991) and president (1991–

1992) of the *American Association for Zoological Nomenclature.* He was also a member of the *American Association for the Advancement of Science, American Fisheries Society, American Institute of Biological Sciences, American Institute of Fishery Research Biologists, American Society of Limnology and Oceanography, Society for Integrative and Comparative Biology* (formerly *American Society of Zoologists*), *Association of Systematic Collections, Ecological Society of America, Kansas Academy of Science,* and *Society for the Study of Evolution.* His editorial activities with various journals and symposia proceedings produced many significant contributions, and his involvement with doctoral and master-level students at various academic institutions led to the development of outstanding carcinologists who now must continue his legacy. His skills as reviewer were highly regarded by editors and grant program managers who were assured of a detailed, unbiased evaluation.

Several of Austin's papers won important awards or honorable mentions. His lobster identification paper (Williams 1987a), for example, won the highly regarded "National Marine Fisheries Service Outstanding Publication Award" for best paper in the 1997 Marine Fisheries Review. In recognition of Austin's life-time work, *The Crustacean Society* presented him in 1997 with their "Excellence in Research Award" during a ceremony at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. [see Lemaitre, R., 1998, Journal of Crustacean Biology 18(3):619–620]. He was also honored with the "1999 Elton Sette Award" from the Marine Fisheries Section of the American Fisheries Society.

Austin will be remembered not only for his impressive scientific accomplishments but also for his human qualities. Unselfish almost to a fault, he made every effort to help colleagues and students alike. His height of 1.85 m (6′1″) gave him a towering physique which combined with his deep knowledge of decapods made him an imposing figure to both students and junior colleagues; however, his modesty was such that he made sure to treat everyone as a friend or colleague of similar stature. He accepted life-time honors bestowed upon him by his peers only hesitantly, and maintained until his end that he was undeserving of such attention. His personality, working habits, discipline, and inspirations date back to his early life experiences which he often mentioned to friends during casual conversations. One of his first jobs prior to entering college was at his family's farm in Sterling, Colorado, where he helped string fences, some of which had to be modified to "first class communications grade" by insulating the top strand of barbed wire to carry telephone signals. This worked fine until it rained and the circuits became grounded by water. During his Sterling days he also taught high school. One of Austin's scientific strengths was his observational and note taking abilities. He had been trained at Kansas to write reflective notes each night as if they were to be published. Those who have examined his field and office notebooks are struck by how remarkably clear and detailed they are.

Austin often mentioned the impact of the Great Plains of Kansas and Colorado on his psyche. One of his closest friends, Gale A. Bishop (Georgia Southern University), has said that he was impressed with Austin's collegiality when he first met him during a visit to the Smithsonian to study fossil decapods. Gale suggested that he might want to join him in the field in South Dakota to collect fossils. Austin did so with much enthusiasm, and the two worked together almost every summer from 1980 until the year of his death. Nancy Brannen Marsh (Science Department, Portal High School, Georgia) also joined them, and the three collaborated in studies of decapods of the Western Interior Cretaceous, collecting numerous fossil crabs, lobsters, and shrimps from the Carlile Shale and the Pierre Shale of South Dakota, Wyoming and Colorado.

These fossil collections have been donated to the Museum of Geology at the South Dakota School of Mines, Rapid City. He confessed to Gale that the timing of their collaboration was most appropriate as his wife Jean had passed away (1983) after a difficult illness (with Austin as major care giver), and his return to the Great Plains was just what he needed to gain closure and healing from the loss. This theme, Gale says, "came up many times and we concluded that getting back to our roots was an extremely healing process, both for Austin's loss and for the loss of both of my parents; it was an annual 'rehealing' as we came back into harmony with our roots and Mother Earth. When working with Austin on fossils in the Western Interior his intellect and collegiality were always apparent. His interests spanned the sciences, arts, education, and humanities. He often would visit the Rapid City Astronomy club to participate in telescopic observations, take us all out dancing at the Broken Boot Saloon in Rapid City, climb Bear Butte or Harney Peak, or head us up to Rushmore for the evening patriotic lighting program. While in the field, he brought new insights to paleontology, often seeing things we took for granted or forcing clearer explanation of our mutual deductions. Our collaboration was clearly very beneficial to Austin as well as to paleontologists Nancy Brennan Marsh, the late Reinhard Förster of Munich, and Georgia Southern students Mike Klug, Mehmet Samiratedu, and Amy Samiratedu. These insights were carried over into the laboratory and into collaborations on papers and research comparing Recent and fossil decapods."

The multi-faceted personality of Austin included a deep appreciation of the simple things of life, his family and friends. During the last decade or so of his life he was fortunate to share many moments with Norma Samuels, of Fairfax, Virginia, whose companionship undoubtedly enriched his life. Austin developed a passion for ballroom and international dancing, and a love for choral music. He actively participated in several choral groups, including the Washington Cathedral Choral Society which performed in the National Cathedral, Washington, D.C. One of his performances is preserved on an audio CD-ROM entitled "Millenium; Russian Choral Music" (1990 Centaur Record Inc.). He worshipped, sang and was an active member of the New York Avenue Presbyterian Church, of Washington, D.C., where well-attended and emotional services were held for him on October 30, officiated by The Rev. Robert H. Craig.

Austin's remains are buried in Marion, Kansas, alongside those of his wife.

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List of taxa named by Austin B. Williams

Taxa are listed alphabetically within each major decapod group. Holotype deposition and number is indicated for all species and subspecies. Asterisk indicates fossil taxa. Abbreviations for repositories are as follows: AHF, Allan Hancock Foundation, University of Southern California (now Natural History Museum of Los Angeles County); AMNH, American Museum of Natural History, New York; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MZUSP, Museu de Zoologia, Universidade de São Paulo, Brazil; SDSM, Museum of Geology, South Dakota School of Mines, Rapid City; SDSNH, San Diego Society of Natural History, California; UKMNH, University of Kansas Museum of Natural History, Lawrence; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Decapoda

Caridea

Alvinocaris Williams & Chace, 1982b.

Alvinocaris lusca Williams & Chace, 1982b. USNM 184534.

Alvinocaris markensis Williams, 1988c. USNM 234286.

Alvinocaris muricola Williams, 1988c. USNM 234288.

Alvinocaris stactophila Williams, 1988c. USNM 234291.

Leptalpheus Williams, 1965b.

Leptalpheus forceps Williams, 1965b. USNM 111084.

Ogyrides hayi Williams, 1981a. USNM 47958.

Ogyrides limicola Williams, 1955a. USNM 96675.

Opaepele Williams & Dobbs, 1995c.

Opaepele loihi Williams & Dobbs, 1995c. USNM 251447.

Rimicaris Williams & Rona, 1986c.

Rimicaris chacei Williams & Rona, 1986c. USNM 228452.

Rimicaris exoculata Williams & Rona, 1986c. USNM 228443.

Astacidea

Homarinus Kornfield, Williams & Steneck, 1995b.

Orconectes eupunctus Williams, 1952a. UKMNH T4250.

Orconectes meeki brevis Williams, 1952a. UKMNH T8140.

Orconectes nana marcus Williams, 1952a. UKMNH T4970.

Orconectes nana Williams, 1952a. UKMNH T6640.

Orconectes neglectus chaenodactylus Williams, 1952a. UKMNH T4420.

Orconectes ozarkae Williams, 1952a. UKMNH T6150.

Thalassinidea

Aethogebia Williams, 1993b.

Aethogebia gorei Williams, 1993b. USNM 251425.

**Axiopsis eximia* Kensley & Williams, 1990c. USNM 219431.

Calocaris (*Calastacus*) *jenneri* Williams, 1974b. USNM 150472.

Calocaris (*Calastacus*) *oxypleura* Williams, 1974b. USNM 101651.

Pomatogebia Williams & Ngoc-Ho, 1990e.

Upogebia acanthops Williams, 1986a. USNM 213194.

Upogebia aestuari Williams, 1993b. USNM 251407.

Upogebia aquilina Williams, 1993b. USNM 251426.

Upogebia baldwini Williams, 1997d. USNM 251486.

Upogebia bermudensis Williams, 1993b. MCZ 12873.

Upogebia burkenroadi Williams, 1986a. SDSNH 3985.

Upogebia careospina Williams, 1993b. USNM 138899.

Upogebia casis Williams, 1993b. USNM 251224.

Upogebia cocosia Williams, 1986a. USNM 213268.

Upogebia coralliflora Williams & Scott, 1989b. USNM 230075.

Upogebia cortesi 2000a. USNM 291186.

Upogebia dawsoni Williams, 1986a. AHF2566.

Upogebia felderi Williams, 1993b. USNM 251430.

Upogebia galapagensis Williams, 1986a. USNM 213223.

Upogebia inomissa Williams, 1993b. USNM 251396.

Upogebia jonesi Williams, 1986a. USNM 213195.

Upogebia lepta Williams, 1986a. USNM 213270.

Upogebia maccraryae Williams, 1986a. USNM 213202.

Upogebia macginitieorum Williams, 1986a. USNM 213219.

Upogebia molipollex Williams, 1993b. AMNH 6820.

Upogebia omissago Williams, 1993b. USNM 222057.

Upogebia onychion Williams, 1986a. AHF 4133.

Upogebia paraffinis Williams, 1993b. MZUSP 8049

Upogebia pillsbury Williams, 1993b. USNM 251435.

Upogebia ramphula Williams, 1986a. USNM 213446.

Upogebia schmitti Williams, 1986a. AHF 3933.

Upogebia spinistipula Williams & Heard, 1991a. USNM 239251.

Upogebia synagelas Williams, 1987d. USNM 233572.

Upogebia tenuipollex Williams, 1986a. USNM 213236.

Upogebia thistlei Williams, 1986a. USNM 213251.

Upogebia toralae Williams & Hernández-Aguilera, 1998b. USNM 285522.

Upogebia vargasae Williams, 1997d. USNM 251484.

Upogebia veleronis Williams, 1986a. (USNM 213272)

Anomura

Munidopsis alvisca Williams, 1988c. USNM 234294.

Munidopsis glabra Pequegnat & Williams, 1995e. USNM 251455.

Munidopsis granosicorium Williams & Baba, 1990b. USNM 240205.

Munidopsis lentigo Williams & Van Dover, 1983b. USNM 191160.

Munidopsis lignaria Williams & Baba, 1990b. USNM 240202.

Munidopsis marianica Williams & Baba, 1990b. USNM 240198.

Shinkaia Baba & Williams, 1998a.
Shinkaia crosnieri Baba & Williams, 1998a. USNM 251480.
Uroptychus edisonicus Baba & Williams, 1998a. USNM 251479.

Brachyura

Allactaea Williams, 1974a.
Allactaea lithorostrata Williams, 1974a. USNM 143770.
Bothromaia Williams & Moffit, 1991b.
Bothromaia griffini Williams & Moffit, 1991b. USNM 250884.
Bythograeoidea Williams, 1980. (Superfamily).
Bythograeidae Williams, 1980. (Family).
Bythograea Williams, 1980.
Bythograea mesatlantica Williams, 1988c. USNM 234300.
Bythograea thermydron Williams, 1980. USNM 172830.
Callinectes similis Williams, 1966b. USNM 113341.
Cyclozodion Williams & Child, 1989a.
Cyclozodion tuberatum Williams & Child, 1989a. USNM 234462.
Epilobocera wetherbeei Rodríguez & Williams, 1995a. USNM 268832.
Eplumula Williams, 1982a.
**Heus* Bishop & Williams, 2000b.
**Heus foersteri* Bishop & Williams, 2000b. SDSM 11016.
Hypsophrys noar Williams, 1974c. USNM 150816.
Latreillia manningi Williams, 1982a. USNM 57071.
Latreillia metanesa Williams, 1982a. USNM 74570.
Menippe adina Williams & Felder, 1986e. USNM 228862.
Mimilambridae Williams, 1979c. (Family).
Mimilambrus Williams, 1979c.
Mimilambrus wileyi Williams, 1979c. USNM 172222.
**Necrocarcinus olsonorum* Bishop & Williams, 1991c. SDSM 11000.
Ovalipes stephensoni Williams, 1976a. USNM 155110.
Panopeus austrobesus Williams, 1984a. USNM 59462.
Panopeus margentus Williams & Boschi, 1990d. USNM 239191.
Panopeus meridionalis Williams, 1984a. USNM 99846.
**Plagiophthalmus bjorki* Bishop & Williams, 2000b. SDSM 11021.
**Raninella manningi* Bishop & Williams, 2000b. SDSM 11018.
Rochinia decipiata Williams & Eldredge, 1994. USNM 251434.
Stilbomastax Williams, Shaw & Hopkins, 1977a.

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A new species of mud shrimp, *Upogebia cortesi,* from Pacific Costa Rica (Decapoda: Thalassinidea: Upogebiidae)

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Abstract.—*Upogebia cortesi,* a new species of mud shrimp from the Pacific side of Costa Rica is described and illustrated. The type series was dredged parallel to shore in water of 30–40 m depth. The species shares lack of a strong proximal mesioventral spine on the merus of the second pereopod with several members of the genus from the western hemisphere; moreover, the species stands alone in having spineless articles on pereopods 1–5 except for fingers of the chelae. The rostrum has no ventral spines. Similarities between this and related species are emphasized in a partial abridgment of the key to upogebiid species in the eastern Pacific.

Eight species of the family Upogebiidae have been reported for the Pacific coast of Costa Rica (Vargas & Cortés 2000). Of these *Pomatogebia cocosia* (Williams 1986) and *Upogebia vargasae* Williams, 1997, were described based on material from Costa Rica. During the 1998 Mollusk Workshop organized by INBio at the "Reserva Absoluta de Cabo Blanco", Península de Nicoya, a dredge sample conducted between the mainland and Isla Cabo Blanco, at 30–40 m depth, yielded three specimens of a new species of *Upogebia* Leach, 1814, described here. The substrate where the specimens were obtained included calcareous algae and rock fragments; at least 10 species of brachyuran crabs and several mollusk species were also found in the sample.

Specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and in Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, San José (UCRMZ), as indicated in the species account.

Upogebia cortesi, new species
Fig. 1

Material.—Costa Rica, NW side of Isla Cabo Blanco, dredged parallel to coast, 30–40 m, 16–17 May 1998: USNM 291186, male holotype; UCRMZ 2220-06, male paratype; USNM 291187, female ovigerous paratype.

Diagnosis.—Rostrum with sides convex in dorsal view, obsolescent pair of spines on submedian anterior margin; projections to either side of rostrum slender and spinelike; no spine on postocular margin; anterior gastric region bearing many spines nearly hidden in patch of dense setae. Abdominal sternites unarmed. Telson subrectangular, sides slightly crenulate. Merus of cheliped lacking subdistal dorsal spine and spines on ventral margin; carpus essentially spineless; palms spineless. Pereopods 2–5 spineless; pereopod 2 without proximal mesioventral spine on merus.

Description.—Rostrum (Fig. 1*a,b*) horizontal in lateral view with tip slightly exceeding eyestalks; convex in dorsal aspect, with pair of submedian obsolescent blunted

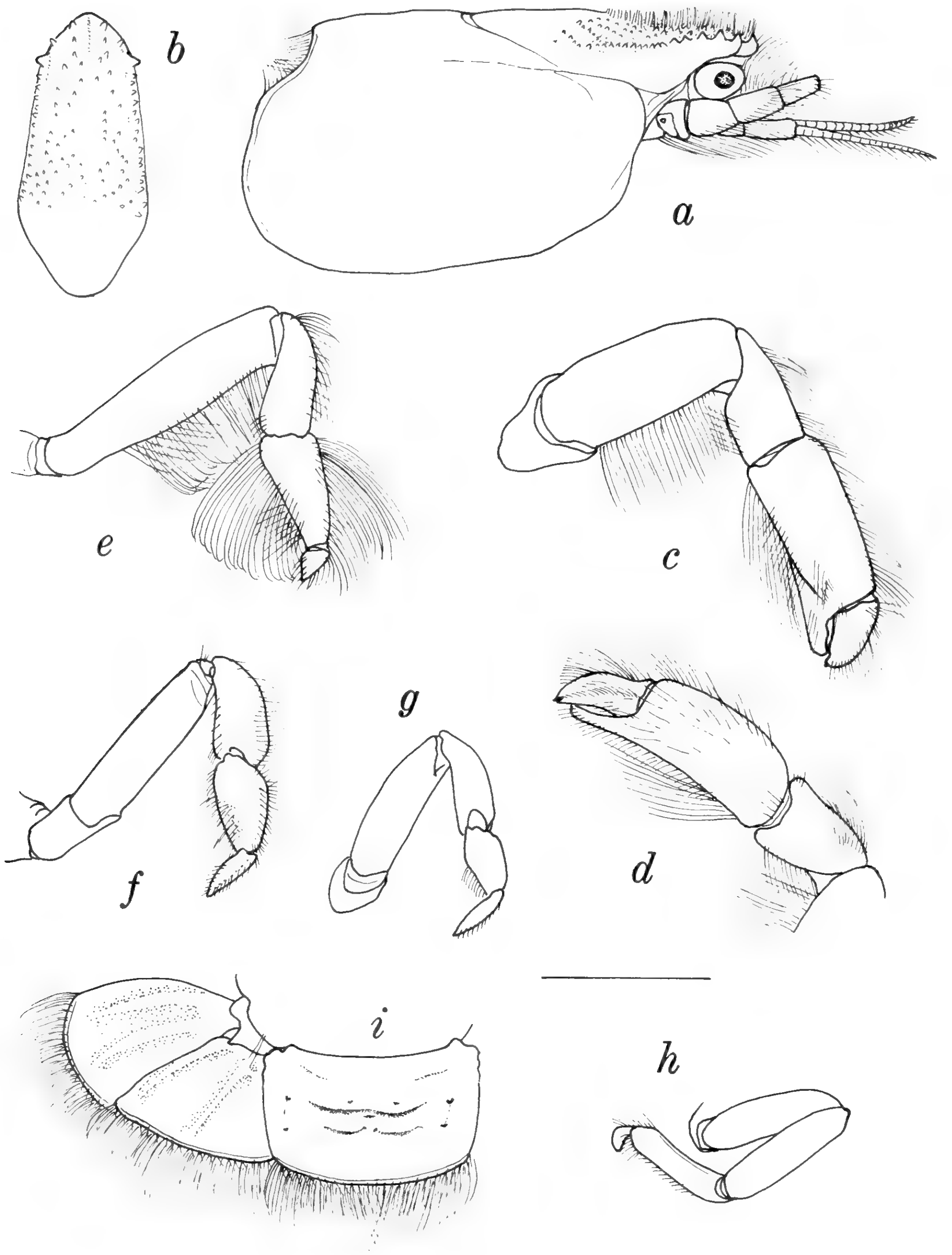

Fig. 1. *Upogebia cortesi,* new species, male holotype, USNM 291187: *a,* Carapace and cephalic region, lateral; *b,* Anterior carapace, dorsal; *c,* Cheliped, right lateral; *d,* Chela and carpus, right mesial; *e,* Right pereopod 2; *f,* Right pereopod 3; *g,* Right pereopod 4; *h,* Right pereopod 5; *i,* Telson, left uropod, and part of abdominal segment 6, dorsal. Scale = 3 mm.

spines on anterior margin; 2 subdistal erect acute dorsal spines followed on each side by about 6 smaller marginal spines along either side of field of small spines on anterior gastric region of carapace, spines on anterior part of field hidden in dense patch of setae. Lateral ridge on either side of anterior gastric region extended anteriorly to spine similar in size to dorsal spines on rostrum, ridge bearing crest of 18 spines, anterior 4 spines larger than succeeding spines. Posterior region of carapace glabrous. Shoulder lateral to cervical groove bearing no spines below intersection with thalassinidean line, latter continuing to posterior margin of carapace without interruption; postocular margin of carapace unarmed.

Abdominal sternites unarmed.

Telson (Fig. 1*i*) subrectangular, wider than long, posterior margin nearly straight, smooth; transverse proximal ridge prominent, rather broad, lateral ridge at each side also rather broad; lateral margins almost imperceptibly crenulate.

Eyestalk stout, horizontal, shorter than rostrum; lower margin slightly convex; cornea narrower than diameter of stalk and directed laterally.

Antennular peduncle (Fig. 1*a*) reaching to about base of terminal article of antennal peduncle, combined length of proximal 2 articles subequal to length of terminal article.

Antennal peduncle (Fig. 1*a*) with distal article and distal half of penultimate article extending beyond tip of rostrum; moderate compressed scale bearing obsolescent anteroventral spine.

Maxilliped 3 bearing epipod.

Epistomial projection rather broad in lateral view, bearing prominent, acuminate apical spine.

Chelipeds (Fig. 1*c,d*) lacking spine on ventral margin of merus. Carpus trigonal, with barely perceptible longitudinal lateral groove, obsolescent spine at anterior ventrolateral corner. Chela length about 2.7 times chela height. Fixed finger slender, with extended tip. Dactyl thick, longer than fixed finger, drawn to corneous tip, and at midlength bearing small tooth on occlusive edge opposing tip of fixed finger.

Pereopod 2 (Fig. 1*e*) reaching about to distal edge of cheliped palm; pereopods 2–4 (Fig. 1*f–h*) spineless. Pereopod 5 of usual form, with cleaning brush on propodus.

Uropods (Fig. 1*i*) with acute spine on protopod above base of mesial ramus; both rami slightly exceeding telson, and with distal margins smooth.

Measurements (in mm).—Male holotype, anterior carapace length 6.1, carapace length 9.1, length of chela including fixed finger 4.1, mid-length height of chela 1.8; male paratype, same, 4.8, 7.8, 3.8, 1.8; female ovigerous paratype, same, 5.4, 7.9, 4.2, 1.5.

Known range.—Known only from the type locality.

Etymology.—The species is named for Dr. Jorge Cortés, Curator of Cnidaria, Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, in recognition of his life-long efforts to advance knowledge of the marine fauna from Costa Rica.

Remarks.—*Upogebia cortesi,* new species, shares with several eastern Pacific and western Atlantic members of the genus a second pereopod on which the merus bears no proximal mesioventral spine (see keys to species in Williams 1986, 1993). The abdominal sternites and pleura bear no ventral spinules.

The species stands alone, however, with respect to several other characters. The rostrum with rounded anterior margin has no ventral spines. The anterior gastric region and rostrum bear an extremely dense patch of setae obscuring spines on this surface. The pereopods are virtually spineless. This condition is most easily demonstrated by emendation of the key to species of the eastern Pacific (Williams 1986) in which the comparative relationship to other species in the region becomes apparent. Although the new species has spineless pereopods, it appears to be related to *U. tenuipollex* Williams, 1986 which has a well developed distodorsal spine on the merus of the cheliped and a cluster of spines on the merus of pereopod 3.

Emended part of Williams (1986:7–10) key distinguishing *U. cortesi,* new species, and *U. tenuipollex*

4. Merus of pereopod 2 lacking proximal mesioventral spine 5
   Merus of pereopod 2 bearing proximal mesioventral spine 12
5. Postocular spine absent 6a
   Postocular spine present and well developed 8
6a. Merus of cheliped and pereopod 3 spineless . . . . *U. cortesi,* new species
   Merus of cheliped and pereopod with spines 6
6. Merus of chelipeds bearing well developed distodorsal spine; merus of pereopod 3 bearing cluster of proximoventral

spines . . . . *U. tenuipollex* Williams Merus of chelipeds lacking distodorsal spine or with spine tiny; merus of pereopod 3 bearing few obsolescent proximoventral spines 7

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Periclimenes murcielagensis, a new species of shrimp (Crustacea: Decapoda: Palaemonidae) living on black coral from the Pacific coast of Costa Rica

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Abstract.—*Periclimenes murcielagensis*, new species, a pontoniine shrimp living on black coral colonies, occurs at depths of 25 m at Isla San Pedrito, Archipiélago de las Islas Murciélago, Guanacaste, Costa Rica. This new species is most similar to *P. veleronis*, Holthuis, and *P. americanus* Kingsley, and is distinguished from these by characters from the rostrum, basal antennular segment, antennular flagellum, and incisor process of the mandible.

Shrimps of the genus *Periclimenes* Costa, 1844, belong to the subfamily Pontoniine, and are distributed widely in subtropical and tropical marine waters worldwide. Some species live freely but the majority are associated with other marine invertebrates. Of the species of this genus known from the eastern Pacific, only *P. infraspinis* (Rathbun 1902), *P. lucasi* Chace, 1937, and *P. veleronis* Holthuis, 1951, have not been reported in association with other invertebrates (Holthuis 1951). Known associates of these shrimps in the western Atlantic are sponges, gorgonians, actinians, corallimorpharians, rhizostome scyphozoans, hydroids, antipatharians, bivalves, ophiuroids and crinoids (Heard & Spotte 1991, Spotte et al. 1994).

While conducting ecological studies of soft corals, specimens of an undescribed species of *Periclimenes* were found living on colonies of black coral (*Antipathes panamensis* Verrill, 1869) at Isla San Pedrito, Archipiélago de las Islas Murciélago, Guanacaste, Costa Rica. This new species is described herein.

Specimens were collected during SCUBA dives at 25 m. Plastic bags were placed over black coral colonies and closed with a rubber band. The shrimps and *Antipathes panamensis* colonies were fixed in a mixture of 10% formalin and seawater, the colonies washed in the laboratory with fresh water, and all the liquid passed through a 0.5 mm mesh. The shrimps were preserved in 70% ethanol.

The material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and Museo de Zoología, Universidad de Costa Rica (UCRMZ). Carapace length (CL) was measured from the tip of the rostrum to the posterodorsal margin of the carapace.

Periclimenes murcielagensis, new species
Figs. 1–5

Material.—Holotype: ovigerous female (CL 7.75 mm), USNM 260931, Isla San Pedrito, Archipiélago de las Islas Murciélago, Guanacaste, Costa Rica, 25 m, coll. Odalisca Breedy, 24 May 1996.—Paratypes: 4 females (CL 7.5–7.9 mm), 2 males (CL 5.256.5), USNM 260932; 9 females (CL 6.25–8.4 mm), 2 males (CL 5.6–6.25 mm), UCRMZ 2247-01, same collection data as holotype.

Diagnosis.—Carapace armed with both hepatic and antennal spine; rostrum well developed, reaching end of antennular peduncle, usually armed with 8–10 teeth dorsally and 2–4 teeth on distal half of ventral margin. Antennular peduncle having basal

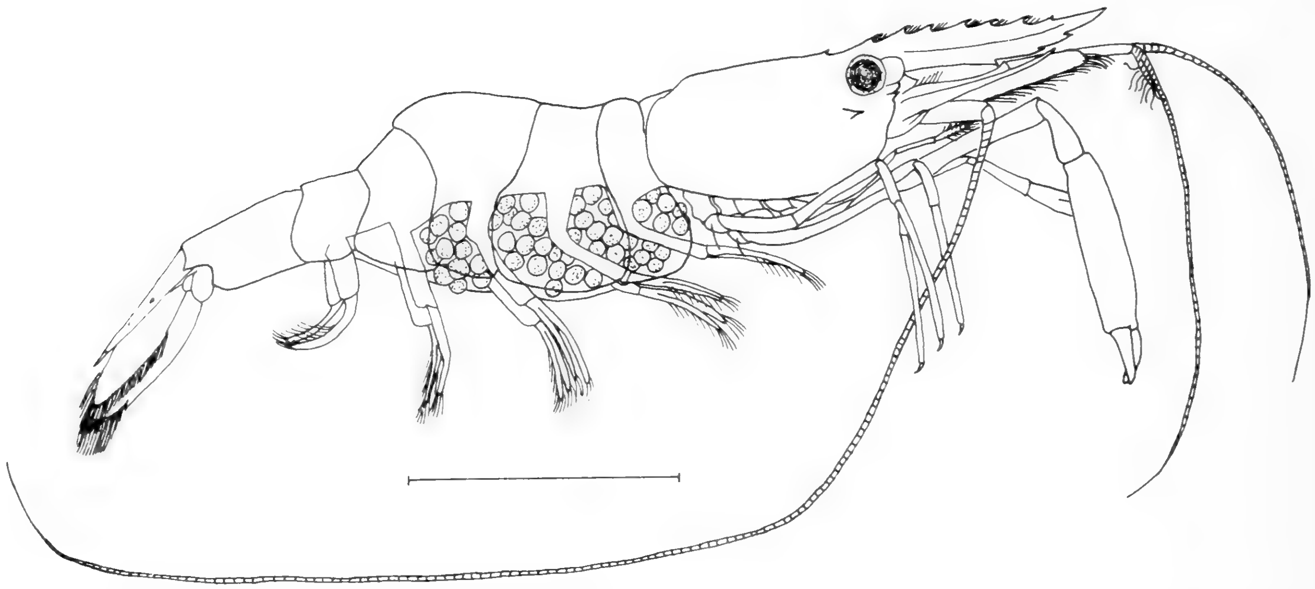

Fig. 1. *Periclimenes murcielagensis*, new species, holotype ovigerous female (CL 7.75 mm), lateral view USNM 260931. Left antennule, antenna and pereopods 1–5 not shown. Scale equals 5 mm.

article armed with 2–4 distolateral spines. Pereopods 3–5 with dactylus simple.

Description.—Rostrum (Figs. 1, 5a–f) nearly straight, slightly reaching end of antennular peduncle; dorsal margin armed with 8–10 teeth interspaced with setae, posteriormost tooth placed on carapace posterior to level of orbital margin, second tooth on carapace usually even with, or anterior to, orbital margin. Distance between first and second tooth, sometimes slightly larger than distance between other teeth, which are regularly spaced over rostrum; ventral margin slightly convex, armed with 2–4 teeth on distal half. No postorbital ridges or supra orbital spines. Antennal spine well developed, acute. Hepatic spine well developed, slightly larger and more robust than antennal spine. Lower orbital angle produced into small, blunt lobe.

Abdominal pleura broadly rounded. Sixth somite (Fig. 1) nearly twice as long as fifth and slightly longer than telson. Dorsal spines of telson (Fig. 2c) distinct, proximal pair situated near midlength of telson, distal pair of spines closer to proximal pair than posterior margin of telson; intermediate marginal spines at posterior end of telson not quite twice as long as mesial pair.

Cornea as broad as peduncle (eyestalk), constricted at junction with eyestalk, accessory pigment spot and associated ommatidia present on dorsoproximal margin of cornea.

Antennular peduncle (Figs. 2b, 4g–h) with stylocerite sharp and slender, reaching to about midlength of basal segment; distolateral margin of basal segment armed with 2–4 spines, second and third segment subequal in length and width. Lateral antennular flagellum with 2 branches fused for about 8 joints; portion of shorter branch not fused consisting of about 6 joints, and about 0.5 times shorter than fused portion.

Antennal scale (Fig. 2a) reaching distal margin of third antennular segment, more than 3 times as long as broad; lateral margin nearly straight, distal tooth falling far short of strongly produced anteromesial angle of blade. Antennal peduncle reaching about to midlength of scale; basal segment with sharp lateral spine near base of scale.

Mouthparts as figured (Fig. 3a–f). Mandible (Fig. 3a) lacking palp; incisor process ending in 4 distinct teeth, distal tooth largest; molar process dentate. Maxilla 1 (Fig. 3b) with upper endite (lacinia) possesing stout apical spine-setae crown, distal to, 10 or more smaller subapical setae; endite with 4 or more stout apical spine-setae and 6 or more subapical setae on each side. Maxilla 2 (Fig. 3c) with entire endite. Maxilliped 1

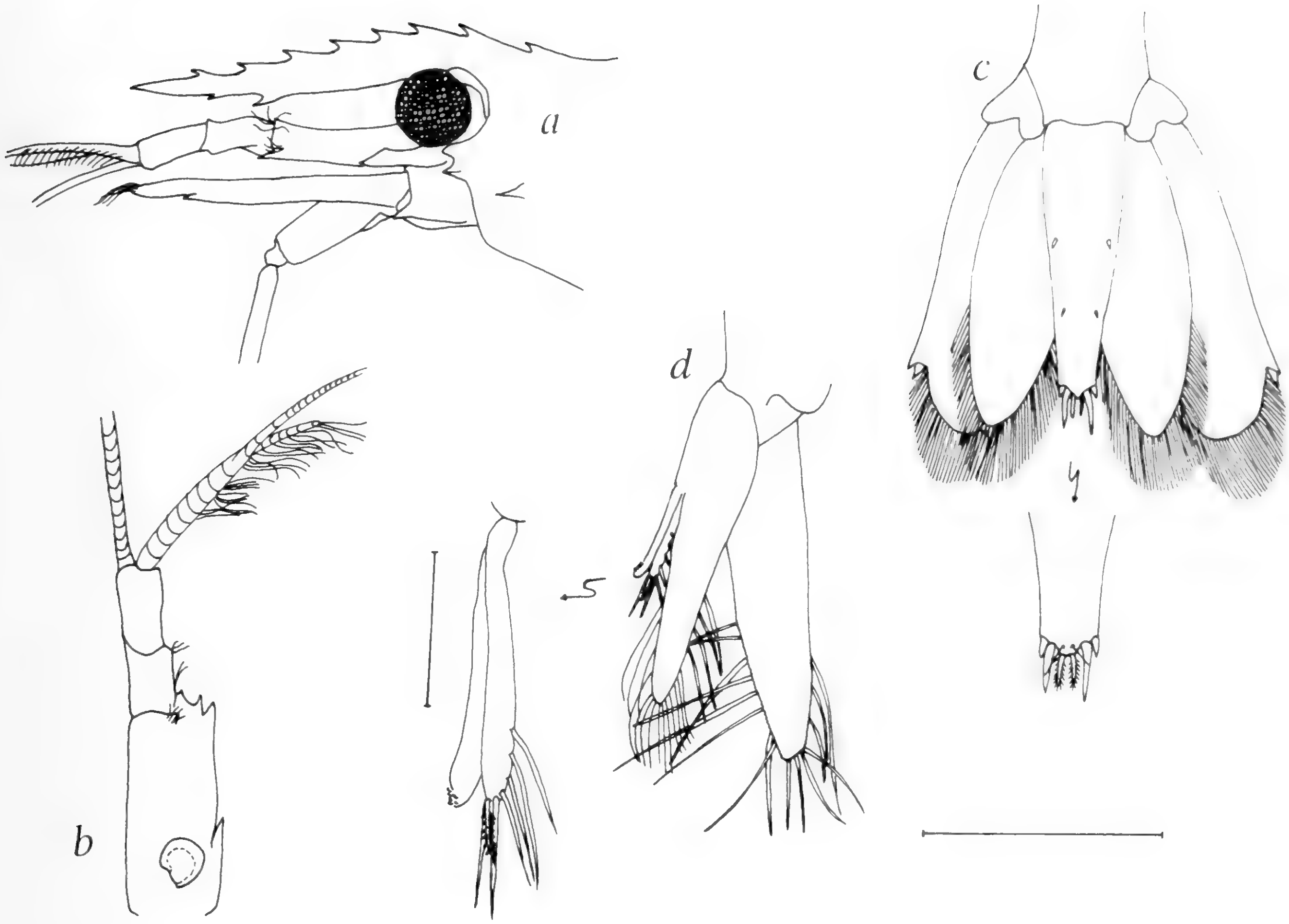

Fig. 2. *Periclimenes murcielagensis,* new species. Paratype male (CL 5.6 mm) UCRMZ 2247-01. a, anterior part of carapace; b, right antennule; c, telson; d, appendix masculina. Scale equal 2 mm (a, c), 1 mm (b), 0.25 mm (d).

(Fig. 3d) with well developed exopodal flagellum (lash) possessing 4 terminal plumose spine-setae; epipod slightly bilobed; palp slender and laching terminal spine setae. Maxilliped 2 (Fig. 3e) possessing well developed exopod with terminal plumose setae; epipod rectangular. Maxilliped 3 (Fig. 3f) extending for proximal 0.25 of scaphocerite; exopod exceeding midlength of proximal segment; with broad, round epipod.

First pereopod (Fig. 4a) reaching end of antennal scale; fingers unarmed, shorter than palm; carpus distinctly longer than chela, subequal to merus. Second pereopod distinctly unequal. Major cheliped (Fig. 4b, c) overreaching antennal scale by approximately length of chela; fingers armed with teeth, distinctly shorter than palm, carpus distinctly shorter than chela, subequal to merus; ischium and merus equal in length. Minor cheliped (Fig. 4d) of second pair overreaching antennular scale by approximately length of fingers; fingers unarmed, shorter than palm; chela, carpus, merus and ischium subequal in length. Pereopods 3–5 (Fig. 4e–g) nearly equal in size and shape; dactyls entire (not bifid), propodi with single spine on distal flexor margin. Third pereopod just reaching end of antennal scale; propodus 4 times length of dactyl, slightly more than twice length of carpus or ischium; merus subequal in length to propodus, with single distal spine on flexor margin. Fourth pereopod extending to distal end of second segment of antennular peduncle; propodus 4 times length of dactyl, slightly more than twice length of carpus or ischium; merus subequal in length to propodus. Fifth pereopod extending to distal end of second segment of antennular peduncle; propodus 4 times length of dactyl, subequal

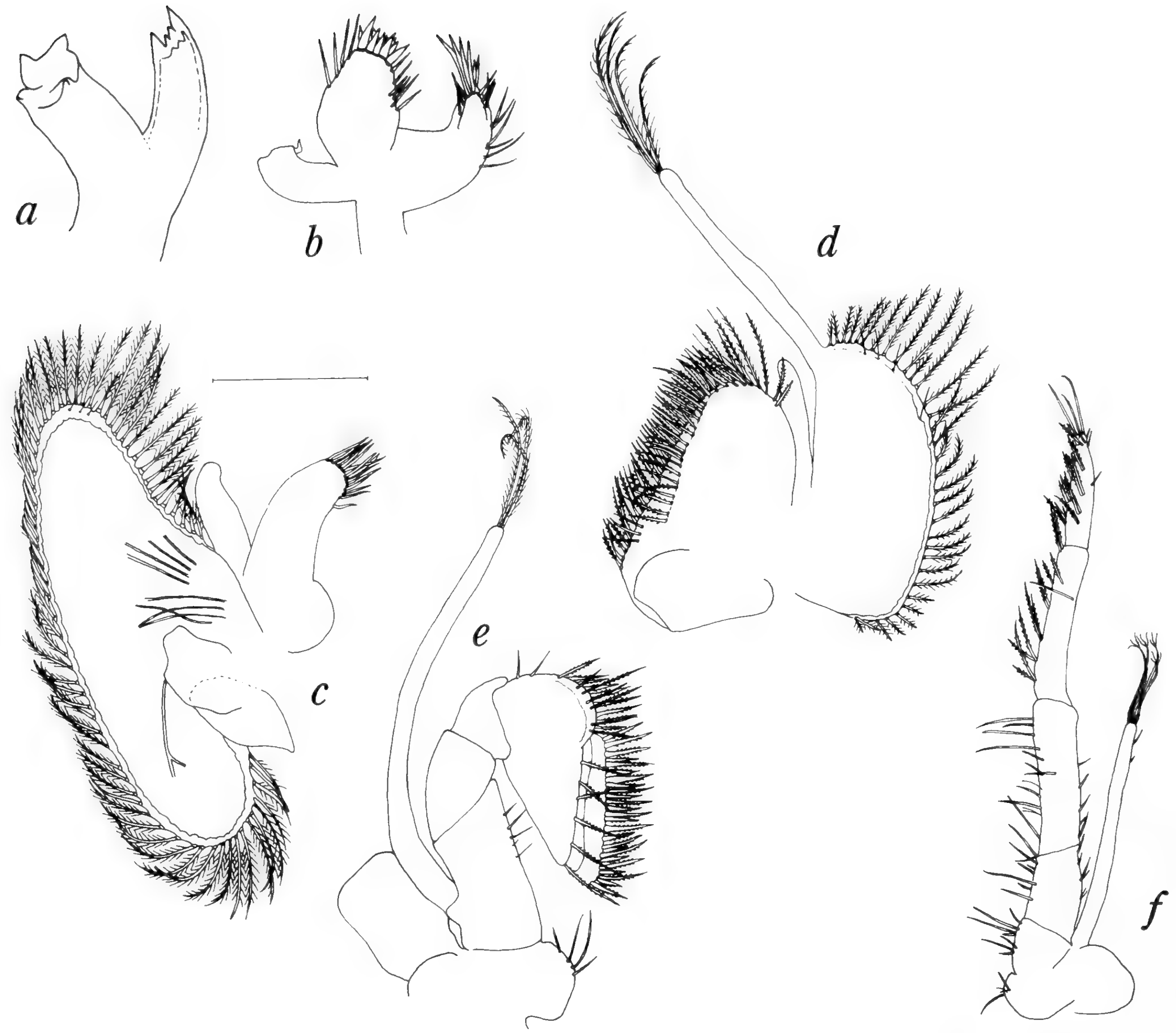

Fig. 3. *Periclimenes murcielagensis,* new species. Paratype male (CL 5.6 mm) UCRMZ 2247-01. a, mandible; b, maxilla 1; c, maxilla 2; d, maxilliped 1; e, maxilliped 2; f, maxilliped 3. Scale equal 0.5 mm (a–e), 1 mm (f).

to merus; carpus and ischium subequal in length.

Males with appendix masculina (Fig. 2d) armed with 3 apical spine-like setae, midle smaller and weakly serrate, and subapical spine-like setae. Eggs size ranging in maximum length from 0.3 to 0.5 mm (hatching stage).

Uropodal exopods extending beyond telson for about 0.8 times length of exopod; with strong movable spine between distolateral tooth and blade; movable spine distinctly longer than distolateral spine.

Color.—Orange after preservation.

Habitat.—Periclimenes murcielagensis, new species, was found living on colonies of black coral *Antipathes panamensis.* Also found on the same colonies with the pontoniin *Waldola schmitti* Holthuis, 1951, cirripeds, mollusks and polychaete worms. Depth: 25 m.

Distribution.—Known only from type locality, Archipiélago de las Islas Murciélago, Guanacaste, Costa Rica.

Etymology.—The species is named for the type locality, Archipiélago de las Islas Murciélago.

Remarks.—Adult males and females differ only in the size of the major cheliped of the second pereopod; in males the major cheliped is markedly smaller than in females. The major cheliped in adult

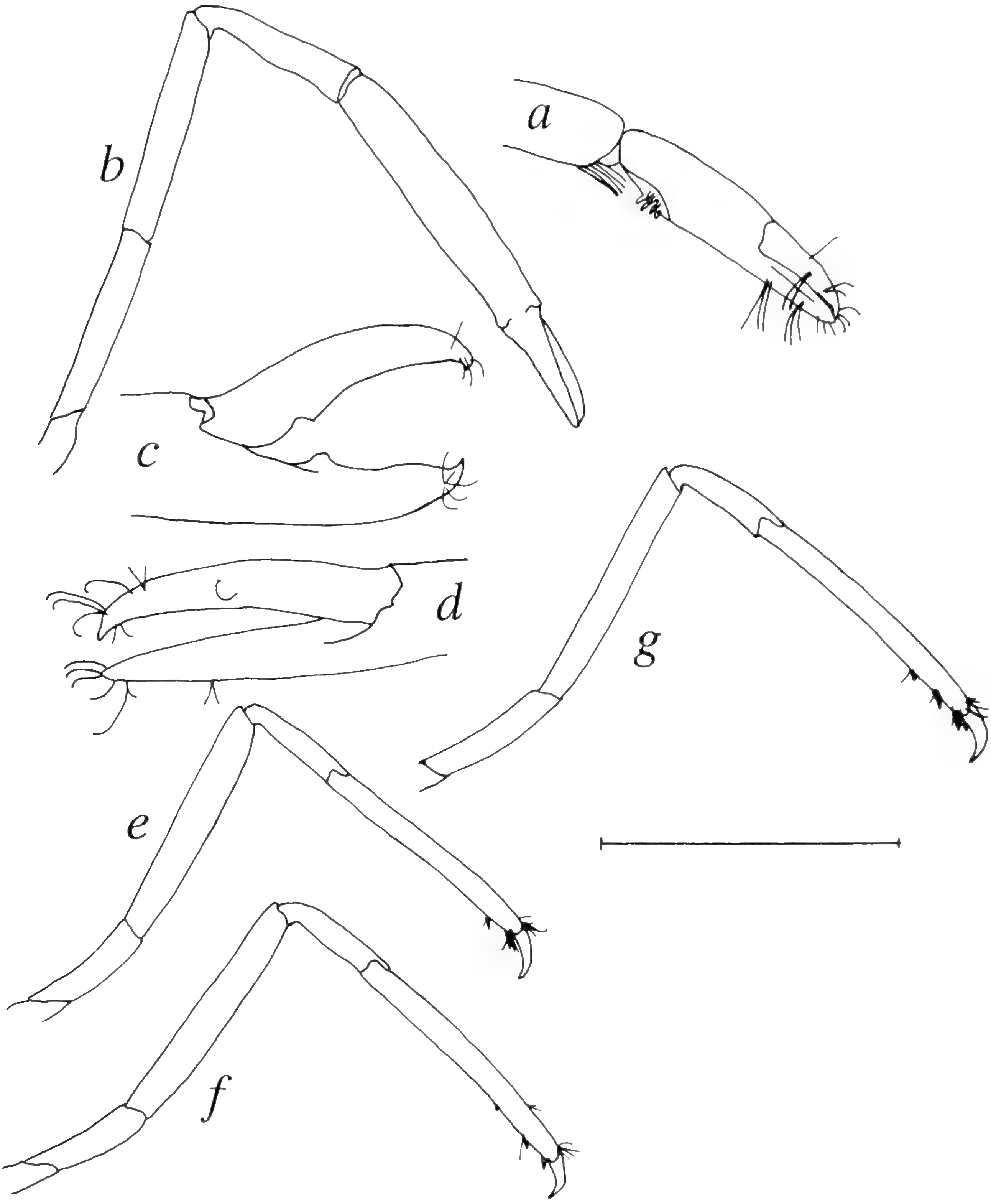

Fig. 4. *Periclimenes murcielagensis,* new species. Paratype male (CL 5.6 mm), lateral view, UCRMZ 2247-01. a, distal portion of chela of first pereopod; b, right second major pereopod; c, enlargement of chela of mayor pereopod; d, distal portion of chela of minor pereopod; e, f, g, third, fourth and fifth pereopods. Scale equal 4 mm (b), 2 mm. (e, f, g), and 1 mm (a, c, d).

males is similar to that of immature females.

Among the eastern Pacific species of *Periclimenes, P. murcielagensis,* new species, is most similar to *Periclimenes veleronis,* from La Libertad, Ecuador (Holthuis 1951). The new species can be distinguished from *P. veleronis* by the slender

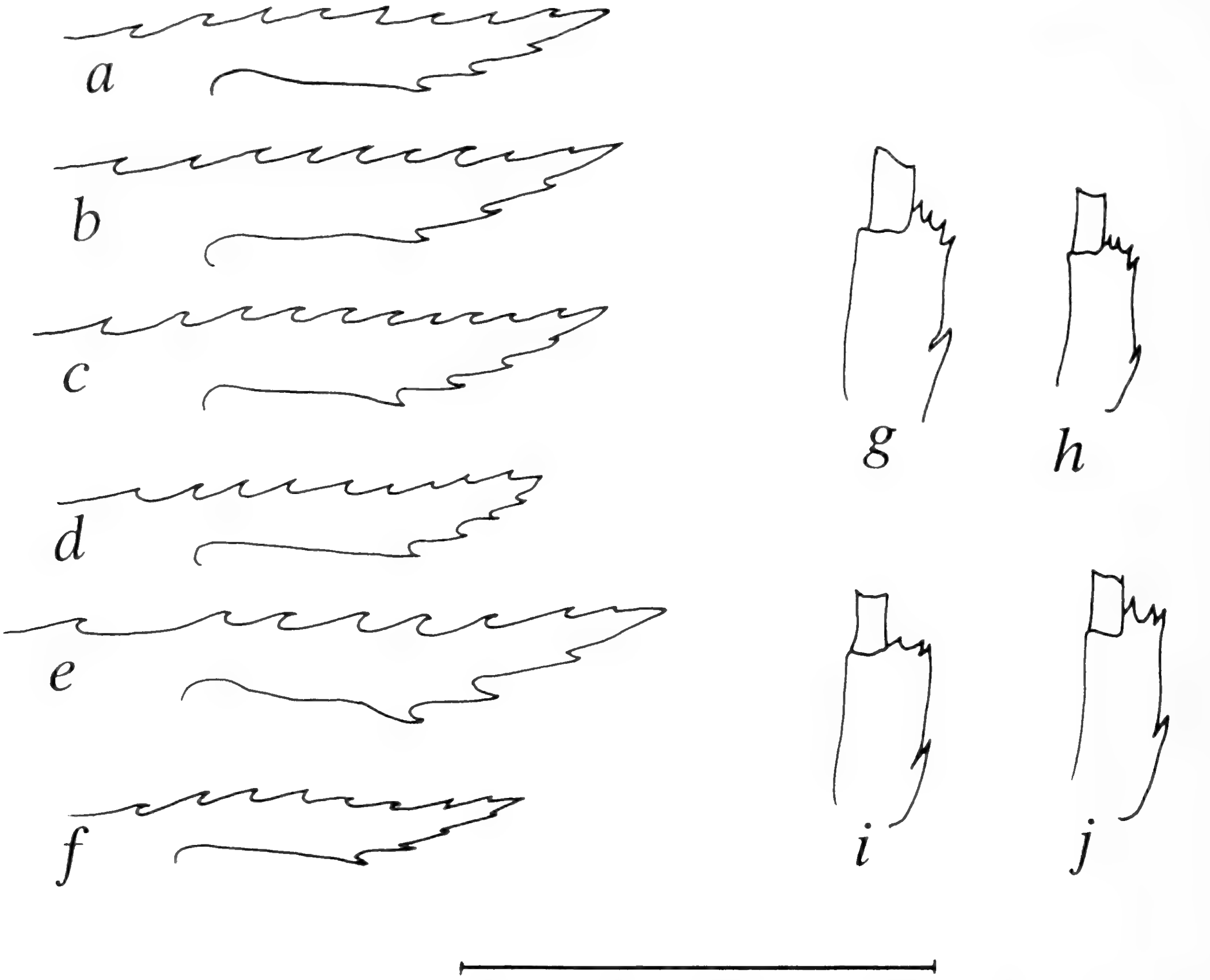

Fig. 5. *Periclimenes murcielagensis,* new species. Variations in rostrum (a–f) and basal segment of antennular peduncle (g–j). (a, f, males; b, c, females; g, i, j, females; h, male). Scale equals 5 mm.

shape and number of teeth on the dorsal (8–10) and ventral (2–4) margins of the rostrum; the presence of two to four subequal spines on the distolateral margin of basal segment of antennular peduncle; the two branches of the antennular flagellum are fused for about eight joints (five joints in *P. veleronis*); the non-fused portion consists of about six joints and is about one-half times shorter than fused portion, whereas in *P. veleronis* the non-fused portion has three joints and is more than half as long as the fused portion.

Periclimenes murcielagensis, new species, also resembles *P. americanus,* from Florida (Kinsgley 1878). The two have a similarly shaped and armed rostrum. The new species can be distinguished from *P. americanus* by the presence of two to four subequal spines on the distolateral margin of the basal segment of antennular peduncle (one in *P. americanus*); no postorbital ridge is present in *P. murcielagensis*; the two branches of the antennular flagellum are fused for about eight joints (eight to 12 joints in *P. americanus*), and the non-fused portion consists of about six joints (three or four in *P. americanus*); the incisor process of the mandible ends in four distinct teeth in *P. murcielagensis* (three in *P. americanus*); the second pereopods are distinctly unequal in *P. murcielagensis* (equal in *P. americanus*).

Acknowledgments

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Office of Fellowships and Grants, Smithsonian Institution, Washington, D.C. I thank "Area de Conservación Guanacaste, Ministerio del Ambiente y Energía" for arranging a visit to Islas Murciélago. I also thank R. Lemaitre and R. Heard for their critical comments on the manuscript; J. Cortés for his constant support, and O. Breedy for sending me the specimens. This is a contribution of the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica.

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A new squat lobster of the genus *Munidopsis* Whiteaves, 1874 (Crustacea: Decapoda: Galatheidae) from Taiwan

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Abstract.—A new species of the squat lobster of the genus *Munidopsis* Whiteaves, *M. formosa,* is described from deep-water off the northeastern coast of Taiwan. The new species is most similar to *M. camelus* Ortmann, but differs in having a much broader and less curved rostrum, the posterior carapace ridge generally armed with a pair of submedian spines, only the chelipeds bearing epipods, and having a lighter coloration. The relationships of this new species with some other similar species are also discussed.

There are about 150 known species of *Munidopsis* Whiteaves, 1874 (see Baba 1988), most of which inhabit deep waters (to 5330 m deep) and generally have small eyes as well as a triangular rostrum. To date, only three species, namely *M. andamanica* MacGilchrist, 1905, *M. cylindrophthalma* (Alcock, 1894) and *M. latimana* Miyake & Baba, 1966, of this genus have been reported from Taiwan (Wu et al. 1998). Recently, several specimens of an undescribed species of *Munidopsis* from Taiwan were collected off the northeastern coast at a depth of about 500 m. Careful examinations of these specimens showed that they are most similar to *M. camelus* Ortmann, 1892 from Japan, and differ from other members of the genus in the rostrum being trifid, as well as the second and the third abdominal tergites each armed only with a pair of large submedian spines. Detailed comparison with *M. camelus* revealed several slight but constant differences between the Taiwanese and Japanese material. The Taiwanese specimens represent a new species described herein.

Specimens of the new species are deposited in the National Taiwan Ocean University, Keelung (NTOU), and those used of *M. camelus* in the personal collection of Prof. K. Baba, Kumamoto University, Japan (KB). The measurements given are of carapace length (cl) excluding rostrum.

Munidopsis formosa, new species.
Figs. 1a, c–e, 2a, c, d, 3

Material examined.—Holotype: Taiwan, northeastern coast, Tai-Shi fishing port, I-Lan County, commercial trawlers, about 500 m, soft bottoms, Aug 1998, 1 ♂, cl 20.4 mm (NTOU-H 1998-08).

Paratypes: Taiwan, northeastern coast, Tai-Shi fishing port, I-Lan County, commercial trawlers, about 500 m, soft bottoms, Apr 1997, 1 ♂, cl 27.8 mm (NTOU-P 1997-04); 15 May 1998, 1 ♂, cl 25.3 mm, 1 ovigerous ♀, cl 22.5 mm (NTOU-P 1998-05-15); 28 Apr 1999, 1 ovigerous ♀, cl 17.4 mm (NTOU-P 1999-04-28).

Description.—Body entirely covered with fine short setae. Rostrum broad, about 2.5 times as long as wide and ⅓ as long as carapace; more or less horizontal, with tip gently curving dorsad; carinate dorsally, with trifid tip. Carapace (Figs. 1a, 2a) slightly longer than wide; frontal margin with 1 spine between rostrum and anterolateral spines; lateral margin feebly convex, armed with 4 stout spines (including anterolateral spine) at distal half; 1 pair of epigastric spines present; gastric region moderately convex, bearing row of 1–3 longitudinal spines; cervical region moderately excavated; cardiac region raised, bearing large median spine; posterior transverse ridge elevated and generally armed only with pair of large submedian spines.

Abdomen (Fig. 1a) with second and third tergites each having pair of large submedian spines. Telson (Fig. 2d) subdivided into 10 plates; lateral margins fringed with dense setae (very thick in male), posterior margin with plumose setae.

Eyes small, lacking dark pigments, movable, extending to about middle of rostrum. A large spine present between eye and antenna. Basal antennular segment (Fig. 1c) bearing 2 strong distolateral spines, with distal one slightly larger. Antennal peduncle (Fig. 1d) with basal segment bearing distomesial and distolateral spines (distomesial one very strong and long), other segments spineless.

Merus of third maxilliped (Fig. 1e) longer than ischium, flexor margin bearing 3 spines, diminishing in size anteriorly, extensor margin armed with large distal spine.

Third thoracic sternite narrowing posteriorly, anterior margin concave; fourth thoracic sternite much wider, about 3 times as wide as preceding (Fig. 2c).

Chelipeds subequal, long and robust (massive in largest male), surface covered with long setae; merus long and with some large spines; carpus short, with spines mainly restricted at distal margin; palm longer than finger and without large spines (but sharply granular in the largest male); fingers not perfectly gaping, inner margins bearing some intermeshing teeth, outer margins nearly straight except at tips (that of fixed finger becoming convex in largest male).

Walking legs robust, similar, all covered with setae. First walking leg having merus with large distodorsal and distolateral spines, and some dorsal spines; carpus generally armed with 2 distodorsal spines; propodus nearly straight, more than 5 times as long as wide; dactylus much shorter than propodus, distally curving ventrad, ventral margin minutely dentate.

Epipod present only on chelipeds.

Eggs subspherical, about 0.5 mm in diameter.

Coloration (Fig. 3).—Body pale orange to orange, with color of females generally deeper. Rostrum except tip, pale orange or whitish. Fourth or fifth abdominal segments to tailfan from pale orange to pale white posteriorly. Eyes pale orange or nearly whitish. Antennules same color as body but antennal flagella orange red. Cervical groove and cardiac depressions sometimes whitish. Ventral surface whitish except mouth parts and chelipeds pale orange.

Size.—Largest male and female cl 27.8 mm and 24.6 mm respectively. Smallest ovigerous female cl 17.4 mm.

Distribution.—So far known only from the northeastern coast of Taiwan, at depths of about 500 m.

Type locality.—Taiwan, northeastern coast.

Remarks.—The present form is closely related to *Munidopsis camelus* Ortmann, 1892 from Japan and can be readily separately from the other species of the genus by the rostrum being trifid, as well as the second and third abdominal tergites each armed with a pair of large submedian spines. Careful comparisons between *M. camelus* (1 ♂ cl 23.2 mm, 1 ♀ cl 21.5 mm, off Hayama, Sagami Bay, Japan, lobster pot, Oct 1987, H. Ikeda coll. deposited at Kumamoto University Faculty of Education; also see Miyake & Baba 1967) and the Taiwanese material revealed the following differences. The anterior three pereiopods bear distinct epipods in the Japanese material but usually only the chelipeds have epipods in the Taiwanese specimens. However, in one of the Taiwanese specimens (NTOU-P 1997-04), a distinct epipod is also present on the left first walking leg. It seems that the presence or absence of epipod are not always consistent as previously thought for galatheids. Nevertheless, further differences between the Taiwanese and Jap-

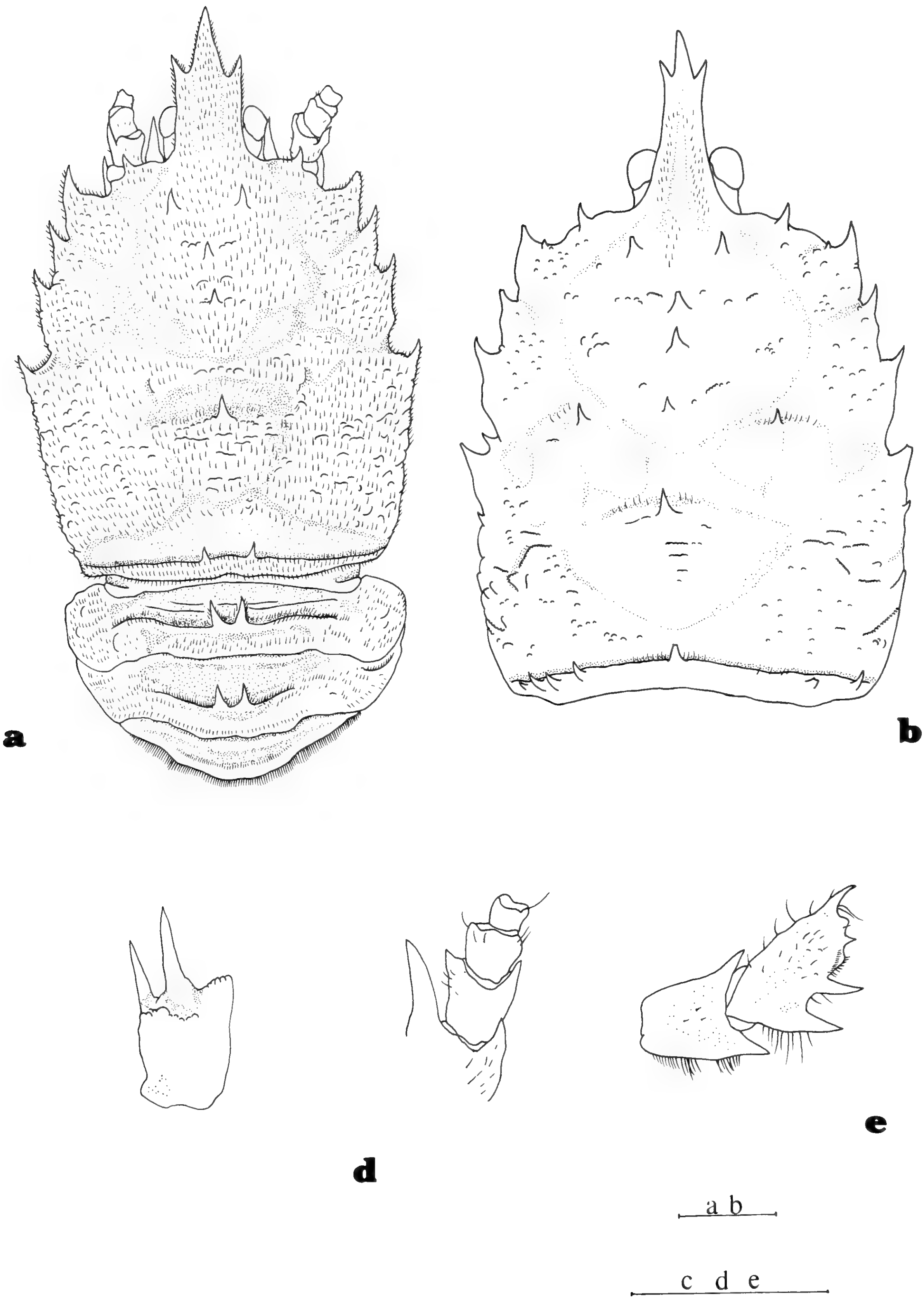

Fig. 1. a, c–e: *Munidopsis formosa,* new species, ♂ holotype cl 20.4 mm, N. E. Taiwan (NTOU-H 1998-08). b: *M. camelus* Ortmann, 1892, ♂ cl 23.2 mm, Sagami Bay, Japan (KB). a, carapace and anterior abdominal somites, dorsal view; b, carapace; c, left basal antennular segment, ventral view; d, left antennal peduncle, ventral view; e, basal segments of endopod of right maxilliped, ventral view. Scale bars = 5 mm.

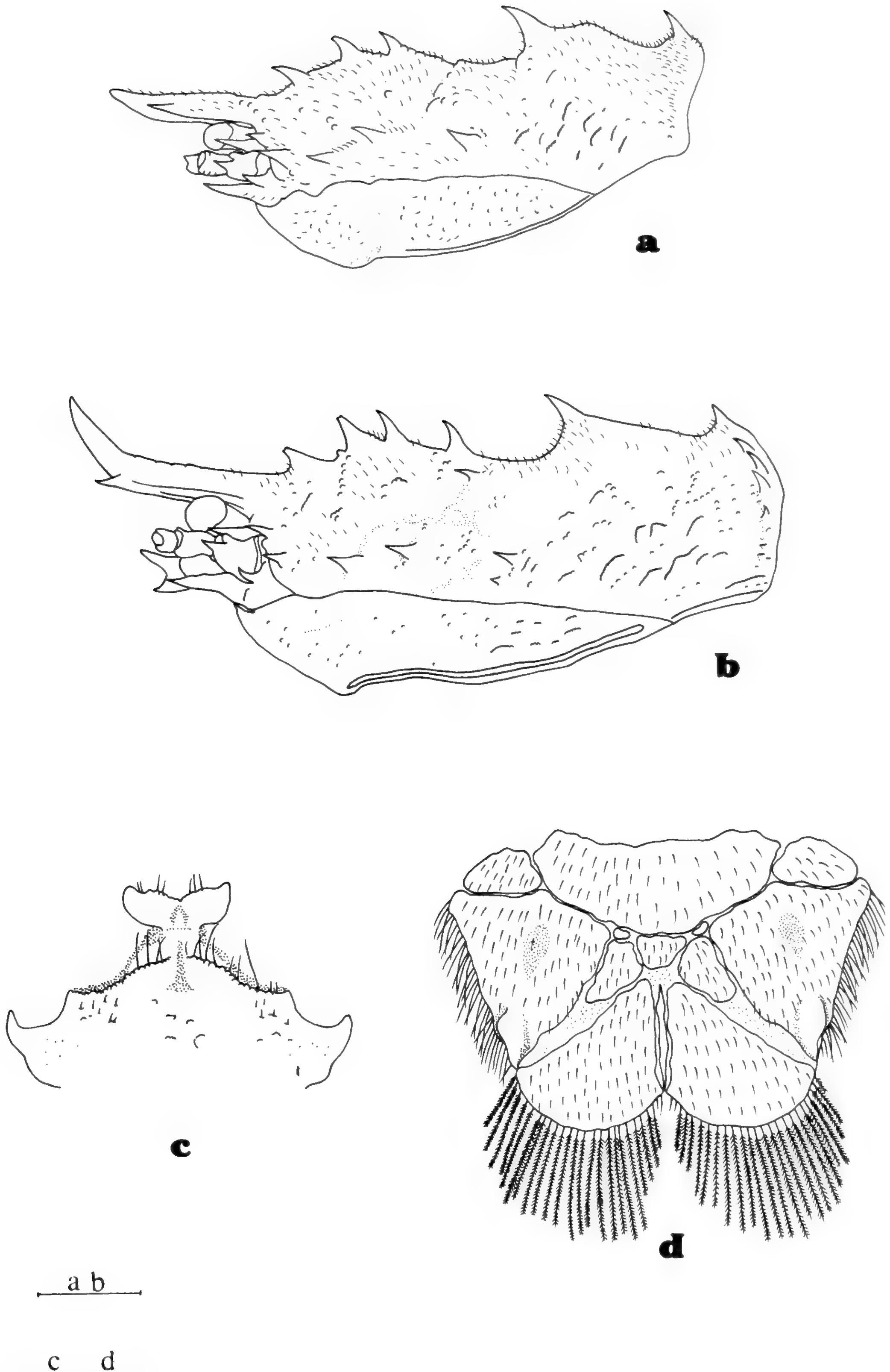

Fig. 2. a, c–d: *Munidopsis formosa*, new species, ♂ holotype cl 20.4 mm, N. E. Taiwan (NTOU-H 1998-08). b: *M. camelus* Ortmann, 1892, ♂ cl 23.2 mm, Sagami Bay, Japan (KB). a–b, carapace, lateral view; c, anterior part of thoracic sternum, ventral view; d, telson, dorsal view. Scale bar = 5 mm.

anese material can be found. The posterior carapace ridge always bear a large median spine which is accompanied with several large lateral spines in *M. camelus* (Fig. 1b). In the Taiwanese form, the posterior carapace ridge generally armed with a pair of submedian spines only (except in one specimen, NTOU-P 1999-1-19, there is one

Fig. 3. *Munidopsis formosa,* new species, ovigerous ♀ paratype cl 22.5 mm, N. E. Taiwan (NTOU-P 1998-05-15).

more small spine present between the large submedian spines) with the lateral parts always devoid of spines (Fig. 1a). Moreover, the rostrum is distinctly narrower (near 4 times as long as wide) and with the tip abruptly curving upward in the Japanese material (Fig. 2b). The rostrum in the Taiwanese form, however, is rather broad (2.5 times as long as wide) and only gently bending upward at tip (Fig. 2a). The coloration of the Japanese material also appears to be more reddish. Color photographs of a live specimen collected off Boso Penisula (180–250 m) showed that the body color of the Japanese material is orange-red. All the above differences show that the Taiwanese form is distinct from *M. camelus* and it is hereby described as new.

The present new species is also similar to *M. regia* Alcock & Anderson, 1894, and *M. plumatisetigera* Baba, 1988. However, *M. formosa* new species, can be readily distinguished from *M. plumatisetigera* by the epipods on the chelipeds and the less spiny body. *M. regia* differs considerably from *M. formosa* in having a much narrower and longer rostrum, and a different spination on the abdomen. Moreover, Alcock (1901) mentioned that the color in life of *M. regia* is "chalky pink".

Munidopsis formosa was collected from about 500 m deep. This is probably the main reason for this species being found only recently. The fishing depth of local deep-water trawlers have extended their trawling depths down to 500–600 m, and many deep-sea animals unknown to Taiwan have been collected, including the present new species.

Etymology.—This species is named after its type-locality Taiwan since it is so far only known from there. Formosa was the old name of Taiwan and is used here as a noun in apposition.

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A new freshwater crab of the genus *Geothelphusa* Stimpson, 1858 (Crustacea: Decapoda: Brachyura: Potamidae) from Yakushima Island, southern Kyushu, Japan

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Abstract.—A new freshwater crab, *Geothelphusa marmorata,* is described from Yakushima Island of Kagoshima Prefecture, southern Kyushu, Japan. It is differentiated from congeners by possession of distally narrowed eyes, chocolate brown or dark red carapace with scattered black speckles in life, stout gastric cristae, a deep H-shaped median gastro-cardiac depression, and laterally curved penultimate segment of the male first gonopod with a mesially curved ultimate segment. This is the second species of *Geothelphusa* Stimpson known from Yakushima Island, and the twelfth species from Japan. Electrophoretic analysis of 15 gene loci suggests that *G. marmorata,* new species, *G. exigua* Suzuki & Tsuda and *G. dehaani* (White) are reproductively isolated.

Freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 are distributed from Taiwan, through the Ryukyu Islands, to the Japanese mainland. Recently, a large number of species were reported from Taiwan and Ryukyu Islands, and 39 species are now recognized in the genus (Shy et al. 1994, Shy & Ng 1998, Tan & Liu 1998). In Japan, 11 species are currently known, i.e., *G. dehaani* (White, 1847), *G. obtusipes* Stimpson, 1858, *G. sakamotoana* (Rathbun 1905), *G. aramotoi* Minei, 1973, *G. tenuimana* (Miyake & Minei 1965), *G. levicervix* (Rathbun 1898), *G. candidiensis* Bott, 1970, *G. miyazakii* (Miyake & Chiu 1965), *G. exigua* Suzuki & Tsuda, 1994, *G. shokitai* Shy & Ng, 1998, and *G. minei* Shy & Ng, 1998 (see also de Haan 1835, Rathbun 1904, Bott 1967, Minei 1974b, Shy et al. 1994). Of these, *G. dehaani* is widely distributed on the Japanese mainland (north of Honshu southward to Nakano-shima of the Tokara Islands, south of Kyushu). The other 10 species are restricted to the southern Kyushu or the Ryukyu Islands, including Amami-ohshima.

During our current study of the population genetics and geographic distribution of *G. dehaani* and *G. exigua* in southern Kyushu, unusual specimens of *Geothelphusa* species were found on Yakushima Island in Kagoshima Prefecture. The unusual eyes, coloration of body, and structure of the male first gonopods of these crabs indicate that they represent a new species that is herein described and illustrated. In addition, a genetic analysis based on electrophoresis is included.

Materials and Methods

For electrophoretic analysis, a total of 201 specimens of *G. dehaani* were collected from three populations (174 specimens from Kotsuki River of the Kagoshima mainland, 20 from Hitotsutani River of the Kagoshima mainland, and seven from Anboh River of the Yakushima Island); 40 specimens of *G. exigua* were collected from two populations (20 specimens from Hitotsutani River and 20 from Kamiharai River of the Kagoshima mainland); and 17 specimens of the new species were collected

Table 1.—List of enzymes and protein, and buffer systems used in electrophoretic analysis. CAPM 6.0; Citric acid-aminopropyl morpholine, pH 6.0: CAPM 7.0; Citric acid-aminopropyl morpholine, pH 7.0: and CT 8.0; Tris-citric acid, pH 8.0.

Enzyme and protein (Abbreviation and E. C. number)	Symbol for locus	Buffer system
Aspartate aminotransferase (AAT, 2.6.1.1)	*AAT**	CAPM 6.0
Adenylate kinase (AK, 2.7.4.3)	*AK**	CAPM 7.0
Glyceraldehyde-3-phosphate dehydrogenase (GAPDH, 1.2.1.12)	*GAPDH**	CAPM 6.0
Glucose-6-phosphate isomerase (GPI, 5.3.1.9)	*GPI**	CAPM 6.0, CAPM 7.0
Hexokinase (HK, 2.7.1.1)	*HK**	CT 8.0
Isocitrate dehydrogenase (IDHP, 1.1.1.42)	*IDHP-1**	CAPM 7.0
	*IDHP-2**	CAPM 7.0
Lactate dehydrogenase (LDH, 1.1.1.27)	*LDH**	CT 8.0
Malate dehydrogenase (MDH, 1.1.1.37)	*MDH-1**	CAPM 7.0
	*MDH-2**	CAPM 7.0
Malic enzyme (ME, 1.1.1.38)	*ME**	CT 8.0
Mannose-6-phosphate isomerase (MPI, 5.3.1.8)	*MPI**	CT 8.0
Phosphogluconate dehydrogenase (PGDH, 1.1.1.44)	*PGDH**	CAPM 7.0
Phosphoglucomutase (PGM, 5.4.2.2)	*PGM**	CT 8.0
General protein (PROT)	*PROT**	CAPM 7.0

from the Anboh River during 1997. Specimens used for electrophoretic analysis were stored at −35°C with a small volume of freshwater. Muscles were extracted and homogenized with an equal volume of cold distilled water. Horizontal starch gel electrophoresis was performed for the detection of enzyme and protein variations (Table 1). Locus and gene nomenclature follows that of Shaklee et al. (1990). Multiple loci for a given enzyme were distinguished by numerals, with "*−1**" representing the most anodally-migrating isozyme. All alleles studied are designated alphabetically. The genetic distance was calculated using Nei's formula (Nei 1972). All the specimens were collected by the junior author.

The holotype and a paratype are deposited in the Kitakyushu Museum of Natural History, Kitakyushu (KMNH), and additional paratypes in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and Marine Biological Laboratory, Faculty of Fisheries, Kagoshima University, Kagoshima (KUMB). Measurements shown in parentheses under "Material examined" indicate the maximum carapace width in millimeters. Abbreviations used include: M, male; F, female.

Family Potamidae Ortmann, 1896
Genus *Geothelphusa* Stimpson, 1858
Geothelphusa marmorata, new species
Figs. 1–3, Tables 1–3

Material examined.—River Anboh: Arakawa, 1280 m alt., 24 Oct 1998: holotype, M (29.4), KMNH-IvR 900005, paratype, F (21.1), KMNH-IvR 900006, M (23.2), F (28.9), USNM 268571, 1120 m alt., 8 Jul 1997; 3 M (30.5, 26.8, 21.8), KUMBcr 1053 (used for the electrophoretic analysis).

Diagnosis.—Penultimate segment of male first gonopod slightly curved laterally, ultimate segment strongly curved mesially, cone-shaped, with terminal aperture. Ocular peduncle swollen proximally, cornea small. Gastric cristae stout, H-shaped median gastro-cardiac depression distinct. In life, carapace and pereopods chocolate brown or dark red with scattered black speckles.

Description.—Carapace much broader than long, smooth, devoid of setae (Fig. 1a); faint, short oblique striae on epibranchial and posterolateral regions; epi- and uro-gastric regions distinct, former divided into 2 stout gastric cristae by deep median groove; H-shaped median gastro-cardiac depression deep, wide; deep transverse

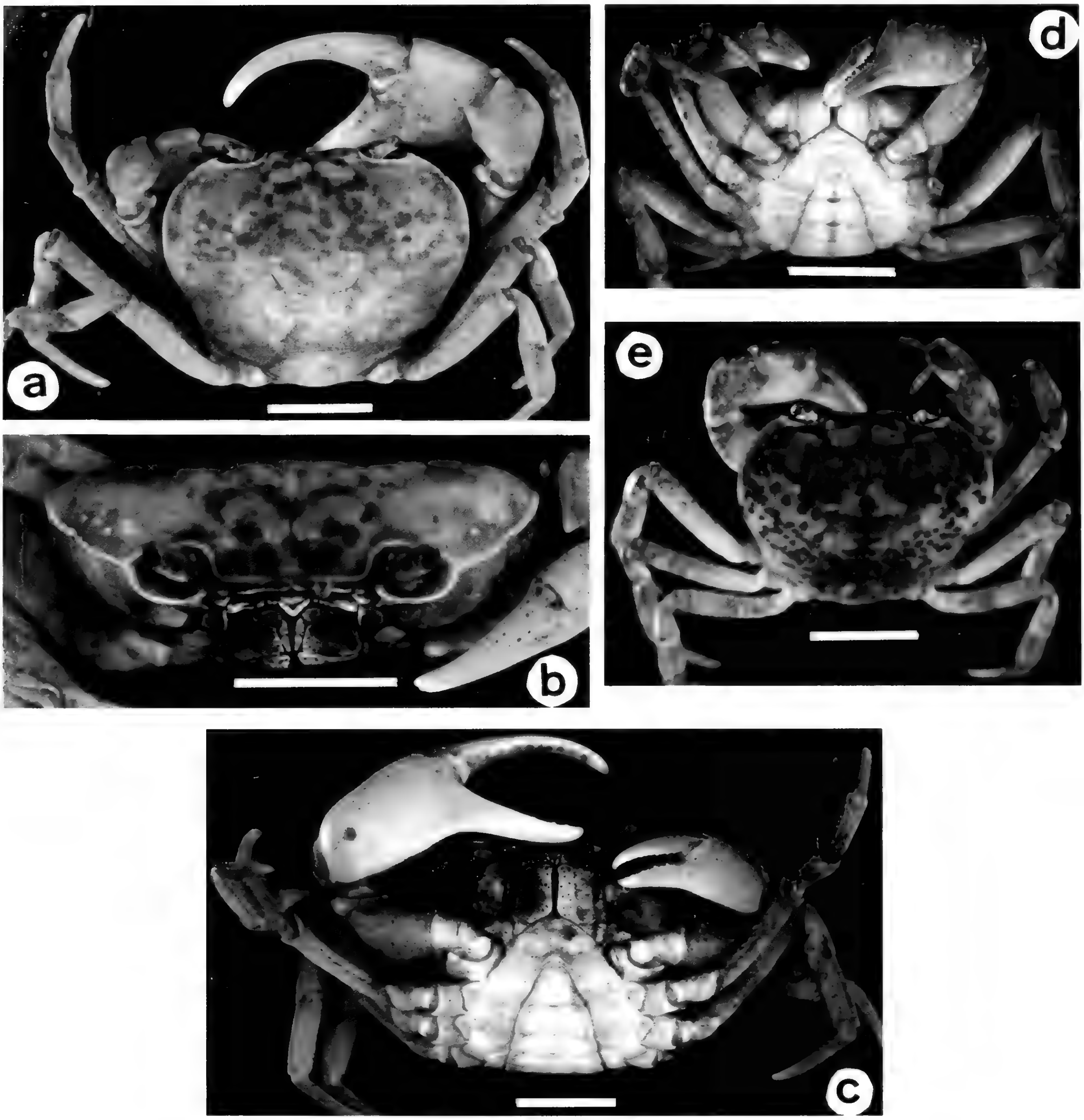

Fig. 1. *Geothelphusa marmorata*, new species, male holotype (KMNH-IvR 900005): a, dorsal view; b, frontal view; c, ventral view. Male paratype (USNM 268571): d, ventral view; e, dorsal view. Scales indicate 10 mm.

groove between cardiac and intestinal regions; cervical groove obsolete on epibranchial region. Anterolateral margin of carapace cristate, lined with fine rounded granules; epibranchial notch rudimentary. Posterior margin of epistome divided into 3 parts by 2 deep notches (Fig. 1b), granules present on lower edge of epistome, absent medially. Lower orbital margin and groove between subhepatic and pterygostomian regions lined with faint granules.

Eyestalk short, proximally swollen, distally slender. Cornea small, slightly wider than distal portion of ocular peduncle (Fig. 1a, b).

Merus of third maxilliped broad, squarish, with deep depression (Fig. 1b). Palp 3-segmented, connected on inner distal angle of merus, tip of palp not below distal margin of ischium. Exopod slender, longer than ischium, with small 5-segmented flagellum (Figs. 1c, d, 2a; exopodal flagellum damaged in holotype).

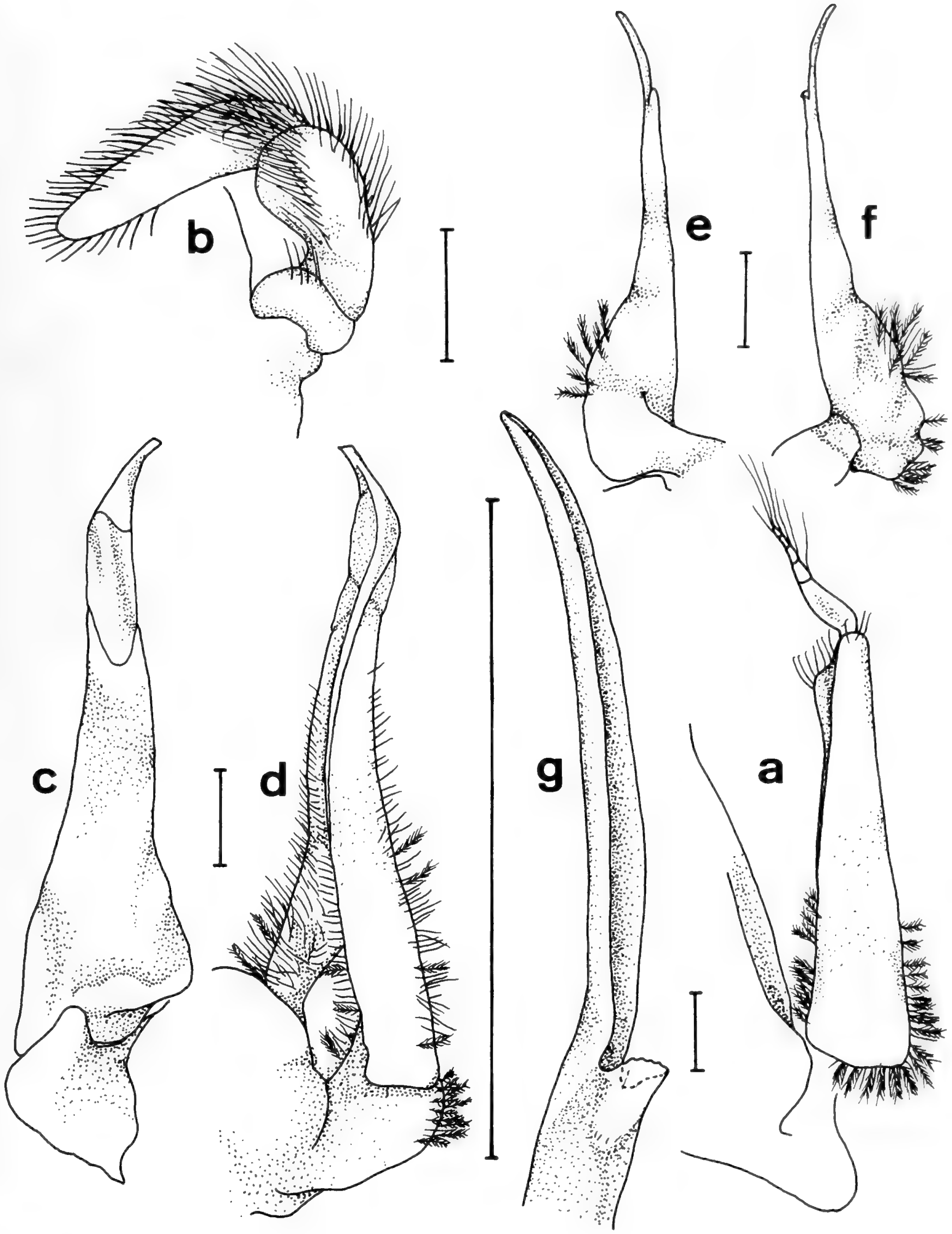

Fig. 2. *Geothelphusa marmorata,* new species, male paratype (USNM 268571): a, exopod of third maxilliped, frontal view; b–g, male holotype (KMNH-IvR 900005): b, left mandibular palp, ventral view; c, left first gonopod, dorsal view; d, same, ventral view; e, left second gonopod, dorsal view; f, same, ventral view; g. tip of left second gonopod, dorsal view. Scales indicate 1 mm.

Chelipeds asymmetrical in males, symmetrical in females; movable finger of large cheliped strongly curved in large male (not so in small male) (Fig. 1a, c–e); palm smooth, outer surfaces convex (Fig. 1a, c, d). Carpus of large cheliped almost smooth, with stout inner tooth, below which is a low projection (Fig. 1a, e). Carpus of small cheliped without any projection below stout inner tooth.

Palp of mandible 3-segmented (Fig. 2b); distal segment uniramous, sickle-shaped; median segment longer than wide, distal half expanded; proximal segment short, stout.

Penultimate segment of adult male first gonopod (G 1) gently curved laterally (Fig. 2c, d), synovial membrane short, about 3 times as long as broad (Fig. 2c), ultimate segment strongly curved mesially (Fig. 2c, d), cone-shaped, with terminal aperture. Male second gonopod (G 2) slender, flat, weakly convex at proximal part, a small cup-like structure on distal one-fourth, tip of G 2 concave (Fig. 2e, f, g). G 2 shorter than G 1, tip of G 2 not protruding from aperture of G 1 when coupled.

Color in life.—Carapace and pereopods (Fig. 1a, e) chocolate brown or dark red with scattered black speckles. Lower part of palm and inmovable finger of both chelipeds white in large male, movable finger and upper part of palm of chelipeds chocolate brown. In small males and females, lower part of palm of both chelipeds white, fingers and upper part of palm dark red. Otherwise, no color variation observed between sexes and sizes.

Genetic characteristics.—Among fifteen gene loci coding for twelve enzymes and one protein, allelic substitution was observed between *G. marmorata,* new species, and *G. exigua* at Lactate dehydrogenase (*LDH**), Isocitrate dehydrogenase-1 (*IDHP-1**), and Phosphogluconate dehydrogenase (*PGDH**) loci (Table 2), and between *G. marmorata* and *G. dehaani* at *PGDH** locus. Nei's genetic distances (*D*) were calculated between all samples based on the fifteen loci (Table 3). The *D* values of *G. dehaani* populations and *G. exigua* populations were low (0.016–0.066 and 0.037, respectively). However, the *D* values between *G. marmorata* and *G. dehaani* were high, ranging from 0.155 to 0.2, and the values between *G. marmorata* and *G. exigua* were higher (0.473 and 0.534).

Etymology.—The specific name is derived from the Latin *marmoratus,* marbled, alluding to the characteristic color pattern of the new species.

Remarks.—The saber-like G 1 and the 3-segmented mandibular palp with uniramous distal segment present in the new species are characteristics of the genus *Geothelphusa* (see Bott 1970). The medium-sized carapace, anterolateral margin lined with small rounded granules and absence of an epibranchial tooth ally *G. marmorata* with *G. dehaani, G. exigua, G. bicolor, G. miyazakii, G. candidiensis, G. ferruginea, G. tali, G. shokitai,* and *G. minei,* from which it is distinguished by several features.

The life color of the carapace with scattered black speckles easily distinguishes *G. marmorata* from *G. dehaani, G. bicolor, G. miyazakii, G. ferruginea,* and *G. tali.* The most definitive differences are in the structure of the G 1. The G 1 ultimate segment in eight related species, except for *G. exigua,* is straight or slightly curved mesially (Bott 1967, 1970; Minei 1973, 1974a; Suzuki & Tsuda 1994, Shy et al. 1994, Shy & Ng 1998). The ultimate segment in *G. exigua* is curved laterally and tapering, and has a subterminal aperture. However, in *G. marmorata,* this segment is strongly curved mesially, ending in a papilla-like tip with a terminal aperture. The eyestalks in the eight related species are constricted medially, and the cornea and proximal part of the ocular peduncle are swollen. In *G. marmorata,* only the proximal part of the ocular peduncle is swollen, while the cornea and the distal part of the peduncle are proportionately narrower as in *G. exigua.*

Previous genetic studies revealed that the different populations of *G. dehaani* in Japan exhibit varying allele frequencies in some gene loci in Japan (Sugawara & Gamo 1984, Nakajima & Masuda 1985, Aotsuka et al. 1995, Ikeda et al. 1998). If allelic substitution is observed at any gene locus among the different morphological groups based on coloration, shape of G 1, and so on, there is a possibility of the groups actually representing different species. In the previous studies, there was no allelic substitution in any gene locus among the different morphological groups. However, Ikeda et al. (1998) observed an allelic replace-

Table 2.—Allele frequencies at 15 loci for 3 populations of *G. dehaani*, 2 populations of *G. exigua* and 1 population of *G. marmorata* in Kagoshima Prefecture.

		G. dehaani			*G. exigua*		*G. marmorata*
Locus	Allele	Koutsuki	Hitotsutani	Anboh	Hitotsutani	Kamiharai	Anboh
*AAT**	**a*	0.027	0.025	0.000	0.975	1.000	0.059
	**b*	0.922	0.975	0.929	0.025	0.000	0.941
	**c*	0.051	0.000	0.071	0.000	0.000	0.000
*AK**	**a*	0.961	1.000	1.000	1.000	0.750	1.000
	**b*	0.028	0.000	0.000	0.000	0.250	0.000
	**c*	0.011	0.000	0.000	0.000	0.000	0.000
*GAPDH**	**a*	1.000	1.000	1.000	1.000	1.000	1.000
*GPI**	**a*	0.253	0.025	0.000	0.600	0.200	0.059
	**b*	0.726	0.475	0.000	0.000	0.275	0.647
	**c*	0.018	0.050	0.000	0.400	0.525	0.000
	**d*	0.003	0.425	1.000	0.000	0.000	0.235
	**e*	0.000	0.025	0.000	0.000	0.000	0.059
*HK**	**a*	0.085	0.000	0.000	0.000	0.000	0.000
	**b*	0.755	1.000	0.786	0.917	0.975	0.735
	**c*	0.160	0.000	0.214	0.083	0.025	0.265
*IDHP-1**	**a*	0.891	1.000	1.000	0.000	0.000	1.000
	**b*	0.070	0.000	0.000	0.000	0.000	0.000
	**c*	0.039	0.000	0.000	0.000	0.000	0.000
	**d*	0.000	0.000	0.000	1.000	1.000	0.000
*IDHP-2**	**a*	1.000	1.000	1.000	0.050	0.000	1.000
	**b*	0.000	0.000	0.000	0.950	1.000	0.000
*LDH**	**a*	1.000	1.000	1.000	0.000	0.000	1.000
	**b*	0.000	0.000	0.000	1.000	1.000	0.000
*MDH-1**	**a*	0.964	0.900	1.000	0.975	0.950	1.000
	**b*	0.036	0.100	0.000	0.025	0.050	0.000
*MDH-2**	**a*	0.994	0.975	1.000	1.000	1.000	1.000
	**b*	0.006	0.025	0.000	0.000	0.000	0.000
	**c*	0.000	0.000	0.000	0.000	0.000	0.000
*ME**	**a*	1.000	1.000	1.000	1.000	1.000	1.000
*MPI**	**a*	1.000	1.000	1.000	1.000	1.000	1.000
*PGDH**	**a*	0.000	0.000	0.000	0.000	0.000	1.000
	**b*	0.991	1.000	1.000	1.000	1.000	0.000
	**c*	0.009	0.000	0.000	0.000	0.000	0.000
*PGM**	**a*	0.875	0.925	0.571	0.925	0.375	0.971
	**b*	0.018	0.075	0.214	0.075	0.625	0.000
	**c*	0.108	0.000	0.214	0.000	0.000	0.029
*PROT**	**a*	1.000	1.000	1.000	0.000	0.000	0.059
	**b*	0.000	0.000	0.000	1.000	1.000	0.941

Table 3.—Genetic distance among 3 populations of *G. dehaani*, 2 populations of *G. exigua* and 1 population of *G. marmorata* in Kagoshima Prefecture.

		G. dehaani			*G. exigua*	
		Koutsuki (I)	Hitotsutani (II)	Anboh (III)	Hitotsutani (IV)	Kamiharai (V)
G. dehaani	(II)	0.016				
	(III)	0.032	0.066			
G. exigua	(IV)	0.469	0.462	0.519		
	(V)	0.520	0.518	0.559	0.037	
G. marmorata	Anboh (VI)	0.156	0.155	0.200	0.473	0.534

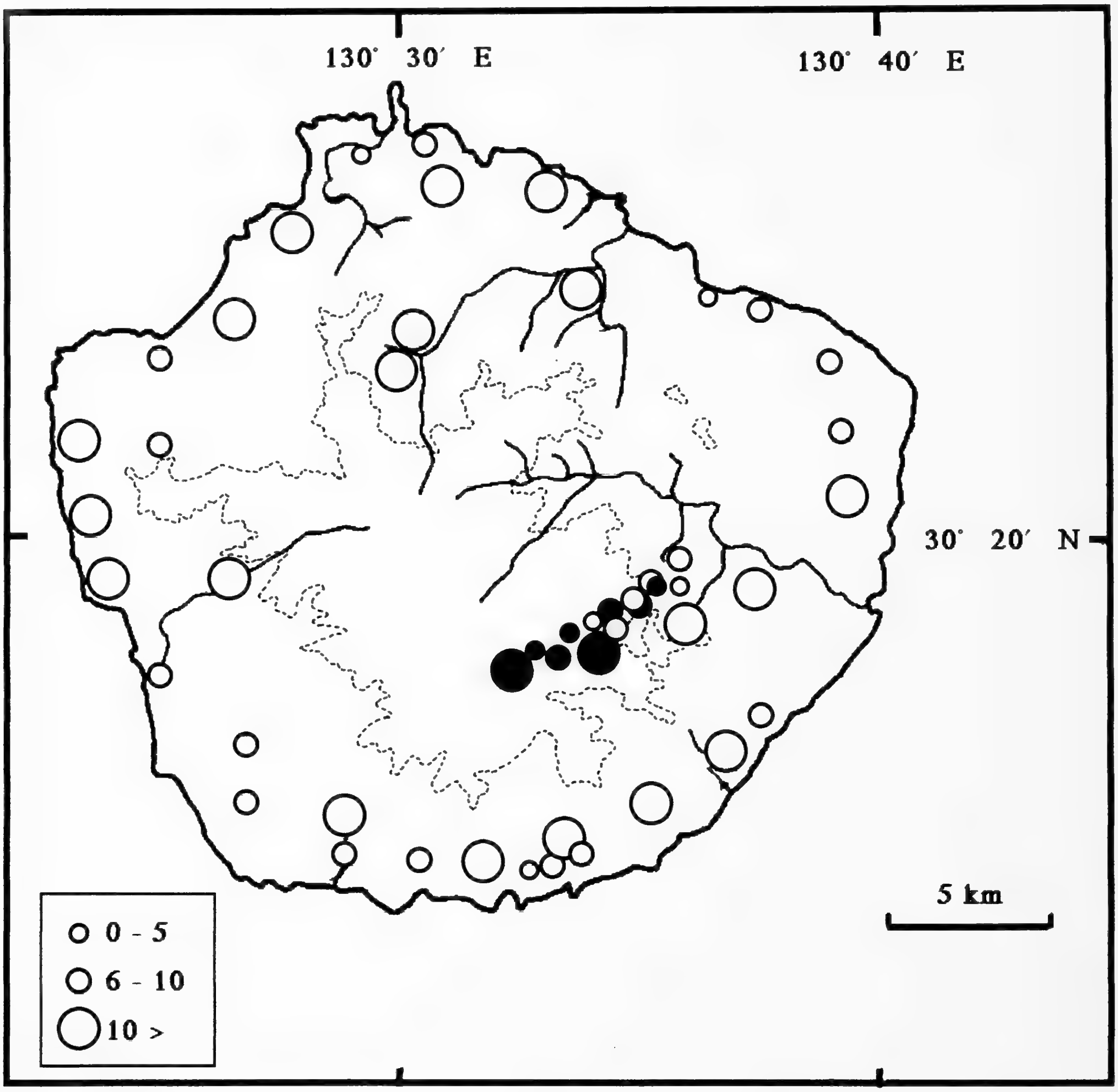

Fig. 3. Distribution and abundance of *G. marmorata,* new species (solid circle) and *G. dehaani* (White, 1847) (white circle) in Yakushima Island, Kagoshima, Japan. Arabic numerals correspond to size of circles in the square at bottom left, and indicate the number of crabs captured per ten minutes by one person. Broken line shows 1000 m contour line.

ment at three loci between color morphs representing allopatric populations. No morphological differences in G 1 structure have been reported among those populations thus far. In this study, allelic substitution was observed at three loci among *G. marmorata, G. dehaani,* and *G. exigua.* In addition, *G. marmorata,* and *G. dehaani* are sympatric in Anboh River, Yakushima Island. The observed allelic substitutions, therefore, strongly indicate the presence of reproductive isolation among three species. The genetic distance (*D* values) further suggest that *G. marmorata,* belongs to a different evolutionary lineage from the Anboh population of *G. dehaani.*

Distribution.—The specimens of *G. marmorata,* examined have been obtained only in the area above 950 m altitude on Yakushima Island, Kagoshima Prefecture (Fig. 3). *Geothelphusa marmorata,* and *G. dehaani* are sympatric, having been taken together at some locations from 950 m to 1350 m altitude.

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A new species of the genus *Neostylodactylus* Hayashi & Miyake, 1968 (Crustacea: Decapoda: Stylodactylidae) from southern Japan

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Abstract.—A new species of stylodactylid shrimp, *Neostylodactylus litoralis,* is described and illustrated on the basis of four ovigerous females collected from sublittoral zones on the Ogasawara and Ryukyu Islands at depths of 3–10.5 m. This new species is readily distinguished from the five described species of *Neostylodactylus* Hayashi & Miyake in having a non-produced posterior margin of the telson, the noticeably elongate mesialmost pair of posterior spines on the posterior margin of the telson, and unarmed meri of the third to fifth pereiopods.

Members of the caridean shrimp family Stylodactylidae are classified in five genera (Hanamura & Takeda 1996), with species known to occur in deep waters exceeding 100 m (Chace 1983; Cleva 1990, 1994, 1997). Only one stylodactylid, *Neostylodactylus amarynthis* (De Man, 1902), has been recorded in shallow waters less than 100 m (Kemp 1925, Chace 1983, Cleva 1990).

While sampling the sublittoral zone (3.0–10.5 m) of the Ogasawara and Ryukyu Islands, southern Japan, we obtained four stylodactylid specimens referable to the genus *Neostylodactylus* Hayashi & Miyake, 1968. Morphologically, our specimens differed from the five previously described species of *Neostylodactylus,* and clearly represent a new species described here.

Specimens were collected by using a hand net, and are deposited in the Coastal Branch of Natural History Museum and Institute, Chiba (CMNH). The method of measurements follows Cleva (1990). The abbreviation CL indicates postorbital carapace length.

Family Stylodactylidae

Genus *Neostylodactylus* Hayashi & Miyake, 1968

Neostylodactylus litoralis, new species

Figs. 1–4

Type series.—Holotype: ovig. ♀ CL 2.9 mm (CMNH-ZC 00071), 27°11.5′N, 142°07.0′E, Takinoura, Ani-jima Island, Ogasawara Islands, 5 m, Aug 1996, coll. Y. Morita. Paratypes: 1 ovig. ♀ CL 2.8 mm (CMNH-ZC 00103), 27°04.6′N, 142°07.1′E, Hyotan-jima Islet, NW of Chichi-jima Island, Ogasawara Islands, 8 m, May 1996, coll. T. Gomi. 1 ovig. ♀ CL 2.4 mm (CMNH-ZC 00119), 26°13.7′N, 127°27.4′E, Gahi-jima Islet, Kerama Group, Ryukyu Islands, 3 m, 3 Sep 1998, coll. A. Ono.

Non-type material.—1 ♀ CL~2.2 mm (molting) (CMNH-ZC 00137), 26°42.0′N, 127°27.4′E, Ie-shima Island, Ryukyu Islands, 10.5 m, 14 Jun 1996, coll. T. Nomura.

Diagnosis.—Small sized stylodactylid species (known specimens CL 2.4–2.9 mm). Carapace armed with supraorbital spine. Rostrum well developed, falling short of distal end of scaphocerite, armed with movable spines on both dorsal and ventral margins. Pleuron of third to fifth abdominal somite each armed with posterolateral spine. Telson armed with 2 pairs of dorsal and dorsolateral spines, posterior margin ending roundly, armed usually with 3 pairs of spines, mesialmost pair longest, with 4 plumose setae between spines. Scaphocerite armed laterally with 5 or 6 movable spines. Third to fifth pereiopods with

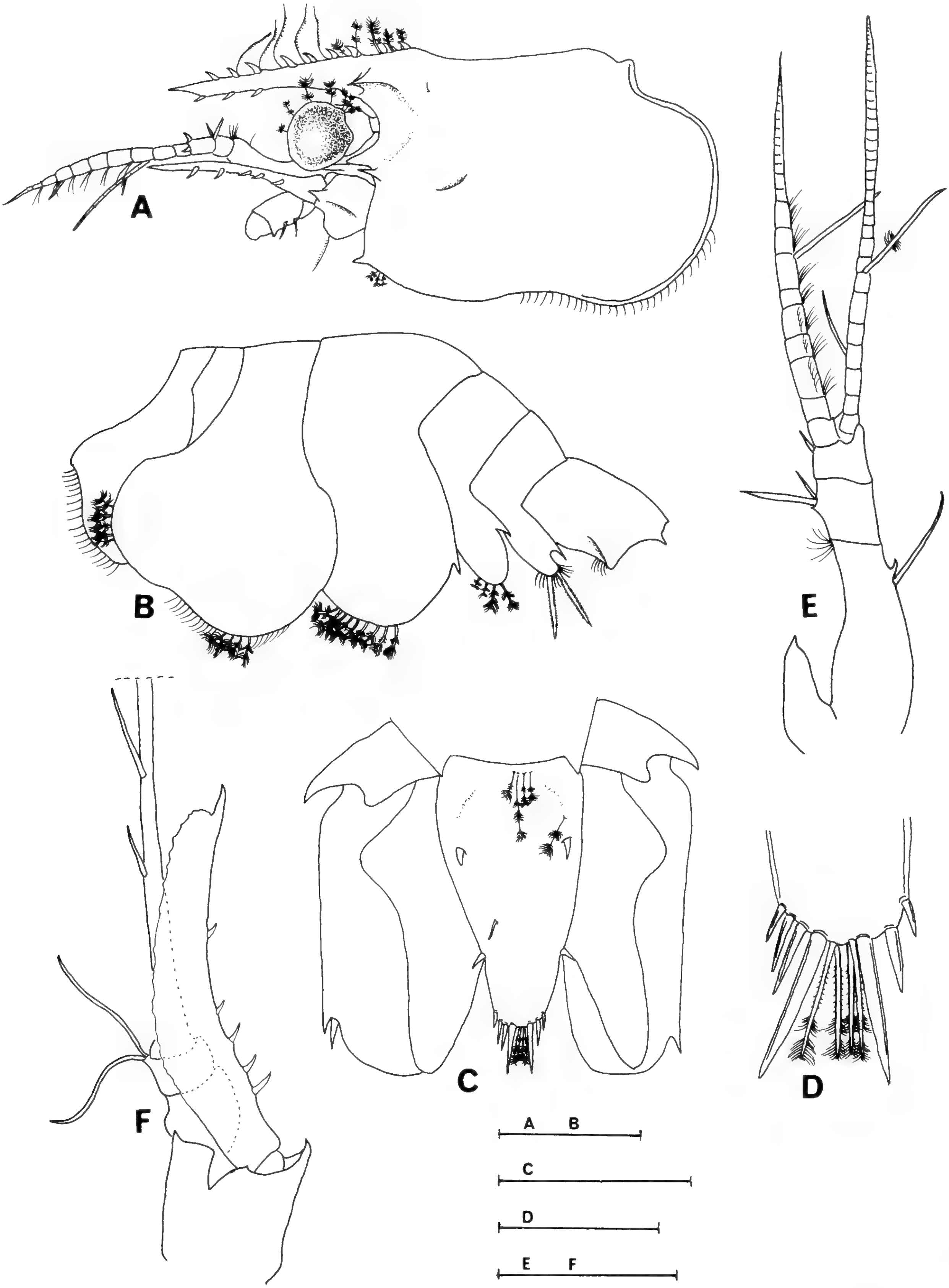

Fig. 1. *Neostylodactylus litoralis,* new species. Holotype (CMNH-ZC 00071). A, left carapace with cephalic appendages, in lateral view. B, right first to sixth abdominal somites, in lateral view. C, telson and uropods, in dorsal view. D, tip of telson, in dorsal view. E, right antennular peduncle, in ventral view. F, right antenna, in dorsal view. Scales equal 1.5 mm (A, B), 1 mm (C, E, F), 0.5 mm (D).

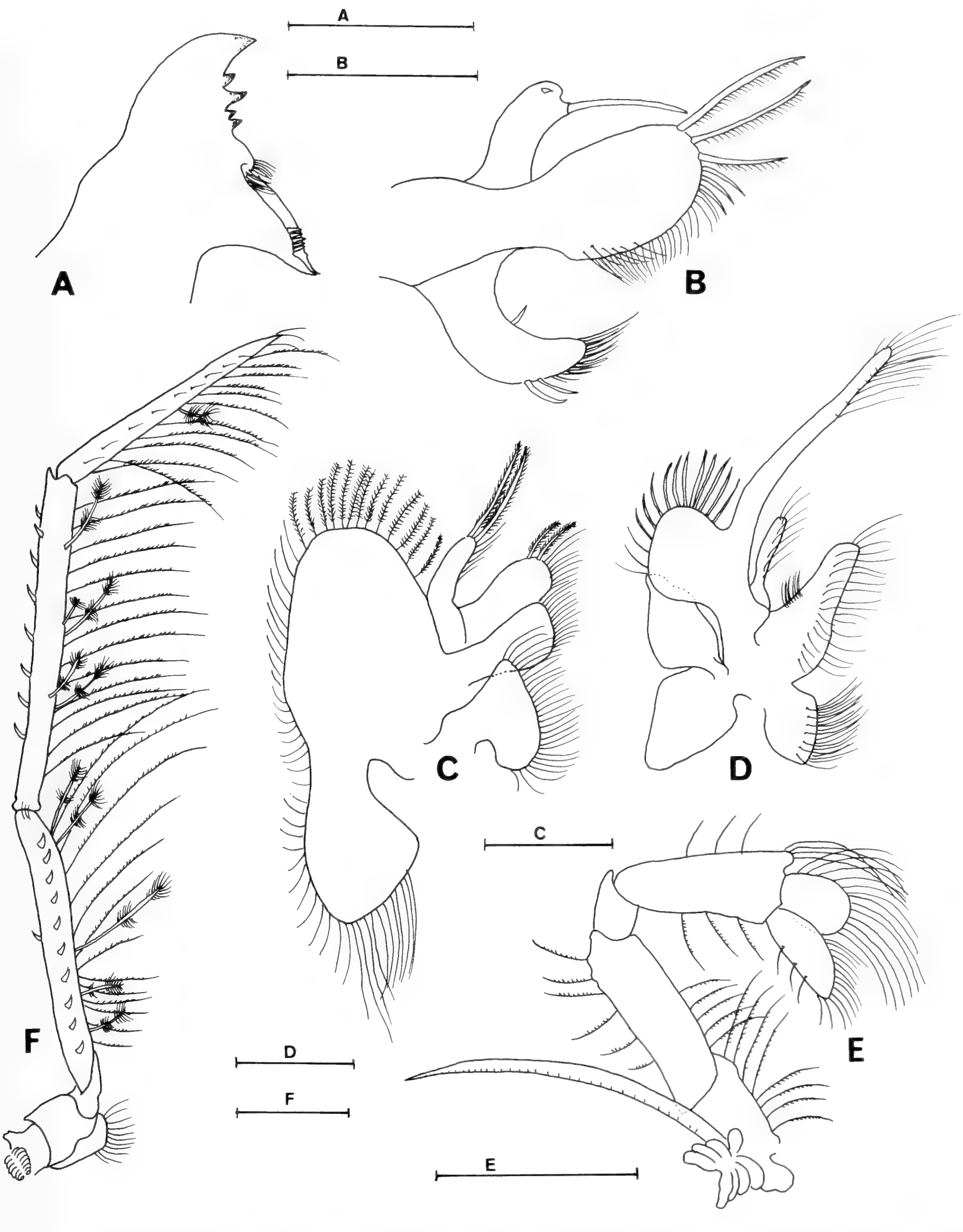

Fig. 2. *Neostylodactylus litoralis,* new species. Holotype (CMNH-ZC 00071). A, right mandible. B, right maxillule. C, right maxilla. D, right first maxilliped. E, right second maxilliped. F, right third maxilliped. Scales equal 0.5 mm (A, B, C, D), 1 mm (E, F).

uniunguiculate dactyli, armed posteriorly with 3 movable spines; meri unarmed.

Description.—Carapace (Fig. 1A) smooth, glabrous; supraorbital spine acute, continuous with feeble postorbital ridge; postorbital region slightly concave; infraorbital margin anteriorly produced in triangular process, distinctly overreaching tip of antennal spine; hepatic depression indistinct; antennal spine submarginal, directed

Table 1.—Branchial formula of *Neostylodactylus litoralis,* new species (female only).

	Maxillipeds			Pereiopods				
	I	II	III	I	II	III	IV	V
Pleurobranchs	—	—	—	1	1	1	1	1
Arthrobranchs	—	—	1	—	—	—	—	—
Podobranchs	—	1	—	—	—	—	—	—
Epipods	1	1	—	—	—	—	—	—
Exopods	1	1	—	—	—	—	—	—

anteriorly; pterygostomian angle armed with spine. Rostrum (Fig. 1A) straight, slightly descending, 0.71–0.79 times as long as carapace; dorsal margin armed with 6–12 articulated teeth, 3–9 teeth anterior to level of postorbital margin, more or less equidistant, interspace with simple long plumose setae, 1 tooth just above level of postorbital margin; dorsal carina with 2 teeth posterior to level of postorbital margin, and with 2 or 3 robust plumose setae; ventral margin armed with 1-3 articulated teeth.

Abdominal somites (Fig. 1B) smooth, glabrous; first somite with pleuron sparsely fringed with simple setae; pleuron of second somite fringed with robust plumose setae along anterolateral and ventromesial margins, with simple setae ventrally; pleuron of third somite armed with small acute tooth posterolaterally, densely fringed with robust plumose setae ventrally; pleuron of fourth somite armed with acute tooth posterolaterally, sparsely fringed with robust plumose setae marginally; pleuron of fifth somite armed with acute tooth posterolaterally, with plus 2 or 3 elongate stout setae bearing setules, and simple setae ventrally; sixth somites 0.33–0.46 times as long as carapace, unarmed posteroventrally.

Telson (Fig. 1C) 0.52–0.68 times as long as carapace, dorsal surface armed with 2 pairs of spines, posterior pair situated more laterally than anterior pair, midline with transverse row of long plumose setae proximally; posterior margin (Fig. 1D) feebly rounded, not produced in acute median process, armed with 3 pairs of spines (an extra spine on left side in holotype), mesialmost pair noticeably elongate, flanking 4 stout plumose setae.

Eye with lightly pigmented cornea, and plumose setae, without ocellus; corneal diameter 0.21–0.29 times as long as carapace; stalk slender.

Antennular peduncle (Fig. 1E) slender, slightly overreaching or falling slightly short of rostral apex; proximal segment armed with ventromesial spine and long spiniform seta posterior to spine, dorsodistal margin fringed with short simple setae; stylocerite reaching midlength of proximal segment, tapering distally in acute point; intermediate segment armed dorsolaterally with 2 spiniform setae; distal segment short, about half length of intermediate segment. Upper flagellum ventrally with short setae, seventh article with long spiniform seta distolaterally; seventh article of lower flagellum with long, plumose seta.

Antenna (Fig. 1F) with scaphocerite with lateral margin distinctly concave, slightly overreaching rostral apex, 0.69–0.75 times as long as carapace, lateral margin armed with 5 or 6 acute movable spines, distolateral tooth distinctly overreaching rounded distal blade; carpocerite fringed with long simple setae distomesially; basicerite armed with spine distolaterally; antennal flagellum armed with long spiniform setae, articulations much indistinct.

Mandible (Fig. 2A) without palp; incisor process well developed, slightly rounded, distal margin armed with 5 blunt teeth; molar process truncated distally, with short sparse setae.

Maxillule (Fig. 2B) with feebly bilobed palp, inner lobe with long simple seta, armed dorsally with small spine proximal to outer lobe; upper lacinia fringed with numerous setae, distal 3 setae considerably longer, plumose; lower lacinia distally with numerous simple setae, midlength of mesial margin with single short seta.

Maxilla (Fig. 2C) with palp distally fringed with long plumose setae; basal endite bilobed, with numerous setae on mesial

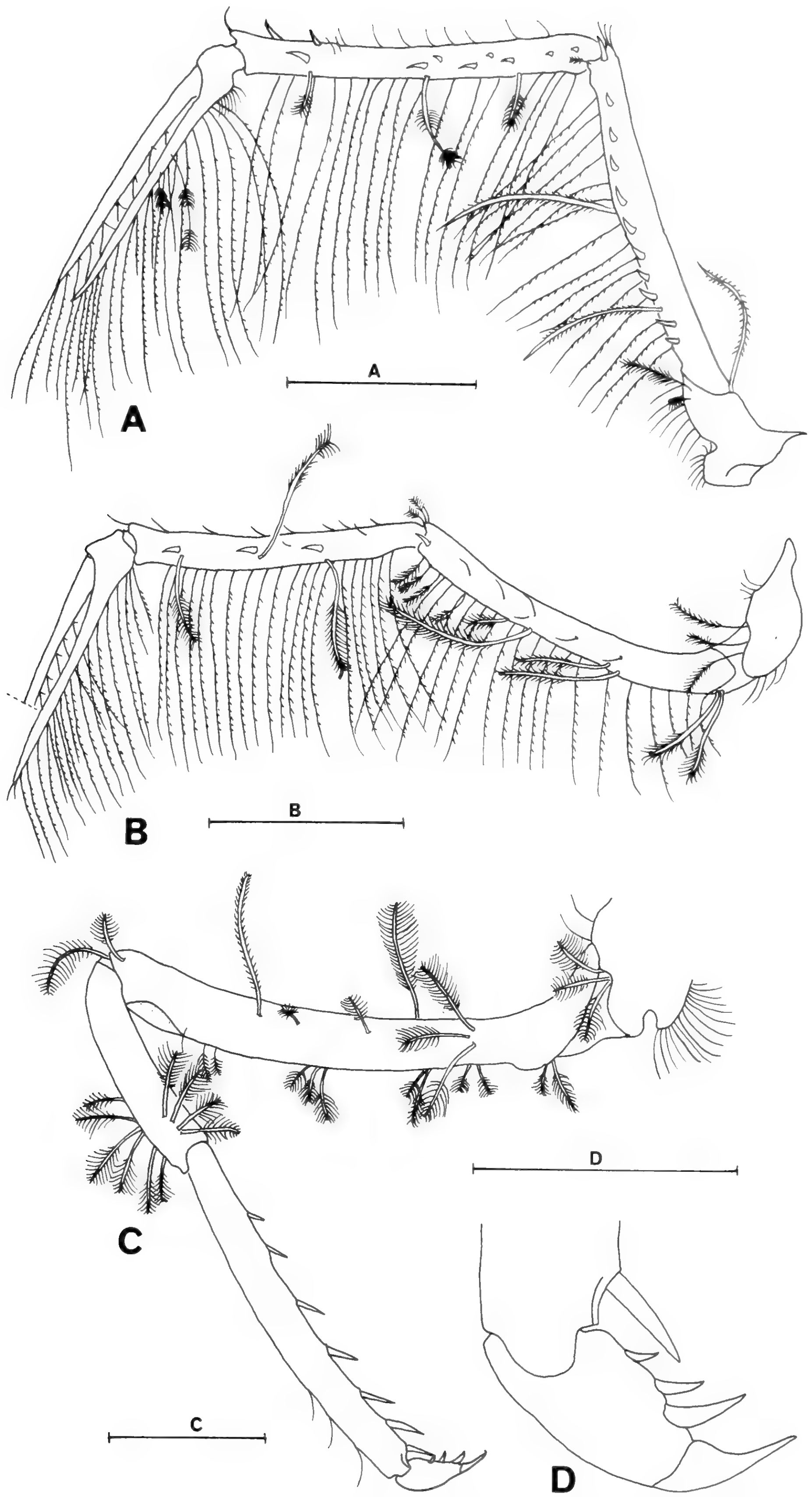

Fig. 3. *Neostylodactylus litoralis,* new species. Holotype (CMNH-ZC 00071). A, left first pereiopod. B, left second pereiopod. C, left third pereiopod. D, same, dactylus. Scales equal 1.5 mm (A, B), 1 mm (C), 0.5 mm (D).

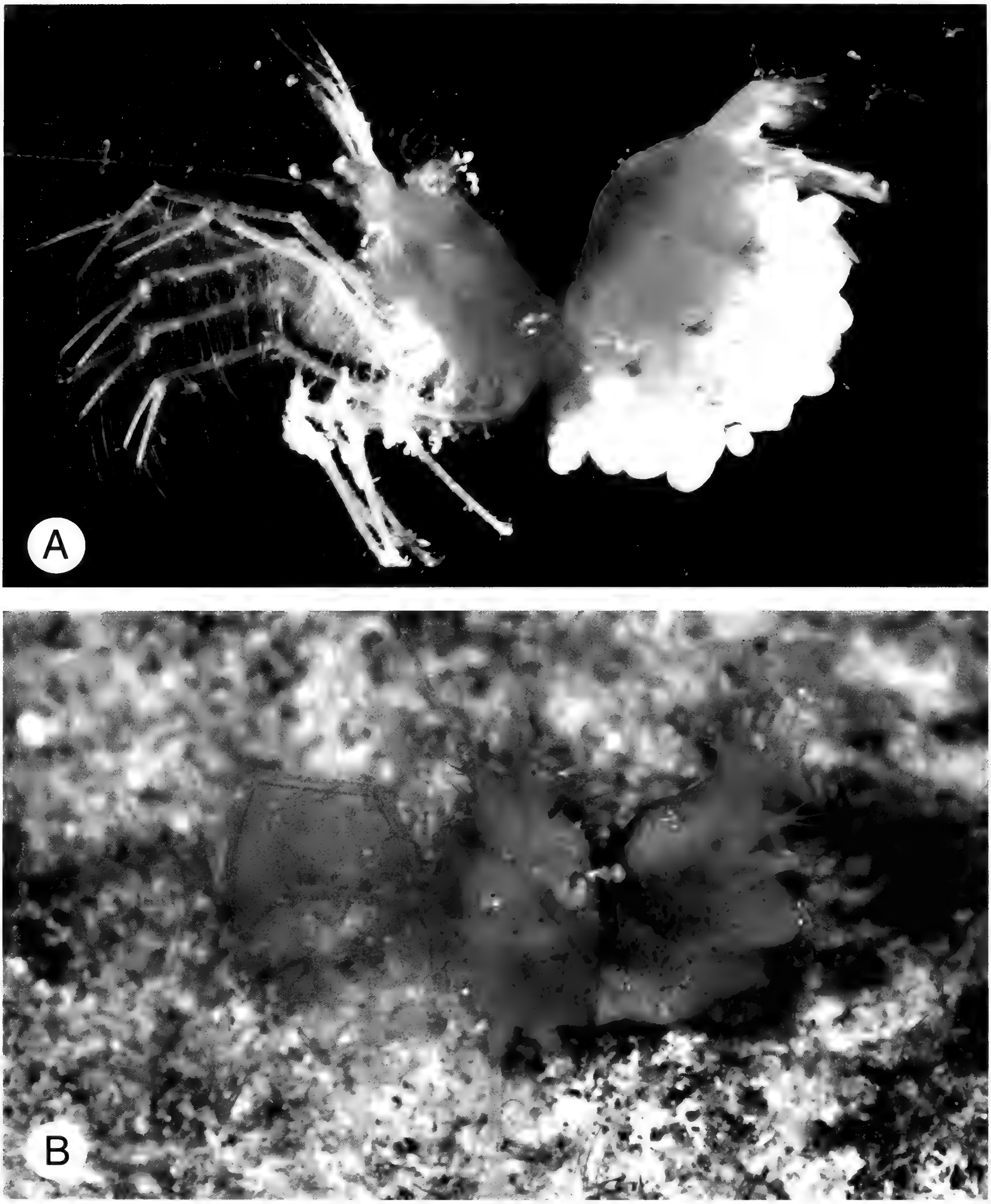

Fig. 4. *Neostylodactylus litoralis*, new species. A, holotype (CMNH-ZC 00071), fresh specimen, lateral view (photo by H. Tachikawa); B, paratype (CMNH-ZC 00119), alive in aquarium (photo by A. Ono).

margin, upper lobe slightly overreaching level of distal margin of lower lobe; coxal endite feebly rounded, with numerous setae. Scaphognathite broad, rounded, marginally with numerous setae.

First maxilliped (Fig. 2D) with well developed exopod; caridean lobe well developed, rounded, palp slender, setose; basal endite distally truncate, with 3 rows of numerous setae; coxal endite distinct, with 2 rows of numerous setae mesially. Epipod bilobed.

Second maxilliped (Fig. 2E) with well developed exopod; terminal 2 segments implanted side by side at distal end of antepenultimate segment, flexor segment slightly longer and narrower than extensor segment, distally fringed with numerous simple setae, flexor margin with 3 simple setae, extensor segment rounded, marginally with numerous long simple setae; antepenultimate segment protruded dorsodistally, with long simple setae, external and mesial margins with long simple setae; carpal segment short, naked; ischiomeral segment with dorsal margin sparsely with setae with setules, mesially with similar setae. Epipod oblong, with well developed podobranch.

Third maxilliped (Fig. 2F) slender, overreaching distal margin of scaphocerite by full length of ultimate segment, without exopod; flexor margins of distal 3 segments densely fringed with long setae with numerous setules and sparsely with short plumose setae; penultimate segment 1.21–1.22 times as long as ultimate segment, armed with row of 5–8 articulated spines; antepenultimate segment with lateral row of 9–12 articulated spines, and 1 spine on dorsal surface. Small arthrobranch present.

Branchial formula as indicated in Table 1.

First pereiopod (Fig. 3A) overreaching distal end of scaphocerite by distal margin of carpus; chela with reduced palm about one-fifth of movable and fixed fingers, proximally convex, cutting edges of both fingers entire, without tooth, movable finger with flexor margin fringed with long setae with numerous setules, fixed finger fringed ventrally with similar setae; carpus 0.83–0.93 times as long as carapace, dorsal margin armed with row of spiniform setae, lateral surface armed with row of spines, ventral margin fringed with long setae with numerous setules and with a few plumose setae; ischiomerus armed laterally with row of spines, with short simple setae distolaterally, ventral margin fringed with long setae with numerous setules and with a few plumose setae.

Second pereiopod (Fig. 3B) overreaching distal end of scaphocerite by proximal margin of movable finger; chela with reduced palm about 0.20 times as long as fingers, proximally convex, cutting edges of both fingers entire, without tooth, movable finger with flexor margin fringed with long setae with numerous setules, fixed finger fringed ventrally with similar setae; carpus 0.67–0.79 times as long as carapace, dorsal margin armed with row of spiniform setae, lateral surface armed with row of spines, ventral margin densely fringed with long setae with numerous setules and with a few plumose setae; ischiomerus armed laterally with row of spiniform setae, distolaterally with spine and short plumose setae, ventral margin densely fringed with long setae with numerous setules and sparsely with long plumose setae.

Third pereiopod (Fig. 3C) slightly overreaching midlength of scaphocerite; dactylus (Fig. 3D) uniunguiculate, armed with 3 movable spines posteriorly; propodus 0.75–0.76 times as long as carapace, 2.20–2.25 times as long as carpus, distomesial margin concave, ventrally armed with short spines; carpus unarmed, with robust plumose setae distolaterally; ischiomerus unarmed, 0.76–0.83 times as long as carapace, 2.20–2.50 times as long as carpus, laterally with long robust plumose setae, dorsodistal margin with short plumose setae, ventrally with short plumose setae. Fourth and fifth pereiopods similar to third pereiopod. Fourth pereiopod falling slightly short of midlength of scaphocerite. Fifth pereiopod overreaching basicerite by full length of dactylus.

Uropod (Fig. 1C) slightly overreaching distal margin of telson. Protopodite armed with strong lateral spine; exopod armed with acute fixed tooth distolaterally, mesially with stout movable tooth; endopod with prominent lateral lobe proximally.

Color in life (Fig. 4).—Carapace and abdominal somites reddish-violet, posterolateral part of carapace and dorsolateral parts of the first to fourth somites darker than other parts, covered with numerous fine red spots. Antennular peduncle transparent-reddish, flagella transparent-whitish. Scaphocerite transparent, antennal basicerite reddish-violet. Telson, third maxilliped, anterior two pereipopods and uropods transparent. Ambulatory pereiopods with coxae and basis reddish-violet with numerous red spots; meri, carpi, propodi and dactyli transparent. Pleopods transparent.

Etymology.—*litoralis,* from Latin *litus,* the shore, in allusion to the habitat in a remarkably shallow depth in the vertical distributional range of Stylodactylidae.

Distribution.—Known only from the Ogasawara and Ryukyu Islands, southern Japan.

Remarks.—Based on the distally acute stylocerite, the prominent supraorbital spine, and the absence of the mandibular palp and arthrobranchs on all pereiopods, the specimens clearly belong in the genus *Neostylodactylus.*

The rostral armature does show marked intraspecific variations. The holotype is armed dorsally with six teeth anterior to the level of the postorbital margin. The dorsal margin anterior to the orbital margin has nine teeth in the paratype from the Ogasawara Islands (CMNH-ZC 00103), and three teeth in that from the Ryukyu Islands (CMNH-ZC 00119).

The non-type material (CMNH-ZC 00137) was molting when captured.

Collectors of the present specimens observed that *N. litoralis* appeared to face upwards. The carapace was bent strongly backwards towards the abdominal somites, with the dorsal surface of the carapace almost in contact with the somites (see Fig. 4B).

In recent taxonomic studies dealing with this genus (Chace 1983; Cleva 1990, 1994, 1997; Komai 1997), five *Neostylodactylus* species were recognized: *N. affinis* Hayashi & Miyake, 1968; *N. amarynthis* (De Man, 1902); *N. hayashii* Komai, 1997; *N. investigatoris* (Kemp, 1925); and *N. sibogae* (De Man, 1918).

The non-produced posterior margin of the telson and the unarmed meri of the ambulatory pereiopods readily distinguish *N. litoralis* from all other congenerics. In other congeneric species, the posterior margin of the telson is acutely produced mesially, and the meri of ambulatory pereiopods are each armed with one or more lateral spines (see De Man 1918, 1920; Kemp 1925, Hayashi & Miyake 1968, Chace 1983, Komai 1997). Moreover, Dr. R. Cleva (in litt.) kindly informed us that the long mesialmost pair of spines on the posterior margin of the telson is also a characteristic of this new species. Furthermore, *N. litoralis* differs from *N. amarynthis,* the type species of the genus, and *N. affinis,* in having the rostrum falling short of the distal end of the scaphocerite, and the telson armed with two pairs of spines instead of five and three respectively. The smooth pleura of the first and second abdominal somites and the lack of the spine on the lateral surface of the sixth abdominal somite also separate the present new species from *N. amarynthis.* The rostral formula separate *N. litoralis* from *N. affinis.* From *N. investigatoris* and *N. sibogae,* the present new species is readily distinguished by having an armed ventral margin of the rostrum, and the presence of marginal spines on the third to fifth abdominal somites. *Neostylodactylus litoralis* differs from *N. hayashii* by having a much shorter rostrum, which falls short of the distal end of the scaphocerite; the rostral armature; the lateral margin of the scaphocerite armed with spines; and the number of spines on the dorsal surface of the telson.

Acknowledgements

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On the male of *Scutumara enodis* Ng & Nakasone, 1993 (Crustacea: Decapoda: Brachyura: Grapsidae)

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Abstract.—The male of the unusual grapsid, *Scutumara enodis* Ng & Nakasone, is described for the first time, and the species is compared with its congeners, *S. laniger* (Tesch) and *S. miyakei* (Nakamura & Takeda). The male characters of *S. enodis,* the type species of the genus, provide further evidence to support the establishment of *Scutumara* Ng & Nakasone, for these three species. The male abdomen and male first gonopods of *S. enodis* are, however, distinctly different from those of *S. laniger* and *S. miyakei.*

A male specimen of the coral reef grapsid crab, *Scutumara enodis* Ng & Nakasone, 1993, was recently collected by the second author in Ishigaki Island, Yaeyama Group, the Ryukyus. This species was originally described from only a single subadult female. This study describes the male specimen of this species, and gives information on the male abdomen and male first pleopod (G1). Our observations provide additional evidence in support of the establishment of the genus *Scutumara* Ng & Nakasone, 1993.

Measurements are given in mm in the order: carapace width by length. Specimens used here are deposited in the Zoological Reference Collection (ZRC), Department of Biological Sciences, National University of Singapore; Natural History Museum & Institute (CBM), Chiba, Japan; and National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM).

Family Grapsidae MacLeay, 1838
Subfamily Varuninae Alcock, 1900

Scutumara enodis Ng & Nakasone, 1993
(Figs. 1, 2)

Scutumara enodis Ng & Nakasone, 1993: 1, figs. 1–2.

Material examined.—Holotype, female (5.8 × 5.9 mm) (ZRC.1993.1), under littoral coral sand, Kunri-Hama Beach, Sesoko Island, Okinawa, Ryukyus, Japan, coll. P.K.L. Ng & Y. Nakasone, Apr 1992. Others—1 male (4.9 × 5.1 mm) (CBM-ZC 3604), beach near Fukido-gawa river-mouth, Ishigaki Island, Yaeyama group, Japan, coll. T. Komai, 24 Mar 1997.

Description of male.—Carapace slightly longer than broad; dorsal surface smooth, glabrous, without setae; regions not defined, strongly convex transversely and longitudinally, gastric region most convex (Fig. 1A). Frontal margin slightly convex, entire; lateral lobes not visible dorsally, slightly deflexed downwards; lateral edges apparently confluent with supraorbital margin from dorsal view, but not confluent from frontal view; inner edges of smooth, entire supraorbital margins strongly deflexed downwards, much more than outer edges of front, forming slight crimp at junction between frontal and supraorbital margins. Infraorbital margin not distinctly cristate, slightly raised; not granulated or striated. Anterolateral margin slightly arcuate, subcristate, very faintly trilobed, lobes separated by very broad, shallow clefts; external orbital lobe most distinct, very broad; second, third lobes more like weak undulations. Posterolateral margins not sharply demarcated from anterolateral margin, appearing almost straight, distinctly converging. Orbits small, eyes completely filling orbit, corneae well developed. Pterygostomial, suborbital, branchial regions smooth. Orbital hiatus completely filled by large basal anntennal segment; flagellum completely enclosed within orbit. Antennules folding obliquely, fossae very large; basal segment large, subtriangular in shape, broader than long. Posterior margin of epistome weakly sinuous, with 3 distinct ridges (1 median, 2 lateral); ridges separated from each other by narrow gap. Endostomial region with 3 well developed longitudinal palatal ridges (1 median, 2 lateral); lateral palatal ridges joining inner edges of lateral ridges of posterior epistomial margin.

Third maxilliped with foliaceous merus, broader than long; anterolateral angle strongly produced, auriculiform; distal margin distinctly bilobed, outer lobe larger, its base with small median cleft. Ischium longer than broad, sulcus not discernible. Small, distinct rhomboidal gape formed between inner margins of meri and ischia of third maxillipeds when closed. Exopod with obtuse, blunt inner subdistal angle, flagellum longer than width of merus (Fig. 1B).

Chelipeds small, subequal, outer, inner surfaces smooth, glabrous; merus, carpus without spines or teeth; inner distal angle of carpus with broad, low, rounded lobe. Outer surface of chela with low but distinct ventral ridge running from near proximal part of palm to almost tip of pollex (Fig. 1C); inner surface without setae at base of fingers. Fingers distinctly longer than palm; cutting edge of both fingers with numerous denticles, ending in recurved, sharp tips; no gape discernible when fingers closed.

Ambulatory legs with second pair longest (Fig. 1D). All segments smooth, without spines or setae. Dorsal and ventral margins of merus sub-cristate, dorsal margin with blunt subdistal tooth. Dactylus tapering to slender, acute tip (Fig. 1E).

Male abdomen triangular (Fig. 1F); lateral margins sparsely setose; first abdominal segment weakly arched, with very weak transverse ridge; second segment narrow, short; third segment broad, slightly swollen laterally but medially depressed with proximal margin broader than distal margin, lateral margins rounded; fourth segment broader but shorter than fifth segment; fifth segment with proximal and distal margins straight, lateral margins slightly concave; sixth segment quadrate, lateral margins trapezoidal, weakly convex, proximal margin slightly concave, convex medially. Telson sub-triangular, lateral margins weakly concave, distal margin rounded.

Lateral margins of first 2 thoracic sternites finely granulated; suture between sternites 2 and 3 slightly convex towards abdomen; lateral margins of sternites 3 and 4 sinuous, with deep, broad notch demarcating edge of suture; median groove between sternites 5 and 6 narrow; space between sternites 8 very narrow throughout length (Fig. 2A).

Penis located at base of eighth sternite (Fig. 2A). G1 relatively slender, weakly curving outwards, reaching to anterior margin of fifth sternite (Fig. 2B); terminal lobe elongate, apparently 2-articulated, dorsally curved; genital opening lateral to base of terminal lobe; subterminal lobe chitinous, rounded, narrower than terminal lobe, densely setose (Figs. C–E). G2 short, small.

Distribution.—Southern Japan (Okinawa south to Ishigaki Islands, Ryukyus).

Remarks.—Ng & Nakasone (1993) established *Scutumara* and transferred two species previously placed in *Pseudograpsus, S. laniger* (Tesch, 1918), and *S. miyakei* (Nakamura & Takeda, 1972), to this new genus. Although the type specimen of *S. enodis* was represented only by a subadult female, Ng & Nakasone (1993) argued that on the basis of differences on the carapace and ambulatory legs, *S. enodis, S. laniger* and *S. miyakei* are distinct enough to war-

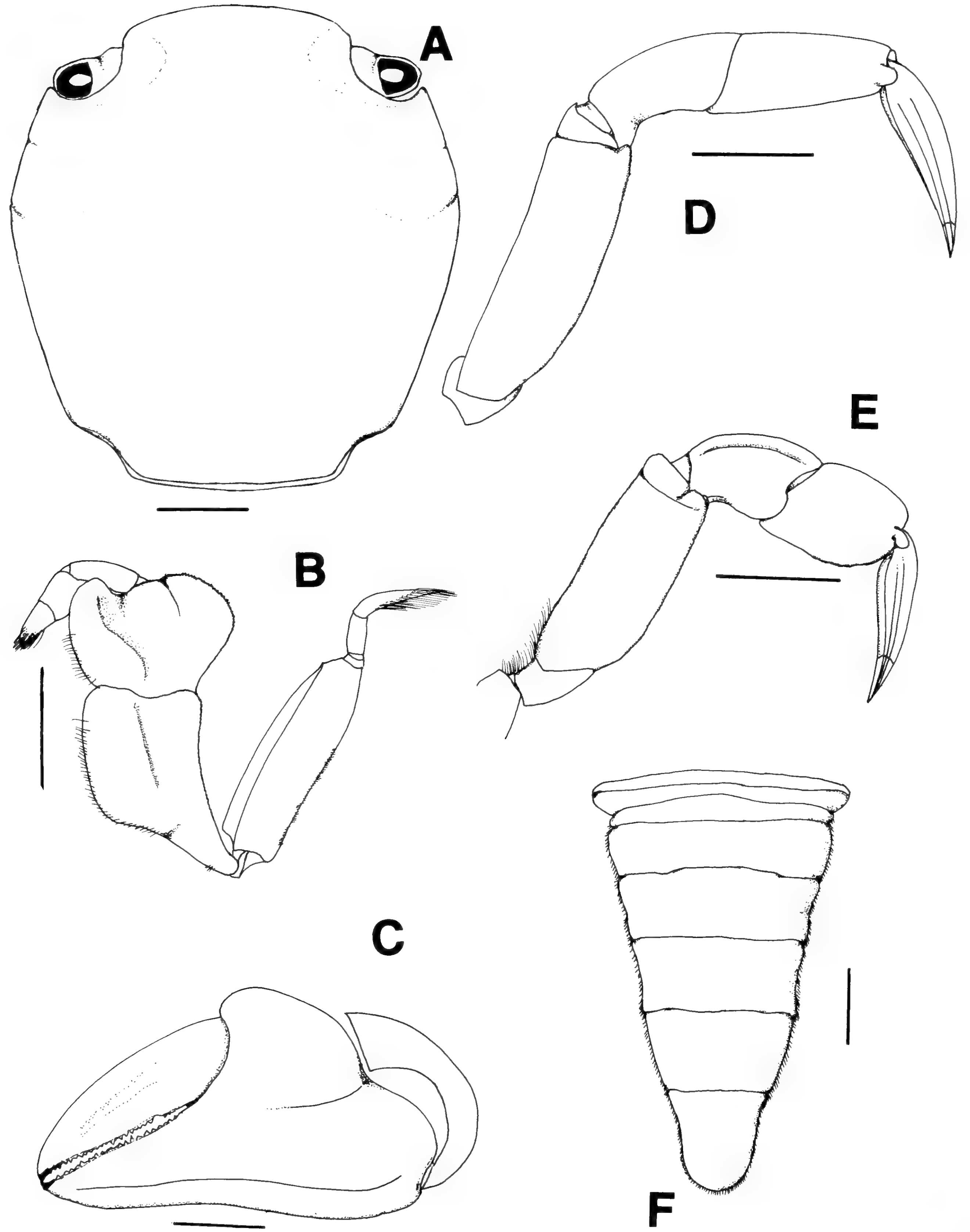

Fig. 1. *Scutumara enodis* Ng & Nakasone, 1993 (male, 4.9 by 5.1 mm, CBM-ZC 3604). A, carapace; B, third maxilliped; C, dorsal view of left chela; D, second ambulatory leg; E, fourth ambulatory leg; F, abdomen. Scales: A, C = 1.0 mm; B, E, F = 0.5 mm.

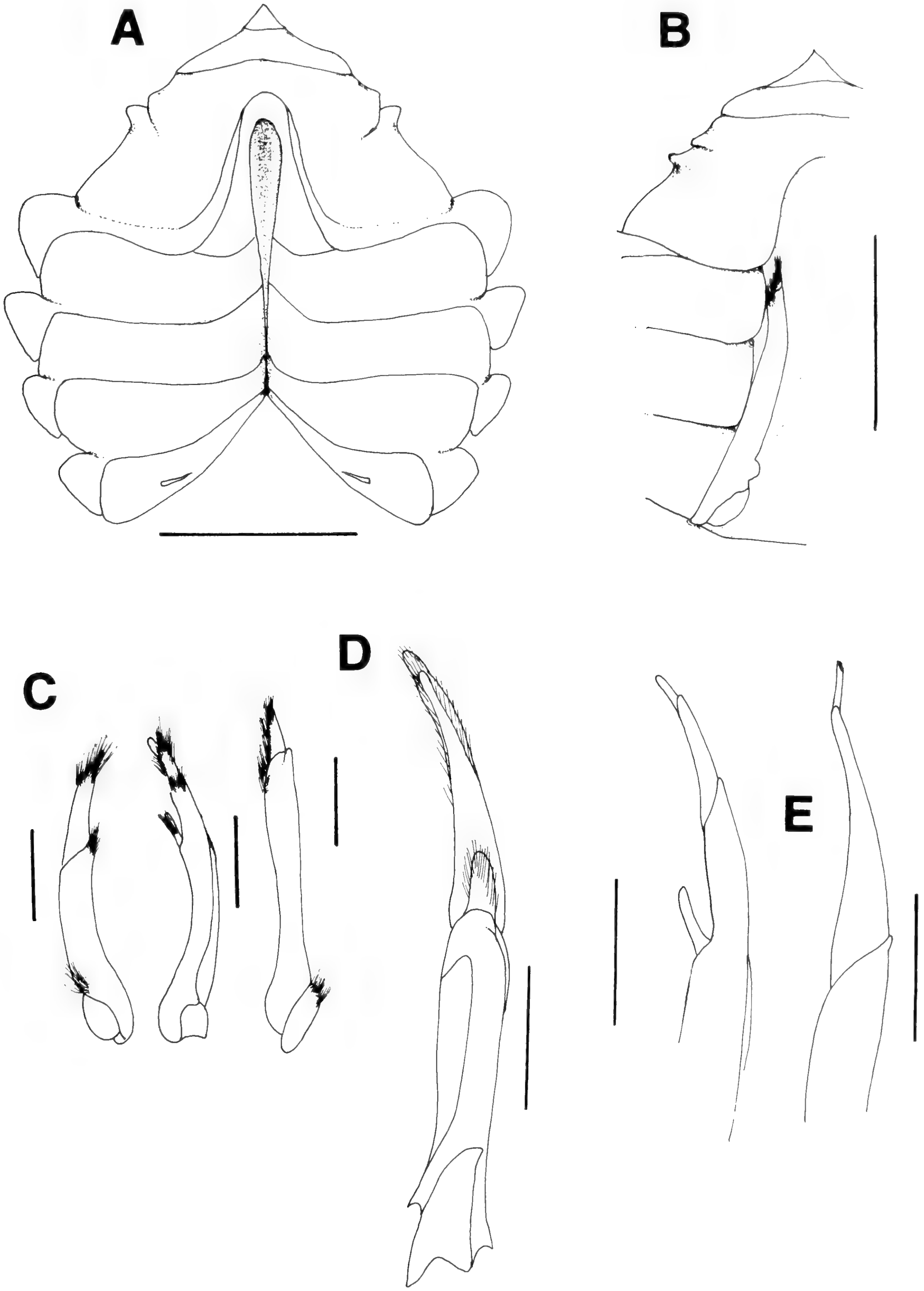

Fig. 2. *Scutumara enodis* Ng & Nakasone, 1993 (male, 4.9 by 5.1 mm, CMB-ZC 3604). A, sternum; B, natural position of male first gonopod; C, male first gonopod in different view; D, enlarge view of the G1; E, different views of the shaven enlarged distal region of G1. Scales: A, B = 1.0 mm, C = 0.5 mm, D, E = 0.25 mm.

rant their placement in *Scutumara.* The discovery of the male *S. enodis* provide further evidence to the establishment of *Scutumara.* We have also found that the exopod of the third maxillipeds of all three species reaches two-thirds the length of the merus, while the exopod of the third maxillipeds in *Pseudograpsus* species reach to half the length of the merus, a character that further seperates these two genera. In addition, all known *Scutumara* species are ivory-cream white when alive, while all *Pseudograpsus* species are chestnut in color. The lateral margins of the sixth abdominal segment are generally rounded in *Scutumara,* however, in *Pseudograpsus,* the lateral margins are angular at the distal region. The sixth abdominal segment in *Scutumara* (length to width ratio between 3.5 and 5.0) is narrow compared to *Pseudograpsus* (length to width ratio between 1.5 to 2.0). Noteworthy is that the dentation on the anterolateral margin of the male specimen of *S. enodis* is less prominent than that of the female holotype. We interpret this as intraspecific variation.

Scutumara enodis is separated from *S. laniger* and *S. miyakei* by the different structure of the frontal margin, the absence of gastric and cardiac grooves, and absence of setae on the inner surface of the palm (Ng & Nakasone 1993). Based on published descriptions and figures of *S. laniger* and *S. miyakei,* the male abdomen and gonopod of *S. enodis* are also different. The third abdominal segment is narrower in *S. enodis* (length to width ratio: ca. 4.1) than for its congeners (ca. 3.5 in *S. laniger,* ca. 3.1 in *S. miyakei*). In the two species of *Pseudograpsus* examined for this character, the length to width ratio of the third abdominal segment ranges from ca. 3.8 (*P. elongata*) to ca. 4.0 (*P. albus*), which is narrower than *S. laniger* and *S. miyakei,* but only slightly broader than *S. enodis.* In *S. enodis,* the lateral margins of the sixth abdominal segment are weakly rounded, while in *S. laniger,* the posterior part of the lateral margins are distinctly convex; in *S. miyakei* the lateral margins are even more convex. The sixth abdominal segment of *S. enodis* is narrower (length to width ratio: ca. 5.0) than that of *S. laniger* (ca. 3.5) and *S. miyakei* (ca. 3.8). The length to width ratio of the telson in *S. enodis* is 1.0, which is similar to *S. laniger,* but is relatively longer in *S. miyakei* (ca. 1.4). Nakamura & Takeda (1972) commented that the G1 of *S. miyakei* differs from *S. laniger* and *Pseudograpsus elongata* (A. Milne-Edwards, 1873) in having a short distal part and obtuse subterminal lobe, while the latter two have long beaks and small subterminal lobes (Nakamura & Takeda 1972: 438). This implies that the G1 of *S. laniger* is also longer and more slender than in *S. enodis* and *S. miyakei.* The G1 of *S. enodis* is characterised by having an elongated tube, and narrow subterminal lobe. The length of the distal part of the G1 of *Scutumara* seem to be variable within the genus. Likewise, in the three species of *Pseudograpsus* examined (*P. elongata, P. albus* and *P. crassus*) for this character, the length of the distal part of the G1 varies greatly, from long (*P. elongata*) to short (*P. albus*), indicating that the G1 is useful character at the species level but not at the generic level.

Specimens of *Scutumara enodis* are small, as are the other two known *Scutumara* species. The holotype female (a subadult) is only 5.8 by 5.9 mm (Ng & Nakasone 1993). The smaller adult male specimen, is only 4.9 by 5.1 mm. Similarly, the holotype of *S. laniger* is only 8.3 mm in carapace length, and that of *S. miyakei* is 3.6 mm. On the other hand, *Pseudograpsus* species are generally larger but it is not consistent. The two smallest species are *P. elongata* and *P. albus*: *P. elongata* ranges from 8.8 by 7.8 mm (USNM 33411) to 9.7 by 8.6 mm (Crosnier 1965); and *P. albus* ranges from 8.2 by 7.3 mm (USNM 81732) to 9.5 by 8.6 mm (Crosnier 1965). *P. crassus* (42.6 by 36.3 mm) is a very large species (USNM 93152).

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Larval development of *Cryptolithodes expansus* Miers (Decapoda: Anomura: Lithodidae) reared in the laboratory

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Abstract.—The complete larval development of *Cryptolithodes expansus* Miers is described based on laboratory rearing. The species has four zoeal stages and a megalopa. The larvae are described and illustrated, and detailed comparisons are made with other lithodid larvae, particularly those of *Cryptolithodes typicus* Brandt.

Cryptolithodes expansus Miers, 1879 is found along the Korean coast (personal observation) and in Japan (Makarov 1938, 1962) on rocky bottoms in the sublittoral region to a depth of about 50–60 m. The family Lithodidae is represented by 16 genera and 95 species (Dawson 1989), but the larval development of only 16 species, representing 9 genera, has been described (Konishi 1986; Haynes 1984, 1993; Konishi & Taishaku 1994).

Sars (1890) described all zoeal stages up to the megalopa of *Lithodes maja* Linnaeus, 1758. Subsequent studies of Lithodidae larvae have been described, at least in part, for 15 species (Konishi 1986; Haynes 1984, 1993; Konishi & Taishaku 1994): *Cryptolithodes typicus* Brandt, 1848, *Dermaturus mandtii* Brandt, 1850, *Hapalogaster grebnitzkii* Schalfeew, 1892, *H. dentata* (De Haan 1844), *H. mertensii* Brandt, 1850, *Lithodes aequispina* Benedict, 1895, *L. antarctica* Jacquinot, 1853, *Lopholithodes mandtii* Brandt, 1848, *Paralithodes brevipes* (H. Milne Edwards & Lucas, 1841), *P. camtschaticus* (Tilesius 1815), *P. platypus* (Brandt 1850), *Paralomis granulosa* (Jacquinot 1852), *P. hystrix* (De Haan 1846), *Placetron wosnessenskii* Schalfeew, 1892, and *Rhinolithodes wonessenskii* Brandt, 1848.

Hart (1965) described all zoeal stages, megalopa and crab 1 stage of *Cryptolithodes typicus* Brandt, 1848 reared in the laboratory. This is the only species of *Cryptolithodes* for which larvae are known so far. The purpose of the present study is to describe complete larval stages of *C. expansus* reared in the laboratory, and to compare them with those of *C. typicus.*

Materials and Methods

On 20 August 1995 a local fisherman caught three berried females of *Cryptolithodes expansus* with a commercial octopus trap in the vicinity of Pusan (35°10′N, 129°10′E), Korea. The ovigerous females were brought to the laboratory, and kept in a container filled with running sea-water. On 10 March 1996, about 250 larvae hatched from one of the females. Of these, 60 were individually reared in 50 ml glass bottles placed in an incubator at 9.5–10.5°C. Some larvae were kept in 11 glass beakers for mass culture.

Larvae were fed with newly hatched *Artemia* nauplii. Moulting and mortality were checked daily. After checking, the larvae were transferred to freshly prepared bottles and beakers. At each developmental stage, dead larvae and exuviae were fixed and preserved with 3% neutralized formalin solution. At least five specimens of each stage were dissected in ethylene glycol for microscopic observation. Drawings were made with the aid of a drawing tube.

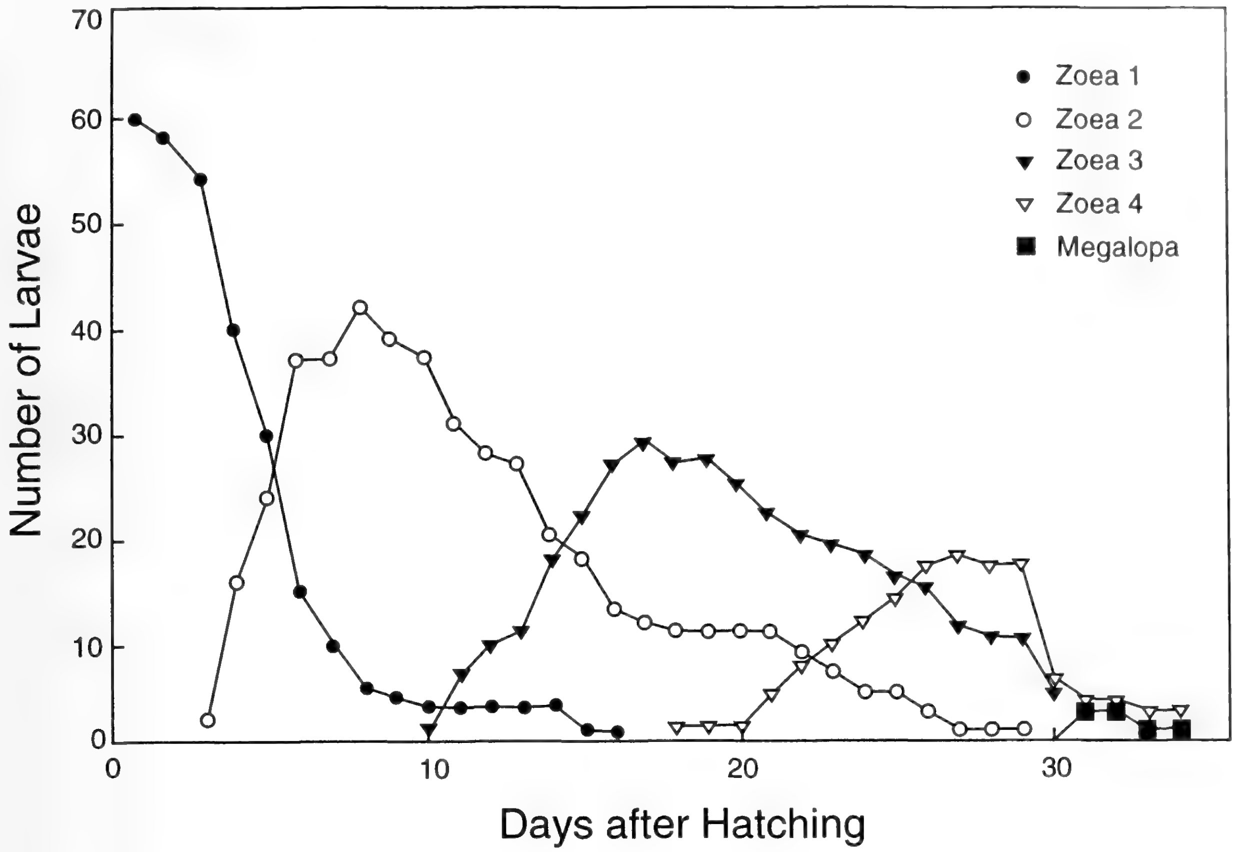

Fig. 1. *Cryptolithodes expansus* Miers. Survival and duration of larval stages reared under laboratory conditions of 9.5–10.5°C and 31.80–32.65‰.

Measurements taken were: carapace length (CL), from the anterior tip of the rostrum to the postero-median margin of the carapace; total length (TL), from the anterior tip of the rostrum to the postero-median margin of the telson excluding telson processes. At least five specimens were measured using a calibrated ocular micrometer.

Results

Development and duration of the larvae.—*Cryptolithodes expansus* passed through four zoeal stages and a megalopa (Table 1, Fig. 1). Of the 60 larvae reared individually, only three molted to the megalopa stage within approximately 37 days.

Table 1.—*Cryptolithodes expansus* Miers. Duration of each larval stage reared at 9.5~10.5°C and 31.80~32.65‰.

	Duration of larval stages (day)		
Larval stages	Mean	Range	*n*
Zoea I	4.8	3–7	47
Zoea II	8.9	6–18	42
Zoea III	8.2	6–17	29
Zoea IV	14.8	13–16	18
Megalopa	10.5	7–15	3

Descriptions

First Zoea.

Size: CL = 1.6–1.8 mm (mean 1.6 mm); TL = 4.0–4.4 mm (mean 4.1 mm).

Duration: 3–7 days.

Color: dark brown color uniformly diffused over the whole carapace.

Carapace (Fig. 2A, B): rostrum well-developed, tapering from broad base to acute tip; ventral and posterior carapace margins with submarginal furrow and raised rim; postero-lateral margin smoothly rounded.

Eyes (Fig. 2A, B): sessile.

Abdomen (Fig. 2 A, B): narrow and slender; 5 somites plus telson; 3rd–5th somites with pair of lateral spines; pair of minute spines on postero-dorsal margin of 2nd–5th somites.

Telson (Fig. 2L): armed with 7 pairs of marginal processes; outermost a naked spine; 2nd a fine hair; 3rd–7th denticulate spines.

Antennule (Fig. 2C): biramous; an endopodal bud naked, a delineated exopod with 10 aesthetascs.

Antenna (Fig. 2D): biramous; scaphocerite of the protopod with 6 long plumose setae and 2 minute naked setae; endopod naked, tapering to sharp terminal point, a spine adjacent to the endopod.

Mandible (Fig. 2E): stout and well armed with median teeth; mandibular palp present as a small bud.

Maxillule (Fig. 2F): coxal endite with 7 serrated and 1 naked spinnule; basial endite with 7 stout denticulate spines and 2 minute setae; endopod 3-segmented with 2+1+3 setae.

Maxilla (Fig. 2G): proximal and distal lobes of coxal endite with 7 and 4 setae respectively; proximal and distal lobes of basial endite with 4 setae each; endopod unsegmented with 3 subterminal and 5 terminal setae; scaphognathite with 10 plumose setae.

First maxilliped (Fig. 2H): coxa naked; basis with 2, 2, 3, 3 setae, endopod 5-segmented with 3, 2, 1, 2, 4+1 setae; exopodite with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 2I): coxa naked; basis with 1, 2 setae; endopod 4-segmented with 2, 2, 2, 4+1 setae; exopod with 4 plumose natatory setae.

Third maxilliped (Fig. 2J): biramous; endopod unsegmented; exopod two-segmented.

Pereiopods (Fig. 2K): elongate but not functional appendages; first pair subchelate.

Second Zoea

Size: CL = 2.1–2.2 mm (mean 2.2 mm); TL = 4.4–5.0 mm (mean 4.8 mm).

Duration: 6–18 days.

Carapace (Fig. 3A, B): slight increase in size, but no change in armature.

Eyes (Fig. 3A, B): stalked and movable.

Telson (Fig. 3L): unchanged.

Antennule (Fig. 3C): similar to first zoea exopod with 9 aesthetascs of varying size.

Antenna (Fig. 3D): exopod with 7 plumose setae and 1 minute naked seta.

Mandible (Fig. 3E): some teeth added.

Maxillule (Fig. 3F): setation of endites and endopod unchanged.

Maxilla (Fig. 3G): proximal and distal lobes of coxal endite with 9 and 4 setae respectively; proximal and distal lobes of basial endite with 5 and 4 setae respectively; endopod unsegmented, with 3 subterminal and 5 terminal setae; scaphognathite with 22 plumose setae.

First maxilliped (Fig. 3H): setation of basis unchanged; 1 plumose lateral seta added on 1st–3rd segments of endopod; exopod with 8 plumose natatory setae.

Second maxilliped (Fig. 3I): setation of basis unchanged; 1 plumose lateral seta added to 1st to 3rd segments of endopod; exopod with 8 plumose natatory setae.

Third maxilliped (Fig. 3J): biramous; endopod bud with 3 setae; exopod with 8 plumose natatory setae.

Pereiopods (Fig. 3K): unchanged in armature; slight increase in size.

Pleopods (Fig. 3B): rudimentary uniramous buds on somites 2nd–5th.

Third Zoea

Size: CL = 2.2–3.2 mm (mean 2.6 mm); TL = 4.9–5.9 mm (mean 5.4 mm).

Duration: 6–17 days.

Carapace (Fig. 4A, B): similar to second zoea.

Telson (Fig. 4L): unchanged.

Antennule (Fig. 4C): exopod with 9 aesthetascs.

Antenna (Fig. 4D): endopod much longer than scaphocerite.

Mandible (Fig. 4E): some teeth added.

Maxillule (Fig. 4F): setation and shape unchanged.

Maxilla (Fig. 4G): proximal and distal lobes of coxal endite with 8 and 4 setae respectively; basial endite unchanged; en-

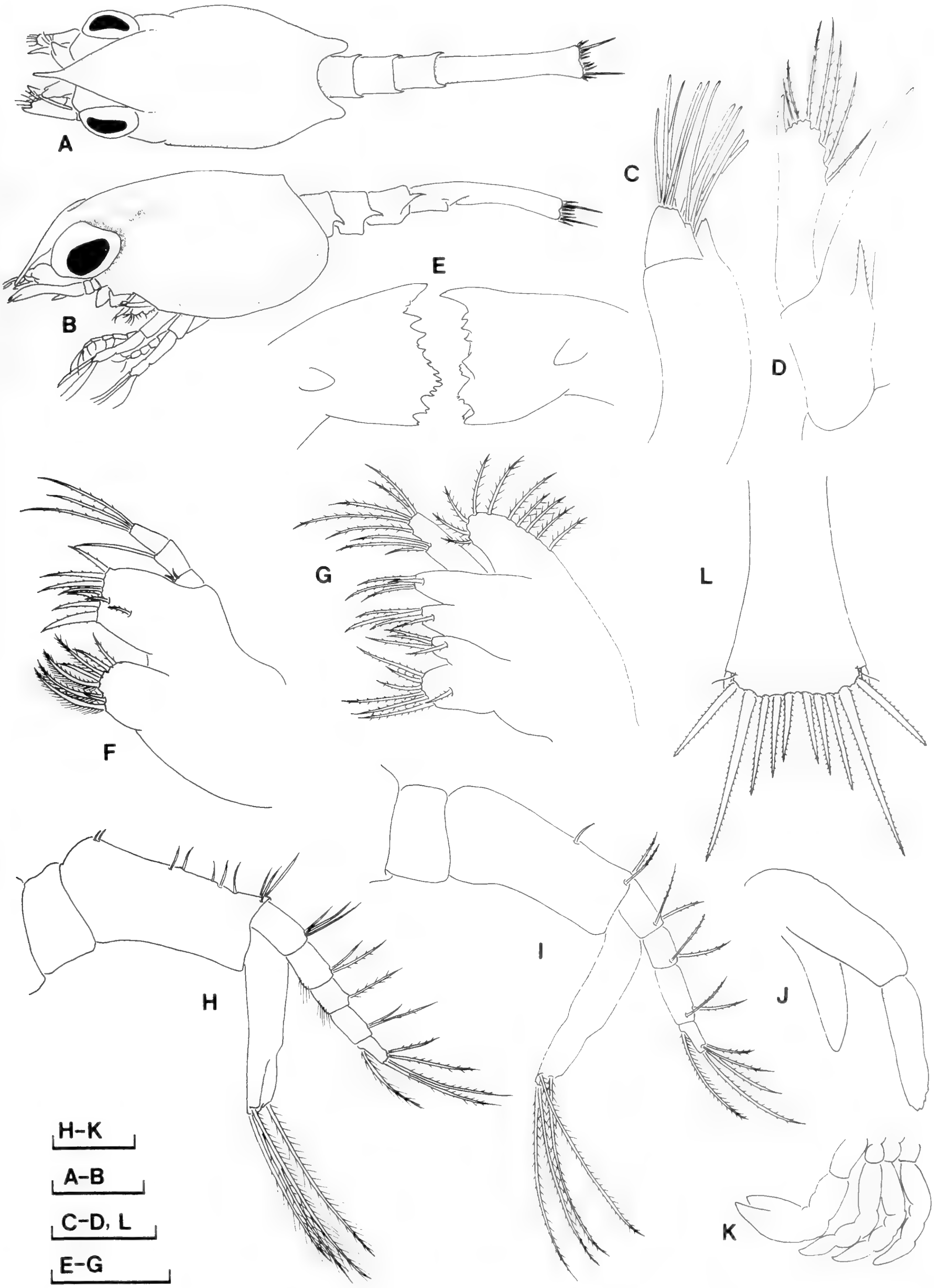

Fig. 2. *Cryptolithodes expansus* Miers. First zoea. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, Pereiopods; L, Telson. Scale bars = 0.2 mm.

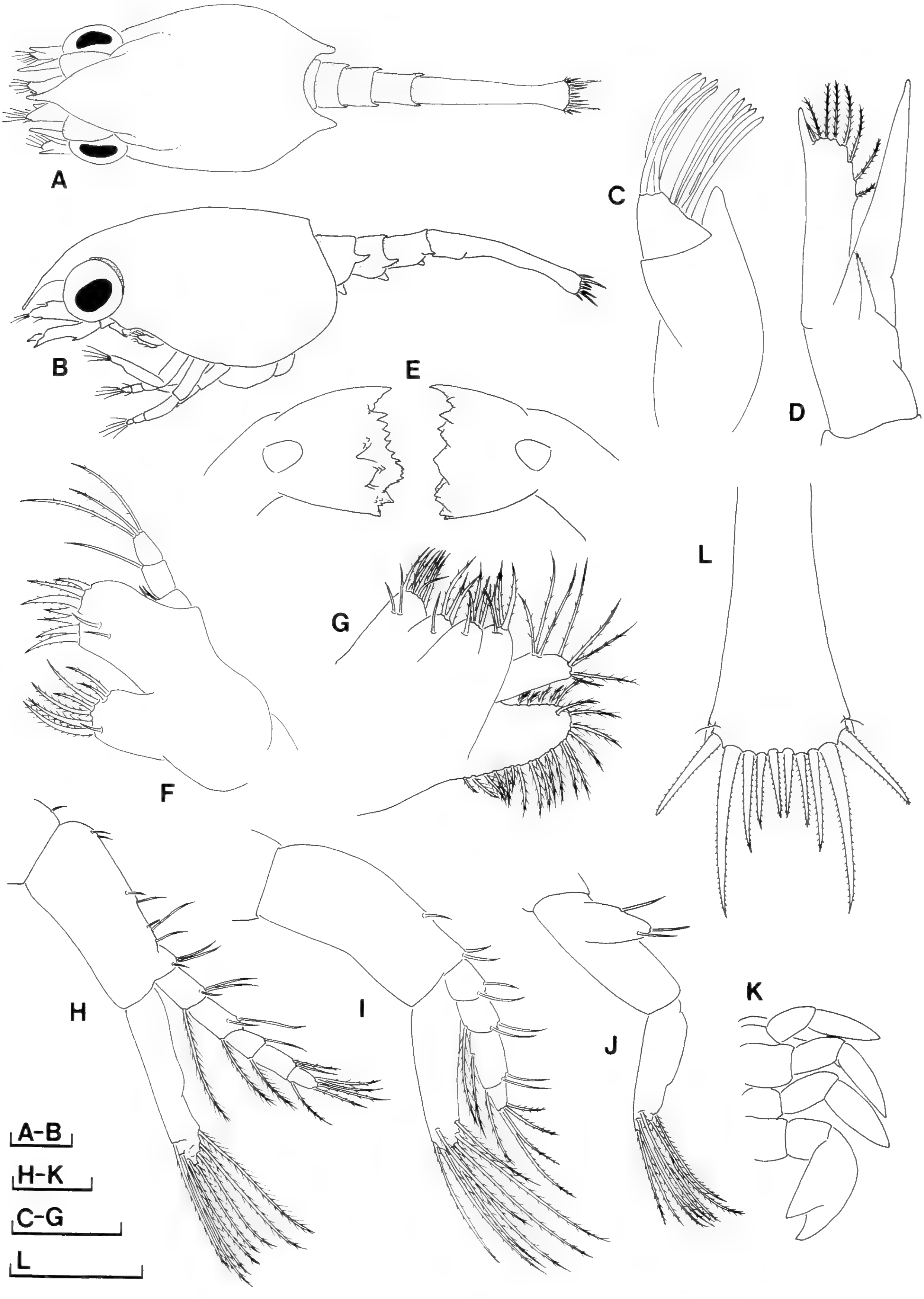

Fig. 3. *Cryptolithodes expansus* Miers. Second zoea. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K; Pereiopods; L, Telson. Scale bars = 0.2 mm.

dopod unsegmented, with 3 subterminal and 4 terminal setae; scaphognathite with 24 plumose setae.

First maxilliped (Fig. 4H): setation unchanged.

Second maxilliped (Fig. 4I): setation unchanged.

Third maxilliped (Fig. 4J): setation unchanged.

Pereiopods (Fig. 4K): unchanged.

Pleopods (Fig. 4B): well developed but not functional appendages.

Fourth Zoea

Size: CL = 3.0–3.4 mm (mean 3.2 mm); TL = 6.1–6.9 mm (mean 6.4 mm).

Duration: 13–16 days.

Carapace (Fig. 5A, B): similar to third zoea.

Telson (Fig. 5T): unchanged.

Antennule (Fig. 5C): similar to previous stage.

Antenna (Fig. 5D): endopod 2-segmented and much longer than exopod.

Mandible (Fig. 5E): some teeth added.

Maxillule (Fig. 5F): setation of coxal endite and endopod unchanged; basial endite with 8 stout denticulate spines and 2 setules.

Maxilla (Fig. 5G): setation of coxal and basal endite unchanged; scaphognathite with 26 plumose setae.

First maxilliped (Fig. 5H): setation unchanged.

Second maxilliped (Fig. 5I): setation unchanged.

Third maxilliped (Fig. 5J): more developed than in third zoea.

Pereiopods (Fig. 5K–O): uniramous; 1st pair unchange; 2nd–4th with apical spine except on 5th.

Pleopods (Fig. 5P–S): unchanged.

Megalopa

Size: CL = 2.4–2.5 mm (mean 2.5 mm); TL = 3.6–3.8 mm (mean 3.7 mm).

Duration: 7–15 days.

Color: intense scarlet.

Carapace (Fig. 6A, B): triangular in dorsal view, with conical rostrum, convex in transverse section; cervical groove distinct; angle between lateral carapace and pleuron acute, with well-marked keel projecting laterally.

Abdomen (Fig. 6A, B, O): 6 somites plus telson; 2nd–5th segments with pleopods; 6th segment with 3 minute hairs on the distal margin.

Telson (Fig. 6O): naked; more elongate and conical; twice as long as 6th abdominal segment.

Antennule (Fig. 6C): biramous; lower ramus 2-segmented with 0, 3+3 setae; upper ramus 4-segmented with 0, 4, 3, 3 aesthetascs plus 3 terminal setae.

Antenna (Fig. 6D): scale naked; flagellum 8-segmented with 0, 2, 0, 0, 4, 1, 4, 4 setae.

Mandible (Fig. 6E): strongly chitinized, smooth and not toothed as in zoeal stages, with broad blade-like process; palp 2-segmented.

Maxillule (Fig. 6F): endites with minute spines; endopod unsegmented.

Maxilla (Fig. 6G): setae of coxal and basial endite reduced and tooth-like; endopod unsegmented; enlarged scaphognathite with 47 plumose setae.

First maxilliped (Fig. 6H): basis with 8 setae; endopod unsegmented and with 5 setae; exopod with 4 terminal setae.

Second maxilliped (Fig. 6I): basis with 2 setae; endopod 4-segmented with 0, 0, 0, 2 setae; exopod 2-segmented with 0, 4 setae.

Third maxilliped (Fig. 6J): basis with 1, 1 setae; endopod 5-segmented with 4, 6, 5, 14, 9 setae; exopod with 3 long plumose setae.

Pereiopods (Fig. 7A–E): well developed and armed with spines; functional chelipeds.

Pleopods (Fig. 6K–N): present on 2nd–5th abdominal somites; endopod small and naked; exopods with 9–11 plumose natatory setae.

Discussion

Morphological characteristics of lithodid larvae have been discussed by Gurney

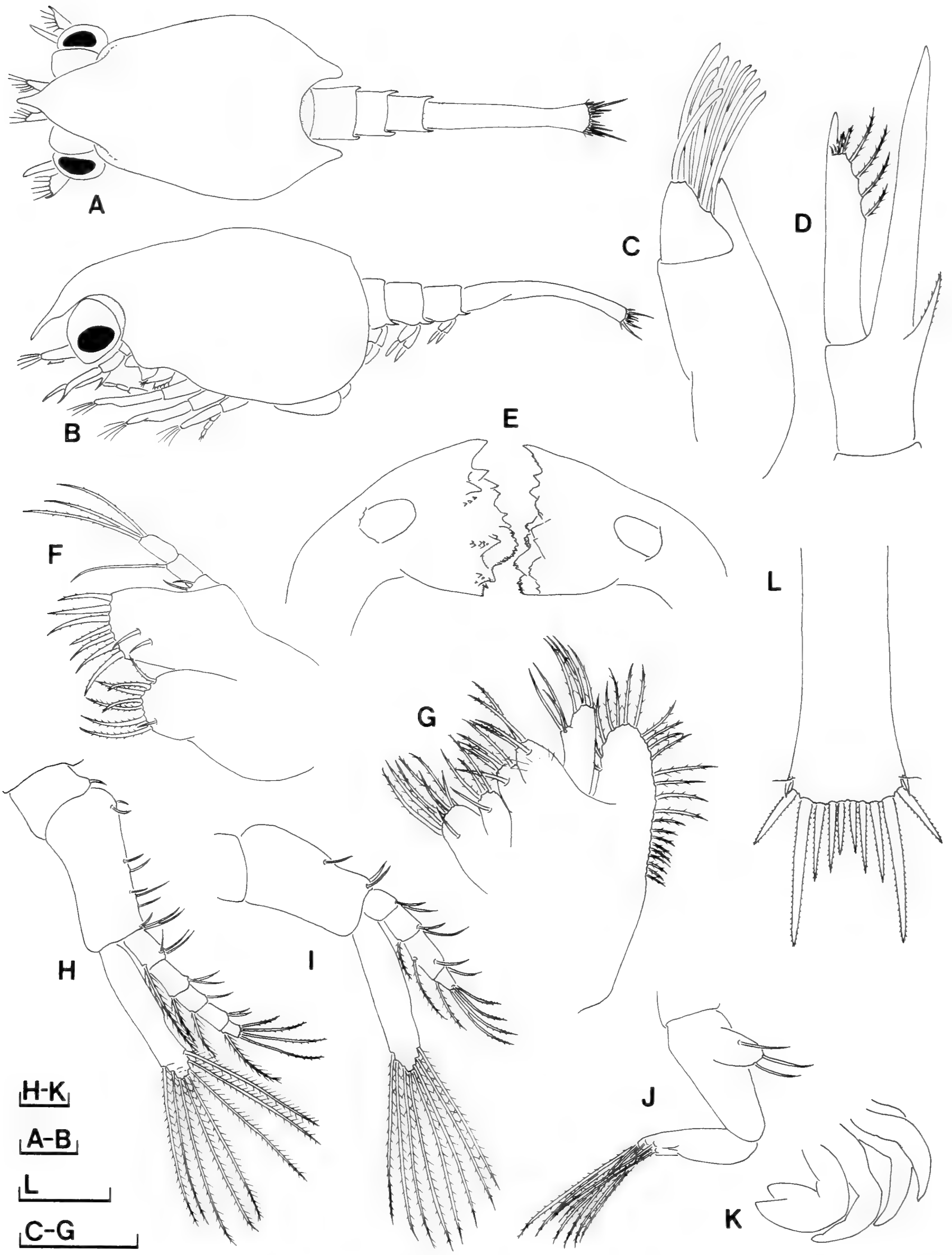

Fig. 4. *Cryptolithodes expansus* Miers. Third zoea. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, Pereiopods; L, Telson. Scale bars = 0.2 mm.

(1942), MacDonald et al. (1957), Pike & Williamson (1960), Kurata (1964), and Konishi (1986). They implied that larval morphology of this family was very similar to that of the Paguridae, except for the reduction or disappearance of uropods.

Although the genus *Cryptolithodes* belongs to the family Lithodidae, it differs

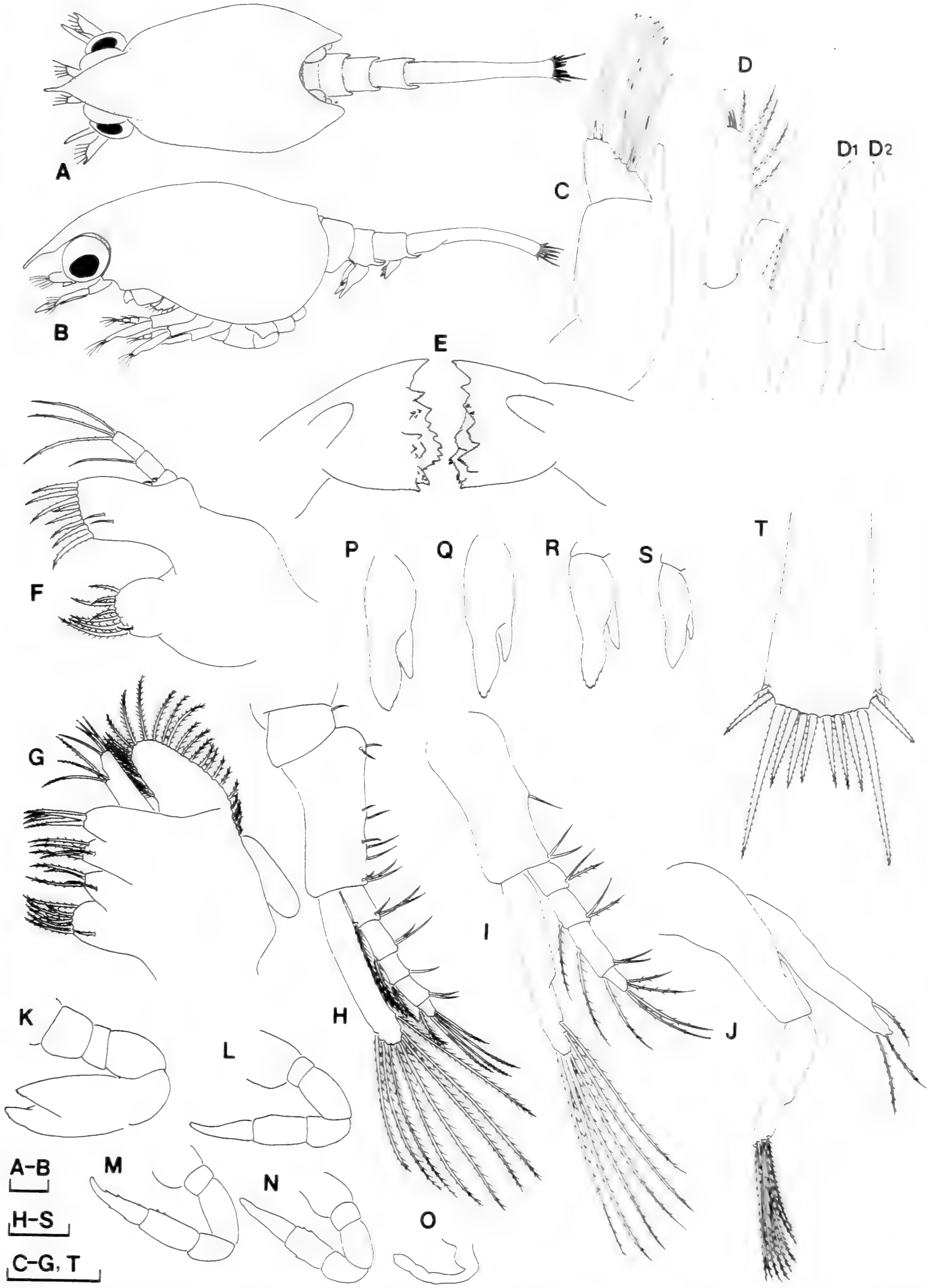

Fig. 5. *Cryptolithodes expansus* Miers. Fourth zoea. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna, D_1-D_2, Endopods of antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, First pereiopod; L, Second pereiopod; M, Third pereiopod; N, Fourth pereiopod; O, Fifth pereiopod; P, Pleopod of second abdominal segment; Q, Pleopod of third abdominal segment; R, Pleopod of fourth abdominal segment; S, Pleopod of fifth segment; T, Telson. Scale bars = 0.2 mm.

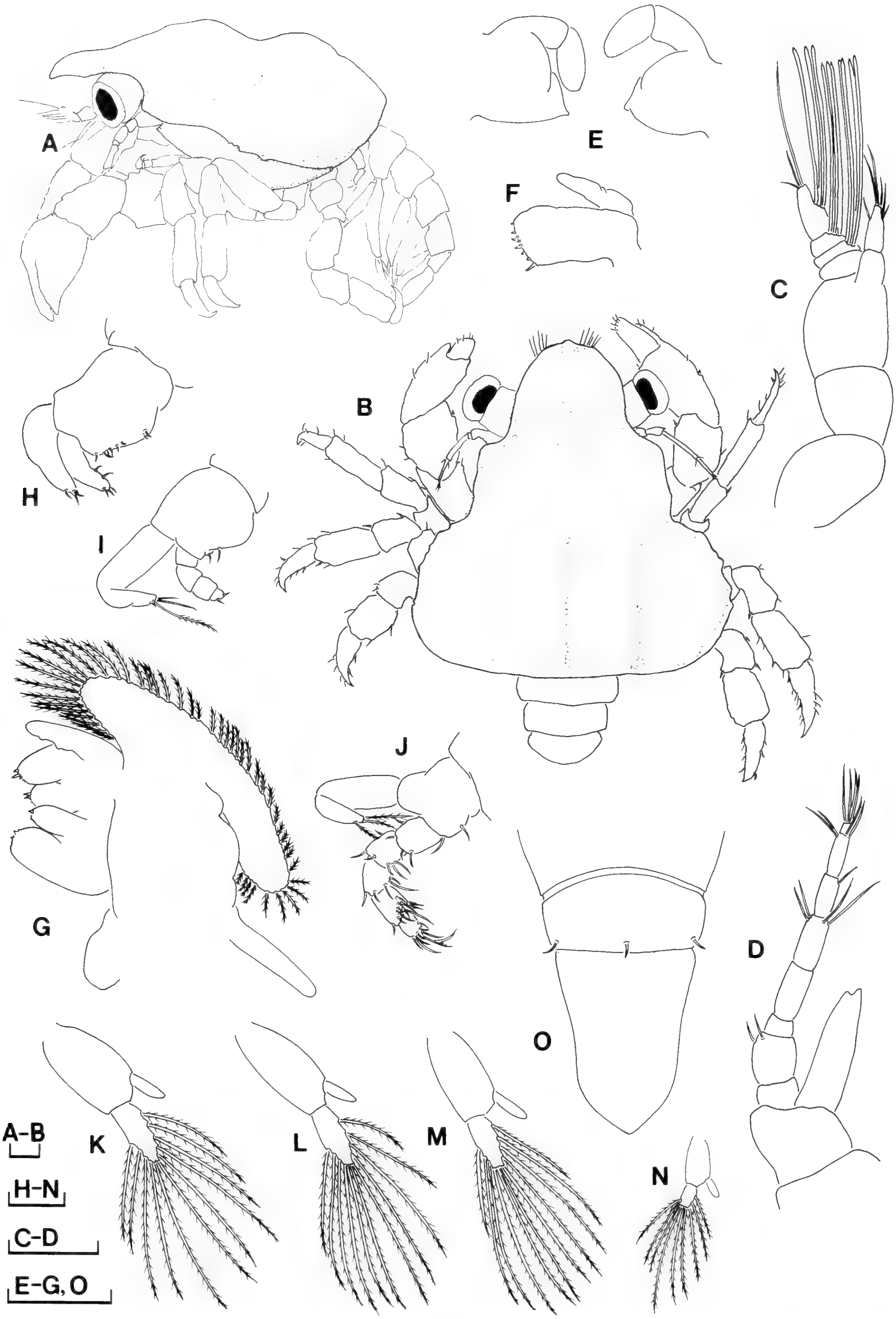

Fig. 6. *Cryptolithodes expansus* Miers. Megalopa. A, Dorsal view; B, Lateral view; C, Antennule; D, Antenna; E, Mandible; F, Maxillule; G, Maxilla; H, First maxilliped; I, Second maxilliped; J, Third maxilliped; K, Pleopod of second abdominal segment; L, Pleopod of third abdominal segment; M, Pleopod of fourth abdominal segment; N, Pleopod of fifth abdominal segment; O, Telson. Scale bars = 0.2 mm.

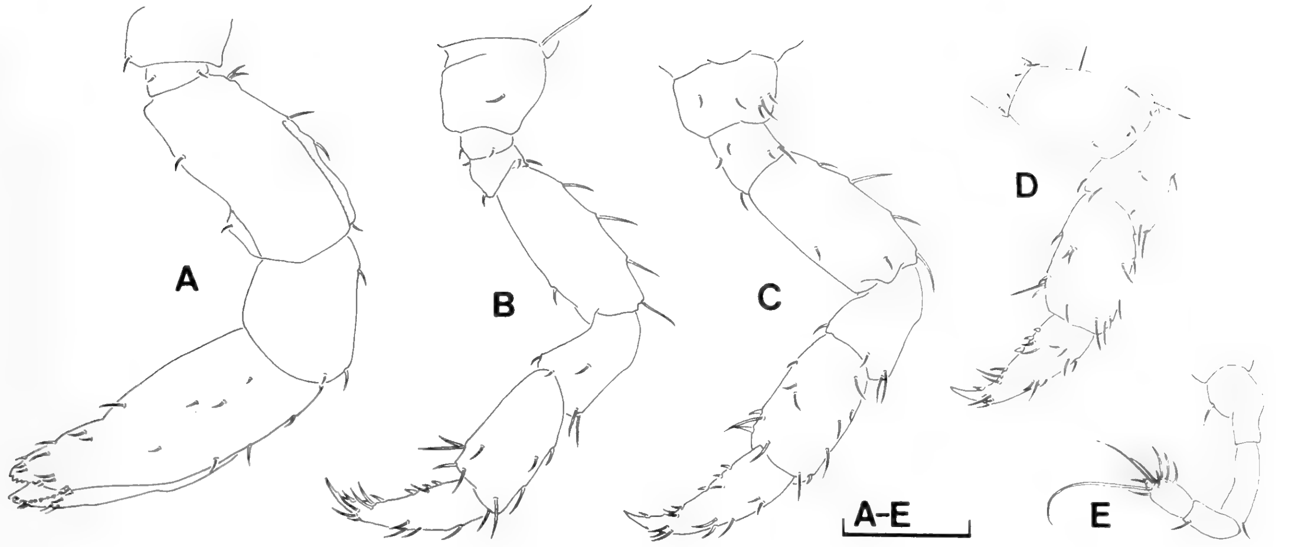

Fig. 7. *Cryptolithodes expansus* Miers. Megalopa. A, First pereiopod; B, Second pereiopod; C, Third pereiopod; D, Fourth pereiopod; E, Fifth pereiopod. Scale bars = 0.2 mm.

Table 2.—Comparison of morphological characters between *C. typicus* and *C. expansus*

	Characters	Species	
		C. typicus (Hart 1965)	*C. expansus* (Present study)
First Zoea			
Size*	carapace length	1.4 mm	1.6 mm
	total length	3.0 mm	4.1 mm
Antennule	aesthetascs	8	10
Antenna	endopod	sharp tip, minute subterminal tooth.	sharp tip
Maxillule	basial endite	7 setae	9 setae
	endopod	7 setae	9 setae
Maxilla	proximal lobes	8, 6 setae	7, 4 setae
Telson	posterior margin	round	straight
Second Zoea			
Antennule	aesthetascs	8	9
Antenna	endopod	segmented	unsegmented
Maxillule	basial endue	8 setae	9 setae
	endopod	1+1+3 setae	2+1+3 setae
Third Zoea			
Antenna	endopod	segmented	unsegmented
Fourth Zoea			
Antenna	endopod	segmented	segmented
Maxillule	basial endue	9 setae	10 setae
Megalopa			
Size*	Carapace length	2.0 mm	2.5 mm
	Total length	2.9 mm	3.7 mm
Carapace	rostrum	wide and flattened	narrow and pointed
Abdomen	5th segment	2 spines	3 spines
Antenna	flagellum	2+1+1+0+3+4+2+7 setae	0+2+0+0+4+1+4+4 setae
Third maxilliped	exopod	4 plumose setae	3 plumose setae
Telson	shape	triangular	spaculate

* Measured from Hart (1965, fig. 1 I, fig. 3)

morphologically from other lithodid larvae. The larvae of *Cryptolithodes* spp. resemble those of some Diogenidae and Coenobitidae in that they lack lateral carinae on the postero-lateral margins of the carapace. Major morphological characteristics of lithodid larvae as reported by Konishi (1986) are as follows: "Uropods, if present, lack an endopod, even in the final zoeal stage; the third maxilliped has an endopod in the first zoeal stage; abdominal somites lack mediodorsal spines; the telson without an anal spine."

Comparative morphological features of *Cryptolithodes typicus* and *C. expansus* are summarized in the Table 2. The larvae of *C. expansus* differed from those of *C. typicus* in body size, number of antennular aesthetascs, setation of the maxillule, and segmentation of the second maxilliped in the zoeal stages.

The zoeal stages of *Cryptolithodes typicus* and *C. expansus* differ from those of the other lithodid larvae in the following: The abdomen is narrower and more slender, and composed of five segments plus telson in all the zoeal stages; uropods are absent in all the zoeal stages; a postero-lateral carinae on the carapace is absent in zoeal stages; a mandibular palp is present at the first zoeal stage.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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A new genus of pinnotherid crab from the Indian Ocean (Crustacea: Decapoda: Brachyura)

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Abstract.—*Abyssotheres,* new genus, is recognized for *Pinnotheres abyssicola* Alcock & Anderson, 1899, known from a single female taken in a bivalve shell from a depth of 787 m off Travancore, India. In this new genus the dactyli of walking legs 1 and 2 are longer than those of walking legs 3 and 4. This is the eighth genus of pinnotherids that shares a two-segmented palp on the third maxilliped.

Alcock & Anderson (1899) described *Pinnotheres abyssicola* from a single ovigerous female found in a lamellibranch taken off Travancore, India at a depth of 430 fm (787 m). It is known only from the holotype kept in the Zoological Survey of India and remains the deepest recorded occurrence of a pinnotherid crab.

One of us (BG) recently visited the Zoological Survey of India (formerly the Indian Museum) and examined the holotype of *P. abyssicola.* It is in very poor condition, possibly having dried out. However, she was able to examine the third maxilliped (Fig. 1*a*) and determined that the palp comprises only two segments. Campos (1996) reviewed the pinnotherid genera with a two-segmented palp on the third maxilliped and reported that the two-segmented palp was found only on members of six genera. Manning (1993) added a seventh, *Epulotheres.* A combination of characters distinguishes *P. abyssicola* from all pinnotherid genera with a two-segmented palp. We recognize a new genus here for it.

We use the following abbreviations in the account below: fm, fathom(s); m, meter(s); MXP3, third maxilliped; WL, walking leg(s).

Abyssotheres, new genus

Diagnosis.—Size medium, carapace length and width described as less than 10 mm in adult. Carapace length and width subequal, front prominent, transverse, projecting anteriorly beyond eyes. Eyes visible in dorsal view. MXP3 with ischium and merus indistinguishably fused, arched, inner margin projecting at about distal third. Palp 2-segmented (Fig. 1a), terminal segment spatulate, shorter than preceding segment. Chela with dactylus slightly less than half of propodus. Walking legs (Fig. 1b) slender, equal right and left; WL1-2 with dactyli longer than dactyli of WL3-4. Abdomen unknown.

Male.—Unknown.

Type species.—*Pinnotheres abyssicola* Alcock & Anderson, 1899, by present designation and monotypy.

Etymology.—From the Latin *abyss,* depth, and the ending *theres.*

Host.—A large bivalve, *Acesta indica* (Smith) (originally described in *Lima*) (Alcock & Anderson 1899).

Distribution.—Known only from off the coast of Travancore, India, at a depth of 787 m. This is the deepest record for a pinnotherid.

Remarks.—Alcock & Anderson's original account, based on an ovigerous female 8 mm wide, is: "Carapace as long as broad, circular, smooth; front rather prominent, about one-fifth the greatest breadth of the

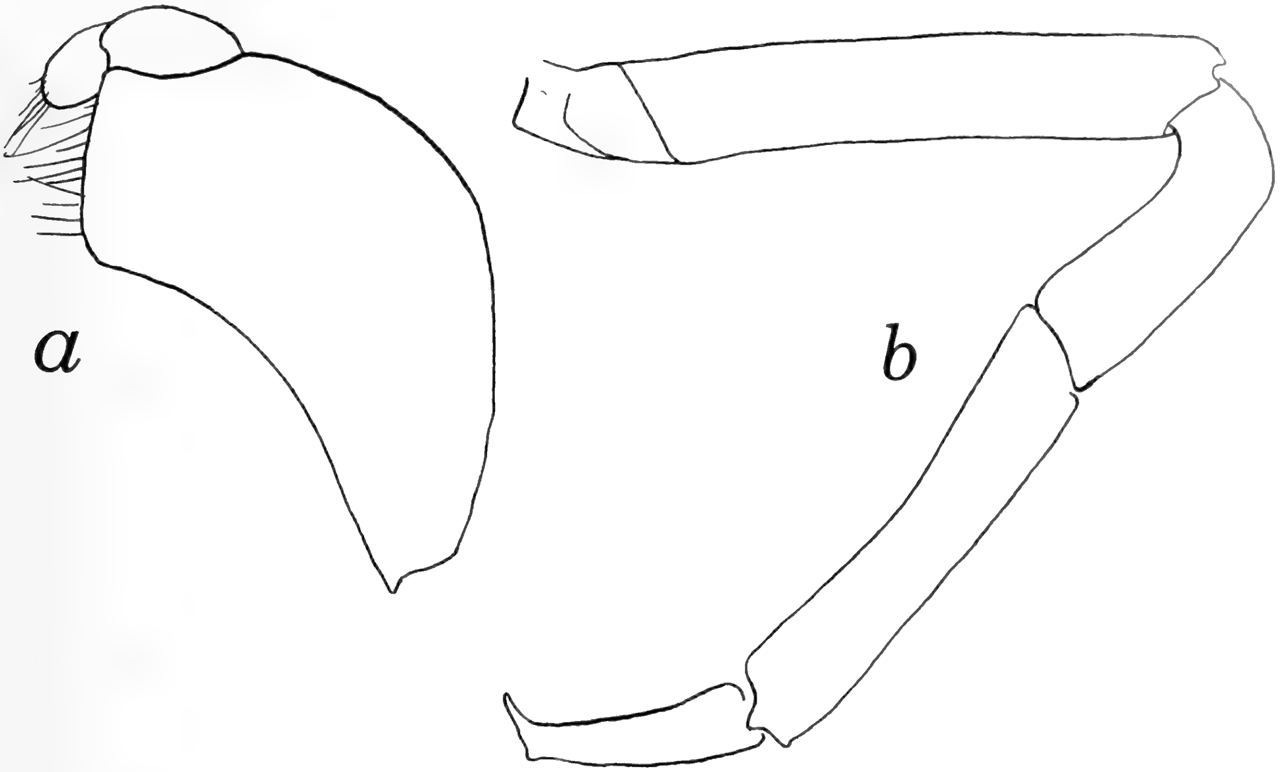

Fig. 1. *Abyssotheres abyssicola* (Alcock & Anderson, 1899). Ovigerous female holotype, carapace length 8 mm: *a,* MXP3; *b,* WL.

carapace. The whole of the eyes and eyestalks and almost the whole of the orbit are visible in dorsal view. The eyes are well developed, but very pale. The dactylus of the external maxillipeds is styliform and is inserted at the end of the preceding joint. The lower border of the thumb is fringed with fine hairs. The legs are slender; the second and third pair are both about 1½ times as long as the carapace, and have the dactylus slightly longer than it is in the other two pairs" (Alcock & Anderson 1899: 14).

This account provides few diagnostic features. First, the carapace is round, as broad as long, and the front is fairly prominent.

Second, the terminal segment of the MXP3 palp is articulated terminally on the subdistal segment. Among those Pinnotherinae with a two-segmented palp, the dactylus of the palp is articulated terminally in members of *Orthotheres* Sakai, 1969 (see Campos 1989, Manning 1993) and in three species described by Bürger (1895), *Pinnotheres glaber, P. impressus,* and *P. laevis,* all presumably shore species known from the Pacific Ocean. In Bürgers's species the dactyli of the walking legs are equally long.

A third distinguishing character of *A. abyssicola* is that the dactyli of WL1-2 are longer than those of WL3-4. This may be an unique feature within the Pinnotheridae.

A fourth characteristic feature of *A. abyssicola* is the arched MXP3, a feature shared with the unrelated *Limotheres nasutus* Holthuis, 1975, from the Caribbean. It also is a commensal of a species of *Lima,* but occurs in shallow water. *Limotheres* has a three-segmented mandibular palp, and differs from *Abyssotheres* in numerous other features.

Campos (1996) studied six genera of pinnotherids that have a two-segmented palp on the MXP3: *Calyptraeotheres* Campos, 1990; *Dissodactylus* Smith, 1870; *Gemmotheres* Campos, 1996; *Ostracotheres* H. Milne Edwards, 1853; *Tunicotheres* Campos, 1996; and *Xanthasia* White, 1846. Members of *Abyssotheres* can be distinguished from members of these genera as follows: the carapace lacks the sharp lateral margins and the dorsal sulci characteristic of *Calyptraeotheres*; the apices of WL dactyli are simple, rather than bifurcated as in *Dissodactylus*; MXP3 with the inner distal margin of the merus obtusely angled rather than curved as in *Gemmotheres, Ostracotheres,* and *Tunicotheres*; carapace lacking upturned lateral margins and median mushroom-shaped tubercle as in *Xanthasia.* All of these other genera comprise shore rather than slope species, and all but *Ostracotheres* and *Xanthasia* are restricted to the Americas.

A seventh genus, *Epulotheres,* was added by Manning (1993), who incorrectly reported that it had a MXP3 with a three-segmented palp. This was corrected by Manning & Felder (1996) who reillustrated the palp, which has the usual three segments. *Nannotheres* Manning & Felder, 1996 does have a two-segmented palp. In it WL4 is the longest walking leg and the dactyli of the walking legs are similar and equal in length.

The obtuse projection on the dorsal surface of the dactylus of the WL (Fig. 1b) may prove to be an unique feature of *A. abyssicola.*

Only one other pinnotherid, *Alain crosnieri* Manning, 1998, is known from depths greater than 400 m. An associate of holothurians, it was taken in depths of 399–461 m off Indonesia.

We are pleased to have the opportunity to include this report in a volume dedicated to our late colleague Austin B. Williams, whose many studies on decapods have contributed much to our knowledge of the group.

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A new genus and species of ghost shrimp from Tobago, West Indies (Crustacea: Decapoda: Callianassidae)

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Abstract.—The new genus *Pseudobiffarius* is the seventh genus of Callianassinae recognized from the Americas. This monotypic genus is based on its type species from Tobago, West Indies, *Pseudobiffarius caesari,* new species. It differs from all members of the subfamily in having a very short, stout upper flagellum on the A1 peduncle.

Collections of a very small callianassid were made on Tobago by two individuals at different times, Lois Nickell in 1989 and Richard Heard in 1992 and 1993. The species was initially identified as a member of *Biffarius* Manning & Felder, 1991, but closer examination after Heard's collections of 1993 revealed that it represented not only a new species but also a new genus as well. The new taxa are named here.

The types have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Carapace length (cl) measured as postorbital carapace length and total length (t1), measured on the midlineare in millimeters (mm). Other abbreviations: A1, antennule; A2, antenna; leg., collector; m, meter(s); Max1–2, maxillae 1–2; Mxp1–3, maxillipeds 1–3; P1–5, pereopods 1–5 (P1 and P2 are chelipeds, P3–5 walking legs); Plp1–5, pleopods 1–5.

Family Callianassidae Dana, 1852
Subfamily Callianassinae Dana, 1852
Pseudobiffarius, new genus

Type species.—*Pseudobiffarius caesari,* new species, by present designation and monotypy.

Etymology.—The generic name is formed by combining the Latin prefix *pseudo-*, false, with the generic name *Biffarius,* alluding to the resemblance of the present genus to the latter. The gender is masculine.

Diagnosis.—Size relatively small, t1 of adults less than 30 mm. Carapace with acute rostral projection, lacking rostral carina or spine. Cornea dorsal, subterminal, disk-shaped, corneal elements distinct. A1 peduncle longer than A2 peduncle; dorsal flagellum of A1 peduncle short and stout, shorter than peduncle. Mxp3 without exopod, ischium-merus operculiform; inner face of ischium with cristate ridge of strong teeth; merus projecting slightly beyond articulation with carpus; last 3 segments slender. Chelipeds unequal in male, equal in female, with meral hook. Plp1 uniramous in both sexes; Plp2 absent in male, biramous in female; Plp3–5 foliaceus, with stubby, projecting appendices internae in both sexes.

Remarks.—Manning & Felder (1991) recognized and named three American genera in this subfamily, *Biffarius, Neotrypaea,* and *Notiax,* and in 1992 added a fourth, *Gilvossius.* Rodrigues & Manning (1992) added a fifth, *Poti.* Heard & Manning (1998) added a sixth, *Necallianassa. Poti* and the type genus of the family, *Callianassa* Leach, 1814, differ from the remainder of these genera by having slender Mxp3, which are pediform rather than operculiform; *Poti* also differs from all other genera in the subfamily by having an incomplete linea thalassinica on the carapace. Members of *Neotrypaea* and *Notiax* are known only from the eastern Pacific; members of the other genera are known only from the western Atlantic.

Members of *Pseudobiffarius* can be distinguished at once from the American genera with broad Mxp3 by the short, stout dorsal flagellum of A1. They further differ from both *Neotrypaea* and *Gilvossius* in having the appendix internae of the Plp3–5 embedded in the edge of the pleopod, whereas they are projecting in *Pseudobiffarius,* as in *Biffarius, Necallianassa* and *Notiax.* In *Notiax* the second male pleopod is present, whereas it is absent in *Pseudobiffarius*; members of *Notiax* also have a strong rostral spine extending almost beyond the cornea and a median distal spine on the telson. Members of *Biffarius* lack the strong ridge of teeth present on the inner margin of the Mxp3 in members of *Pseudobiffarius.*

Pseudobiffarius caesari, new species

Figs. 1, 2, 3a–k, n–o, 4, 5a

Material.—Tobago: Lover's Beach, northwest corner of Man O'War Bay [11°19'N, 60°34'W], protected beach and shallow reef, depth ca. 2 m, leg. R. Heard, sta 3, 6 Apr 1992: 1 male, cl 3.2 mm (paratype, USNM 260965).

Pirate's Cove, east side of Man O'War Bay, depth 2–3 m, leg. R. Heard, 12 Jan 1992: 3 females, 2 non-ovigerous, cl 2.6 and 3.8, 1 ovigerous, cl 4.1 (paratypes, USNM 260970).

Buccoo Reef [11°11'N, 60°49'W], back reef area with sand bottom, depth ca. 2 m, leg. R. Heard, sta 10A (1992 sta 2), 11 Jan 1993: 1 male, cl 4.7 mm (holotype, USNM 260966).

Coral Gardens, Buccoo Reef, depth 5 m, leg. Lois Nickell, 6 Jul 1989: 1 female, cl 3.6 mm (paratype, USNM 260968).—Coral Gardens, Buccoo Reef, depth 2 m, leg. Lois Nickell, 2 Aug 1989: 1 female, cl 6.0 mm, tl 26 mm (paratype, USNM 260969).

Pigeon Point [11°10'N, 60°51'W], depth 1 m, on sand, leg. R. Heard, 15 Jan 1993: 1 female, cl 4.4 mm (paratype, USNM 260967).

Lowlands Lagoon [= Petit Trou; 13°50'N, 61°05'W], leg. R. Heard, sta. 9, 7 Apr 1992: 1 male, cl 5.4 mm (paratype, USNM 260971).

Diagnosis.—Size very small, cl 6.0 mm or less and tl 30 mm or less in adults. Telson subrectangular, with small submarginal spines posteriorly and distinct median and posterolateral spines. Mxp3 ischium-merus operculiform, without exopod, inner surface of ischium with strong crest of teeth. Major cheliped not dimorphic in males; merus of both chelipeds with ventral hook. Male lacking Plp2. Uropods unarmed.

Description.—Carapace (Figs. 1, 4a–c) smooth, with dorsal oval, without cardiac prominence; cervical groove distinct; linea thalassinica distinct, parallel to longitudinal axis of body; rostrum short, acute, not produced into distinct spine; lateral frontal projections present, low, obtuse.

Abdominal somites (Figs. 1, 4a, d) smooth, somite 1 saddle-like, shortest; somite 2 longest, almost twice as long as somite 6, with small tuft of setae posterolaterally, set in submarginal longitudinal crease; somites 3–5 subequal in length, each with small lateral row of setae set in submarginal crease; somite 6 about as long as telson, with median carina. Telson (Fig. 4e, f) subrectangular, tapering posteriorly, slightly longer than wide, with anterior tuft of setae mid-dorsally and some isolated setae and small spinules dorsally, submarginal row of spinules present posteriorly; posterior margin setose, emarginate, with median spine and 2 pairs of posterolateral spines.

Eyes (Figs. 1, 4a–c, 5a) flattened, slightly convex, about as long as first segment of A1 peduncle, external margins moderately convergent, mesial margins parallel, tips pointed; cornea rounded, darkly pigmented, subterminal.

A1 peduncle (Figs. 4a, b, 5a) extending beyond A2 peduncle; segment 3 more than

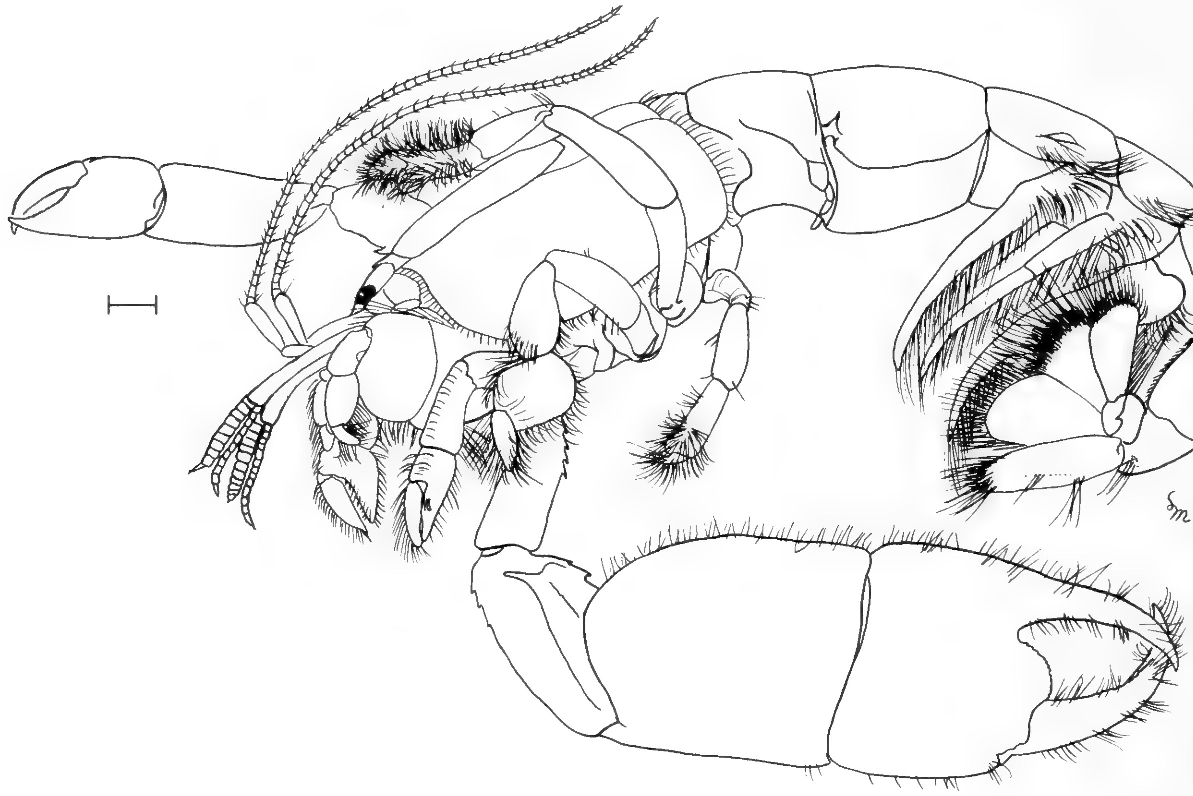

Fig. 1. *Pseudobiffarius caesari,* new genus and species, male holotype (USNM 260966), cl 4.7 mm, Buccoo Reef. Lateral view. Scale = 1 mm.

twice as long as segment 2, segment 1 subequal to segment 2; upper flagellum stout, much shorter than distal segment of peduncle. A2 peduncle (Figs. 4a, b, 5a) with segment 4 slightly shorter than segment 3 and as long as segment 1 and 2 together; antennal scale not evident; flagellum much longer than peduncle.

Mandible (Fig. 3a, b) with numerous small teeth on incisor process; molar process unarmed; palp 3-segmented, segment 3 elongate, longer than segments 1 and 2 combined, tapering distally. Max1 (Fig. 3c) with broad basal endite, distal lobe almost forming right angle; coxal endite elongate, triangular; palp slender, with curved tip. Max2 (Fig. 3d) with protopodal endites bilobed, distalmost lobe elongate, triangular; palp slender; exopod broad, with crenulated margins. Mxp1 (Fig. 3e) with protopodal endites very slender, bilobed; palp very small but distinct, longer than wide; exopod bilobed, mesial margin densely setose with short, spatulate setae (Fig. 3f); epipod subrectangular, elongate. Mxp2 (Fig. 3g) with 5-segmented endopod, terminal segment short, spatulate; exopod unsegmented, shorter than endopodal merus; protopod with small setose epipod, apparently lacking arthrobranch. Mxp3 (Fig. 3h–k) ischium-merus sub-operculiform; ischium about as wide as long, mesial surface with dentate crest of large teeth; merus more than 1.5 times wider than long, almost 4 times wider than carpus and propodus, distal margin of outer face projecting beyond articulation with carpus; propodus much longer than wide, tapering distally, only slightly wider than digitiform dactylus.

Males with very unequal chelipeds. In larger cheliped of male (Figs. 1, 2a, b): ischium with ventral margin spinulose in largest of 3 males; merus with dorsal margin spinulose in proximal fourth, smooth distally, posterior margin with spinules proximal to distally-directed hook, with distal portion serrated; carpus distinctly longer than wide, smooth dorsally and ventrally, broadly rounded proximally; palm shorter than carpus, length less than height; fingers

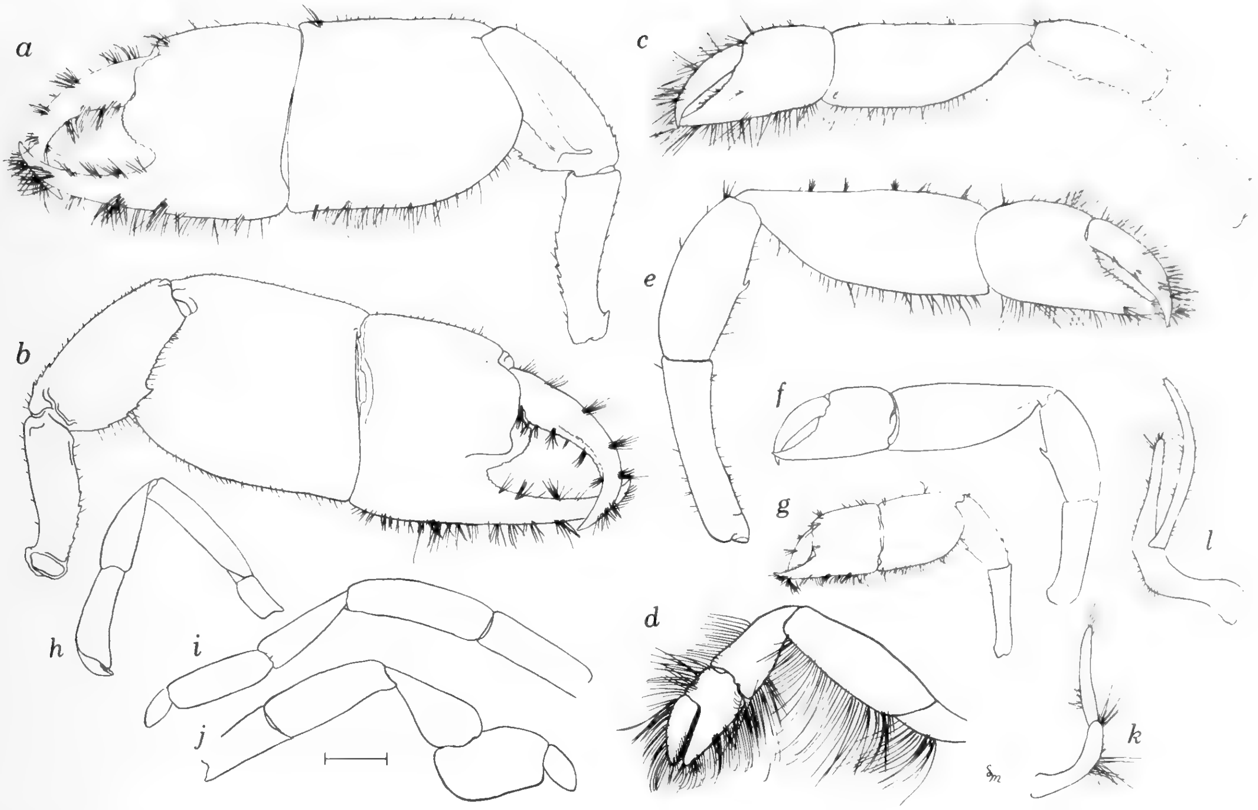

Fig. 2. *Pseudobiffarius caesari,* new genus and species. a, Male major P1, outer aspect; b, Male major P1, inner aspect; c, Female P2; d, Male P2; e, Male minor P1; f, Juvenile male minor P1, setae omitted; g, Juvenile male major P1; h, Male P3; i, Female P4; j, Female P5; k, Female Plp1; l, Female Plp2. a, b, d, male holotype (USNM 260966), cl 4.7 mm, Buccoo Reef; c, g, h, k, l, female paratype (USNM 260967), cl 4.4 mm, Pigeon Point; e, f, juvenile male paratype (USNM 260965), cl 3.2 mm, Lover's Beach. Scale: a–j, 0.5 mm; k, l, 1.0 mm.

about as long as palm, gaping, tips acutely pointed, crossing; cutting edge of movable finger minutely serrated; gape conspicuous, base with dorsal convex lobe, edge serrate, above smoother, deep invagination in distal border of propodus.

Smaller cheliped of male (Fig. 2d, e) and both chelipeds of female (Fig. 2c) similar in size (chelipeds symmetrical in female): ischium smooth, unarmed, about as long as merus; merus with small, acute hook at mid-length of ventral margin; carpus longer than other joints, length about 2.5 times height; palm less than half as long as merus, length and height subequal; fingers subequal, curved, slightly longer than palm, sharply pointed, with some serrations on cutting edge of fixed finger, tip of fingers crossing.

Table 1.—Gill formula of *Pseudobiffarius caesari*, new genus and species.

	Maxillipeds 1	Maxillipeds 2	Maxillipeds 3	Pereopods 1	Pereopods 2	Pereopods 3	Pereopods 4	Pereopods 5
Pleurobranchs	–	–	–	–	–	–	–	–
Arthrobranchs	–	–	2	2	2	2	2	–
Podobranchs	–	–	–	–	–	–	–	–
Epipods	1	1	–	–	–	–	–	–
Exopods	1	1	–	–	–	–	–	–

P2 (Fig. 2c, d) with fingers not gaping, cutting edges straight, smooth. P3 (Fig. 2h) with ischium and merus of about same width, merus longer than ischium; carpus broadening distally; propodus wider than carpus, anterior and posterior margins convex, posterior margin much longer than anterior; dactylus as long as wide, spatulate. P4 (Fig. 2j) lacking subchelar projection. P5 (Fig. 2i) distinctly chelate, fingers small, tips curved.

Branchial formula, differing from normal callianassid formula in complete absence of arthrobranch on Mxp2, as shown in Table 1.

Plp1 of male uniramous, 2-segmented. Male lacking Plp2. Plp1 of female (Fig. 2k) uniramous, 2-segmented, proximal segment

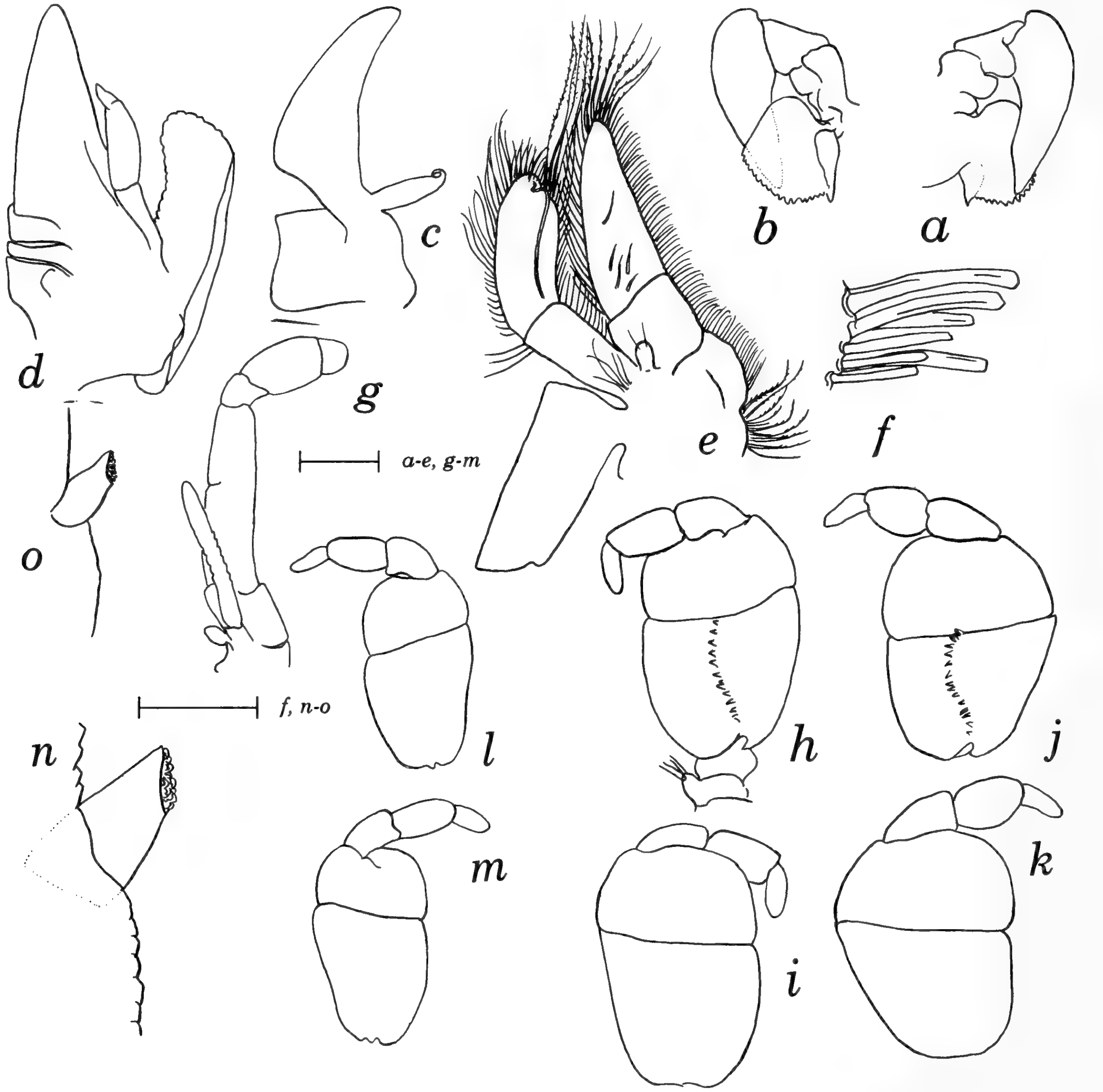

Fig. 3. *Pseudobiffarius caesari,* new genus and species: a–k, n, o, male holotype (USNM 260966), cl 4.7 mm, Buccoo Reef. *Pseudobiffarius caesari,* new genus and species: h, i, female paratype (USNM 260968), cl 3.6 mm, Buccoo Reef.—*Biffarius biformis* (Biffar, 1971): l, m, male (USNM 266071), cl 5.5 mm, Fort Pierce, Florida (USNM 266071): a–b, Mandible; c, Max1; d, Max2, e, Mxp1; f, Marginal setae of Mxp1, enlarged; g, Mxp2; h, Mxp3, inner face; i, Mxp3, outer face; j, Mxp3, inner face); l, Mxp3, outer face; m, Mxp3, inner face; n, o, Plp3 appendix interna. Upper scale, a–e, g–m = 0.5 mm; lower scale, f, n, o, = 1.0 mm.

with subterminal and terminal patch of short setae; distal joint about as long as proximal, with a patch of small setae at midlength and 4 spiniform apical setae. Plp2 of female (Fig. 2l) biramous; endopod straight, with long terminal setae and a few setae scattered along its length; exopod similar to endopod but curved and lacking longer apical setae. Plp3–5 with stubby, projecting appendices internae (Fig. 3n, o) in both sexes.

Uropodal endopod (Fig. 4a, e) slightly longer than wide, margins densely setose; exopod slightly longer than and much wider than endopod, upper plate more than half as wide as lower.

Size.—cl of males ($n = 3$), 3.2 to 5.4 mm; tl of largest male, 20 mm; cl of females ($n = 6$), 2.6 to 6.0 mm, of ovigerous female, 4.1 mm; tl of largest female, 26 mm.

Remarks.—Although this species superfi-

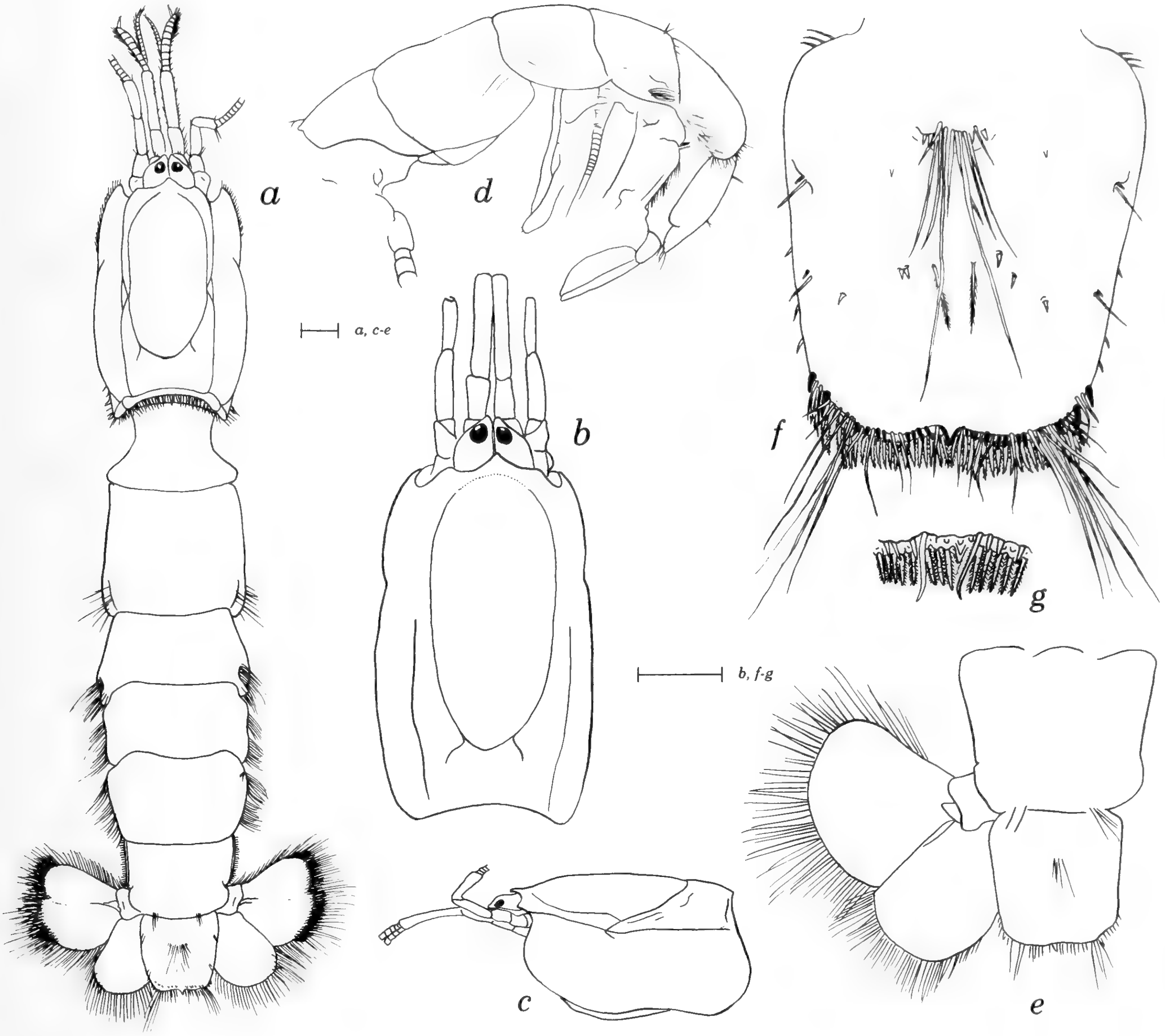

Fig. 4. *Pseudobiffarius caesari,* n. gen., n. sp. a, Dorsal view (pereopods omitted); b, Carapace and anterior appendages, dorsal view; c, Carapace and anterior appendages, lateral view; d, Abdomen, lateral view; e, Sixth abdominal somite, telson, and left uropod, dorsal view; f, Telson, dorsal view, enlarged; g, Details of telson margin, enlarged. a–d, f–g, female paratype (USNM 260967), cl 4.4 mm, Pigeon Point; e, female paratype (USNM 260968), cl 3.6 mm, Buccoo Reef. Scale: a, c–e, 2 mm; b, f, 1 mm; g, 0.5 mm.

cially resembles the type species of *Biffarius, B. biformis* (Biffar 1971), it differs in many features. In contrast to *B. biformis,* males have only one type of cheliped rather than two types, as reported by Biffar (1971) in *B. biformis. Pseudobiffarius caesari* also differs from *B. biformis* in having the A2 peduncle shorter than the A1 peduncle, the upper A1 flagellum much shorter, stouter, and with 9 or 10 rather than 18 to 20 segments. In *B. biformis* the inner face of the ischium of Mxp3 (Fig. 3m) lacks spinules, whereas there is a line of strong spinules on the inner surface of Mxp3 (Fig. 3h, j) in *P. caesari.*

Examination of the telson under high magnification (Fig. 4f, g) yielded a very different picture of its marginal ornamentation than can be obtained under the magnification available from a dissecting microscope. In addition to being lined with short, plumose setae and some much longer ones, especially laterally, the posterior margin of the telson has a distinct median spine and a series of small, thick marginal spines and shorter submarginal spines, with two larger spines posterolaterally.

The shore fauna of Tobago is very rich in species of burrowing decapods. Among

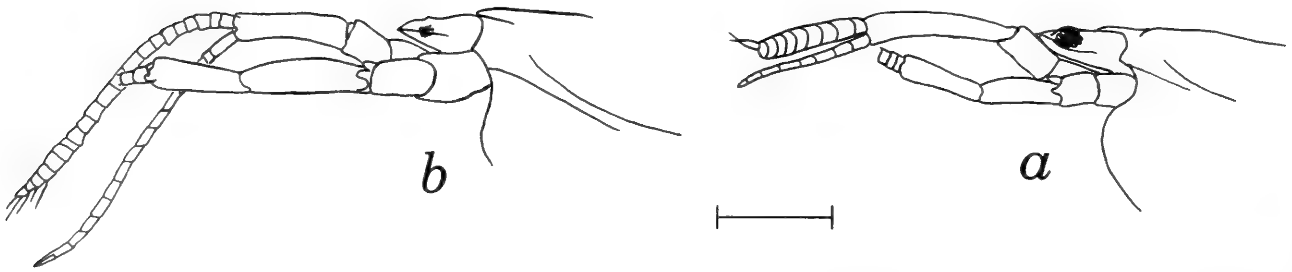

Fig. 5. Carapace and anterior appendages in lateral view. a, *Pseudobiffarius caesari,* new genus and species, female paratype (USNM 260967), cl 4.4 mm, Pigeon Point; b, *Biffarius biformis* (Biffar 1971), male, (USNM 266071, cl 5.5 mm, Fort Pierce, Florida. Scale = 1 mm.

the new species discovered by us (RH) are another callianassid, *Neocallichirus nickellae* Manning, 1993 and the commensal pinnotherid crab, *Austinixa hardyi* Heard & Manning, 1997.

We are pleased to acknowledge our respect for our late colleague, Austin B. Williams, by being able publish this report in a volume of the Proceedings of the Biological Society of Washington dedicated to him.

Etymology.—Named for Errol Caesar of the Fisheries Division, Ministry of Agriculture, Land, and Marine Resources, Tobago. His enthusiastic support and interest in Heard's fieldwork on Tobago materially improved collecting opportunities.

Acknowledgments

We thank both Errol Caesar and J. David Hardy for their support of Heard's investigations on Tobago; Lois Nickell, then with the University Marine Biological Station, Millport, Scotland, for the gift of her collections; and Lilly King Manning for preparing the figures. Manning's studies on callianassid systematics are supported by the Smithsonian Marine Station at Fort Pierce; this is contribution no. 455 from that facility.

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Griceus buskeyi, a new genus and species of calanoid copepod (Crustacea) from benthopelagic waters off Hawaii

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Abstract.—The new genus and species of deep-sea, benthopelagic calanoid copepod, *Griceus buskeyi,* differs from other calanoid copepods in the following derived character states: dorsal interlocking extensions of abdominal somites; antenna 2, mandible, and maxilla 1 originate posterior to the labrum and paragnaths; coxal endite of the mandible outside of the labral-paragnathal envelope; praecoxal and coxal endites of maxilla 1 unarmed; praecoxal endites of maxilla 2 unarmed; endopod of maxilliped with four articulating segments. Two setae on middle endopodal segment of swimming legs 3 and 4 suggests the new genus and species belongs to the superfamily Augaptiloidea. A mandibular endopod which is reduced in size to a small unarmed lobe and absence of an endopod on maxilla 1 suggests an affinity with the arietellid genus *Paraugaptilus* Wolfenden.

Samples from deep-sea, benthopelagic habitats continue to reveal a diverse fauna of calanoid copepods which often express unusual morphologies. Here we describe an unusual species of calanoid which we believe can be placed in the family Arietellidae as it is presently understood (Ohtsuka et al. 1994), but not in any of its known genera.

Methods

This adult female calanoid copepod was collected 6 July 1997 from seawater flowing from a flexible plastic pipe maintained by Natural Energy Laboratory of Hawaii Authority near Kona, Island of Hawaii, 19°43′27.01″N, 156°04′35.46″W. The intake of the pipe (1 m diameter) is located at 675 m, about 30 m from the bottom, and draws in about 132 cubic m/min. Because of its flexibility, the position of the intake may vary vertically ± 10 m with the movement of the tide. Water from one outflow pipe (10 cm in diameter) drains through a 53 micron mesh net placed in a large, dark tank. The sample was collected after 12 hrs; the animal reported here may have been dead prior to sample fixation with 4% formaldehyde. The specimen was later cleared in steps through 50% lactic acid/50% water to 100% lactic acid, stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% water, and examined with bright-field and with differential interference optics.

Cephalic appendages are abbreviated A1 = antenna 1; A2 = antenna 2; Mn = mandible; Mx1 = maxilla 1; Mx2 = maxilla 2. Appendages on thoracic somites are Mxp = maxilliped (thoracopod 1); P1–5 = swimming legs (thoracopods 2–6). The caudal ramus is CR. Designations of appendage segments are according to Ferrari (1995) as follows: medial lobe of a segment = li, lateral lobe = le; rami are exopod = Re and endopod = Ri; ramal segments of Mx2 are exopodal; the Mxp has a basopod with a distal medial lobe, and with at most five endopodal segments in calanoids (Ferrari & Dahms 1998). Armament elements of appendages are termed setae regardless of their position or degree of rigidity. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite.

Calanoid superfamily names follow Andronov (1974) with the exception of Clausocalanoidea for Pseudocalanoida (Bowman 1987, International Commission on Zoological Nomenclature 1988). The changes proposed by Andronov (1991) are not followed here because there is no requirement that a family group name be derived from the oldest included genus name, or by coordination here the oldest included family name (International Code of Zoological Nomenclature 1985, articles 62–64). The correct names in question are Augaptiloidea, Centropagoidea and Megacalanoidea.

Griceus, new genus

Diagnosis.—The following derived character states are assumed to be shared by all species of this genus discovered subsequently: dorsal interlocking extensions of abdominal somites; A2, Mn and Mx1 originating posterior to the labrum and paragnaths; coxal endite of Mn outside of the labral-paragnathal envelope; praecoxal and coxal endites of Mx1 unarmed; praecoxal endites of Mx2 unarmed; endopod of Mxp with four articulating segments.

Type species.—*Griceus buskeyi,* by monotypy.

Etymology.—The name honors Dr. George D. Grice for his contributions to the exploration of the deep-sea benthopelagic fauna, and to the taxonomy of calanoid copepods. Dr. Grice's family name is latinized to form *Griceus.* The gender of the name is masculine.

Griceus buskeyi, new species

Specimens.—Holotype (National Museum of Natural History, Smithsonian Institution USNM 288058) a dissected female, 0.90 mm in length; prosome—0.74 mm and urosome—0.16 mm.

Female.—Pr (Fig. 1C): 6 segments; 1st a complex of 5 cephalic somites plus Th1; Th2–4 simple and articulated; arthrodial membrane between Th5 and 6 incomplete; reduced in width dorsally. Rostral area a simple, bilobe plate (Fig. 1A, C) without spinules or attenuations of cephalon. Location of base of A2, Mn, Mx1, Mx2 and Mxp as in Fig. 1A, B. Base of A2 posterior to labrum; base of Mn outside of labral-paragnathal envelope. Base of Mxp lateral to base of Mx2; base of Mx1 lateral and posterior to base of Mx2. Rostrum, labrum, and paragnaths as in Fig. 2D.

Ur (Fig. 1D): 4 segments; anterior segment a genital complex of Th7 and Ab1; as viewed dorsally, genital complex symmetrical (Fig. 2A). Viewed laterally (Fig. 2B, C), genital complex with a thickened ridge laterally on right side. Right laterally and dorsad, posterior margin of abdominal somites 1–3 asymmetrical, each with attenuate, finger-like process which engages socket-like depression on anterior margin of following somite (Fig. 2E).

A1 (Fig. 3): A large segmental complex proximally (Fig. 4A) of 19 setae separated by incomplete ventral (anterior) arthrodial membranes into 8 groups of 3, 2, 2+1, 3, 2, 3, 1, 2 setae+aesthetascs with setae of same group laterally displaced relative to each other; aesthetasc of the 3rd group short, triangular with distal sensilla. Distal to the complex an incompletely articulating segment with 2 setae and short, triangular aesthetasc with distal sensilla followed by 13 completely articulating segments with 2+1, 2, 2, 2, 2, 2+1, 2, 2, 2, 2, 2+1, 2, 6+1 setae+aesthetascs.

A2 (Fig. 4B, C): coxa and basis without setae. Re 8 articulating segments with 0, 1,

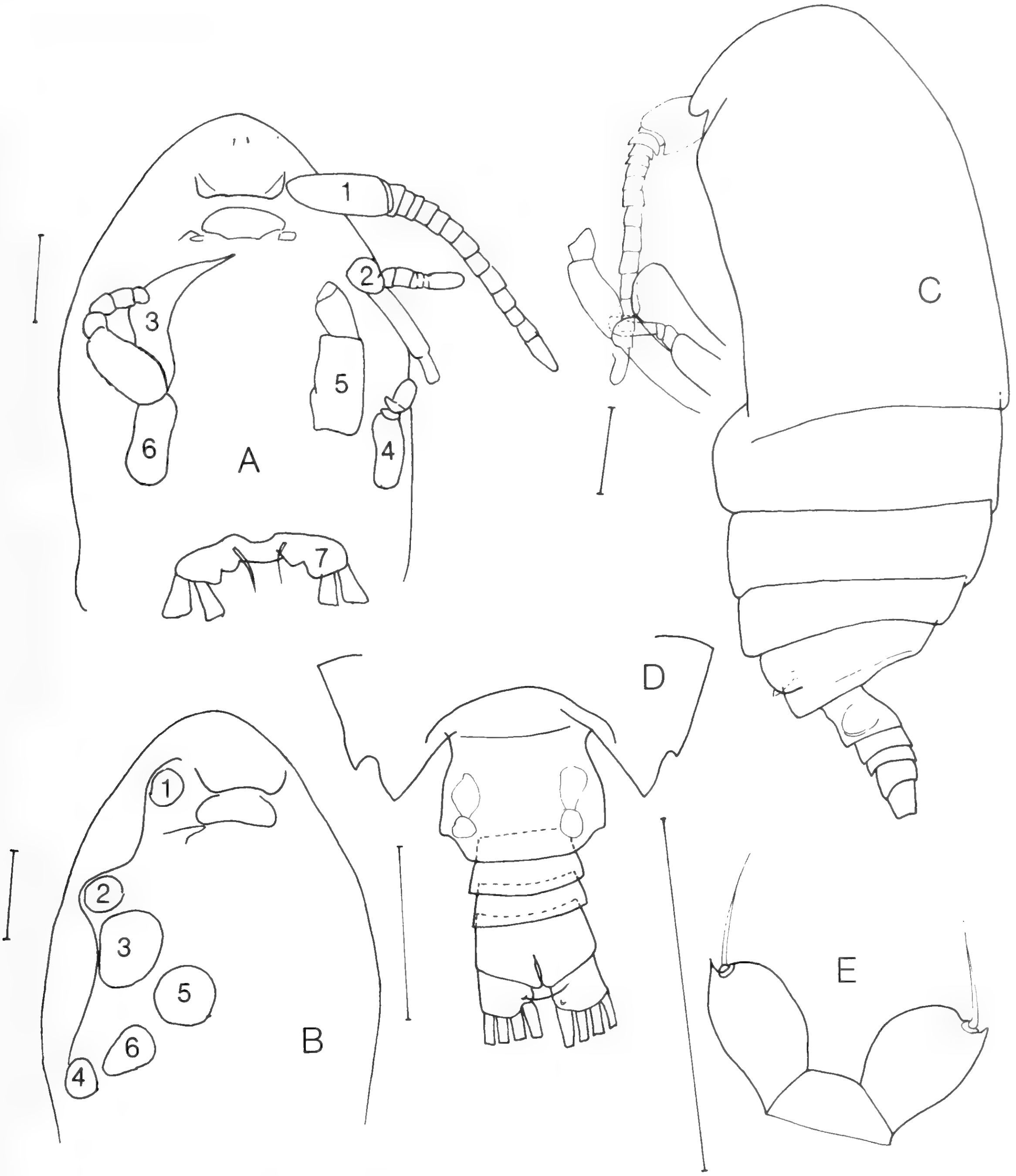

Fig. 1. *Griceus buskeyi* new genus, new species. A, Oral area, ventral, showing location of only one of antenna 1 (1), antenna 2 (2), mandiblar gnathobase (3), maxilla 1 (4), maxilla 2 (5), maxilliped, obscuring mandibular palp (6); both swimming legs 1 (7); B, same, showing location of origin of antenna 1 (1), antenna 2 (2), mandible (3), maxilla 1 (4), maxilla 2 (5), maxilliped (6); C, animal, left lateral; D, Th5–6 and urosome, dorsal; E, leg 5. All scale lines are 0.01 mm.

1, 1, 1, 1, 0, 3 setae. Ri 2-segmented with 1 and 8 (4 terminal, 4 subterminal) setae.

Mn (Fig. 4D): coxa elongate with lobe at mid-length and attenuations medially; basis unarmed. Re 5-segmented with 1, 1, 1, 1, 1 setae. Ri apparently a lobe on the basis medial to the exopod.

Mx1 (Fig. 4E): Praecoxa, coxa and basis with poorly-developed, unarmed lobes. Ri not distinguished. Re 1-segmented with 1 medial and 3 terminal setae.

Mx2 (Fig. 4F): Proximal and distal praecoxal endites poorly-developed, unarmed; no arthrodial membrane separating praecoxa and coxa. Proximal coxal endite with 2 setae, distal coxal endite with 2 setae. Endites of basis indistinct with 1 and 2 setae. Re unsegmented with 7 setae.

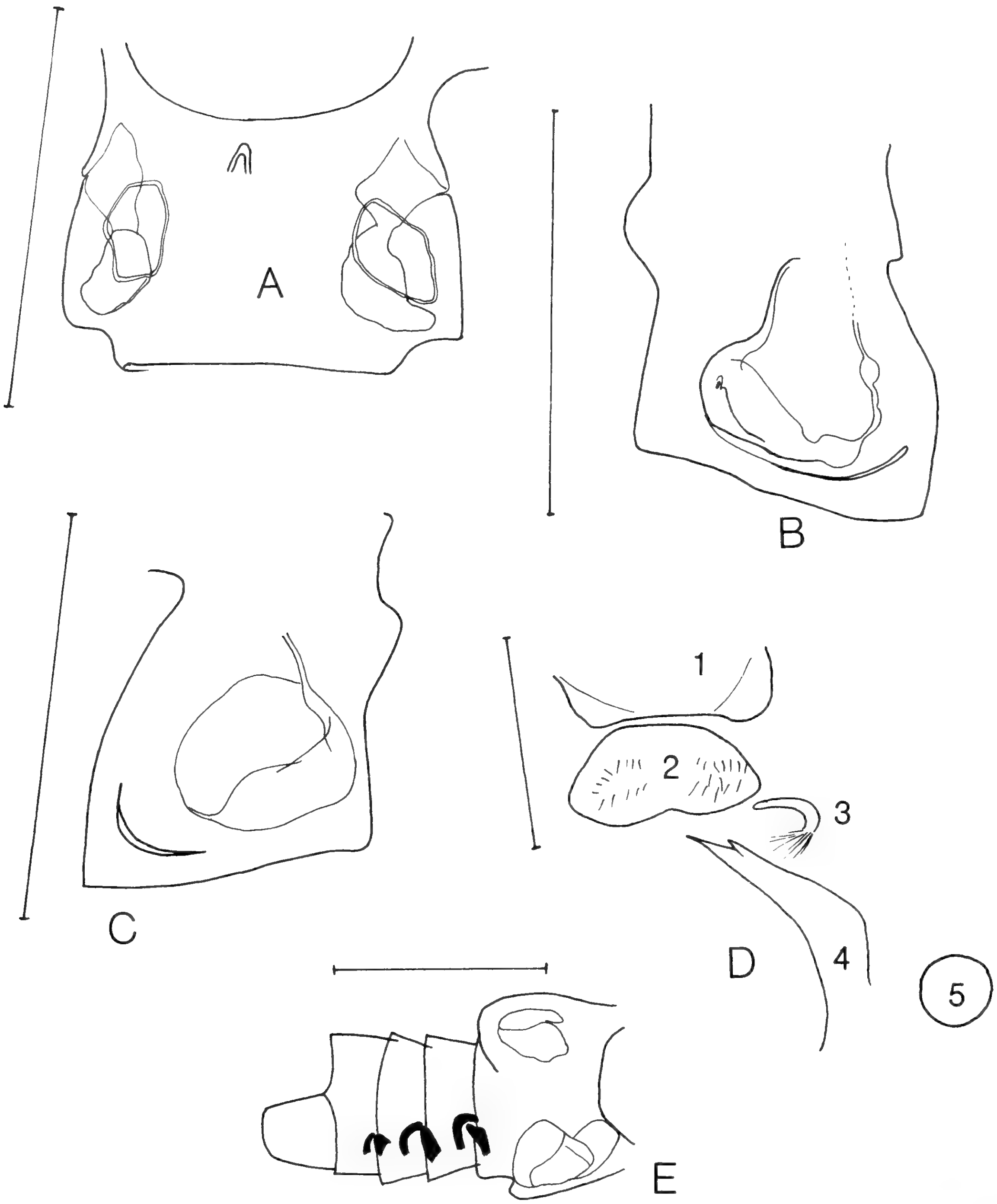

Fig. 2. *Griceus buskeyi* new genus, new species. A, Genital complex, dorsal; B, Genital complex, left lateral, C, Genital complex, right lateral; D, Mouth area, ventral, showing location of rostrum (1), labrum (2), paragnath (3), tip of mandibular gnathobase (4) and origin of antenna 2 (5); E, urosome, dorsal and slightly lateral, with attenuate finger-like processes and socket-like depressions darkened. All scale lines are 0.01 mm.

Mxp (Fig. 5A): syncoxa with 1 seta but without distinct lobes. Basis with 3 setae (2 on a distal medial lobe which is poorly developed and weakly sclerotized) and anterior denticles not organized into a clear pattern. Ri 4-segmented proximal to distal with 1, 2, 3, 4 setae (4, 3, 1, 2 by segmental age).

P1 (Fig. 5B): coxa with medial seta. Basis with medial denticles; medial seta curved only toward its tip with setules along the proximal straight part; lateral seta absent. Re apparently 3-segmented with distal segment missing; proximal segment with 2 (medial and lateral) setae; middle segment with 2 (medial and lateral) setae. Ri 3-segmented; proximal segment with medial seta, a pore on anterio-distal margin (with the inner seta of the basis comprising

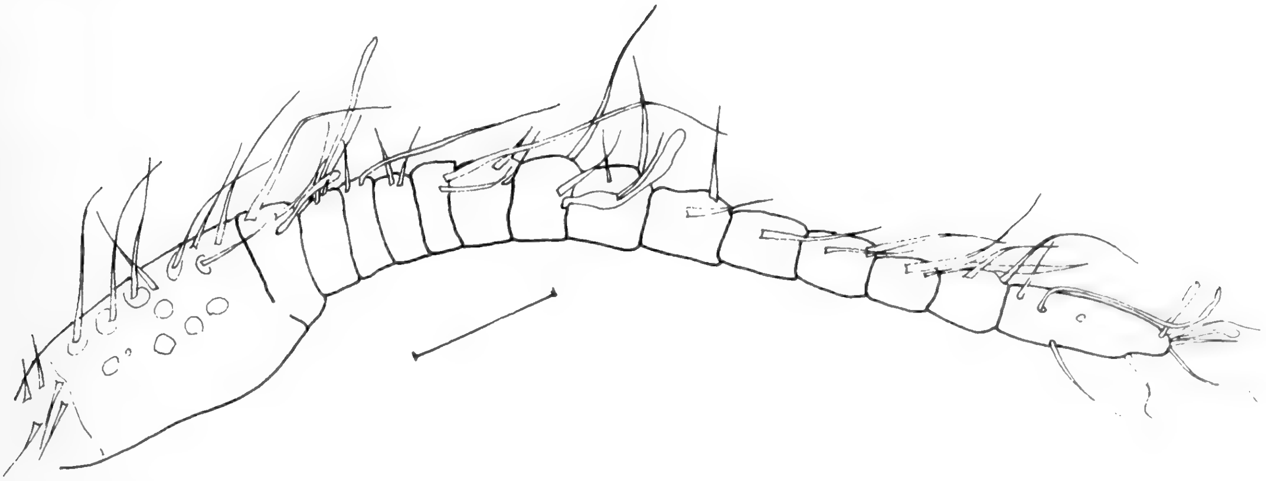

Fig. 3. *Griceus buskeyi* new genus, new species. A, antenna 1, left. Scale line is 0.01 mm.

Von Vaupel Klein's organ) and a lateral attenuation; middle segment with 2 medial setae; distal segment with 1 medial, 2 terminal and 2 lateral setae.

P2 (Fig. 5C): coxa with medial seta. Basis unarmed. Re apparently 3-segmented with distal segment missing; proximal segment with 2 (medial and lateral) setae; middle segment with 2 (medial and lateral) setae. Ri 3-segmented; proximal segment with medial seta and middle segment with 2 medial setae; distal segment with 3 medial, 2 terminal and 2 lateral setae.

P3 (Fig. 5D): coxa with medial seta. Basis unarmed. Re apparently 3-segmented with distal segment missing; proximal segment with 2 (medial and lateral) setae; middle segment with 2 (medial and lateral) setae. Ri apparently 3-segmented; proximal segment with medial seta and middle segment with 2 medial setae; distal segment missing.

P4 (Fig. 5E): coxa with medial seta. Basis with lateral seta. Re apparently 3-segmented with distal segment missing; proximal segment with 2 (medial and lateral) setae; middle segment with 1 medial seta (lateral seta apparently missing). Ri apparently 3-segmented; proximal segment with a medial seta and middle segment with 2 medial setae; distal segment missing.

Leg 5 (Fig. 1E): coupler uniting limbs which each bear a terminal seta.

CR (Fig. 1D): 4 thick apical setae; dorsal seta small and thin.

Male.—unknown.

Etymology.—The name recognizes Edward Buskey for collecting the sample which contained this copepod. The specific epithet is a noun in the genitive singular.

Remarks.—The unknown, but possibly extensive, period of time this specimen may have remained unfixed in the collecting net makes difficult the determination of several possible synapomorphies involving setae or spinules. For example, a rostrum without spinules (filaments), antenna 2 basis without setae, antenna 2 endopod with four terminal setae and mandibular exopod with one seta on the terminal segment all represent potential apomorphies that should be verified when better preserved specimens are available. For this reason, we have chosen to emphasize the apparently derived nature of the following changes in shape of somites and appendage segments which are presumed apomorphies for species of *Griceus*: interlocking extensions of abdominal somites dorsally; antenna 2, mandible and maxilla 1 originating posterior to the labrum and paragnaths; coxal endite of the mandible lying outside of the labral paragnathal envelope; praecoxal and coxal endites of maxilla 1 unarmed; praecoxal endites of maxilla 2 unarmed; endopod of maxilliped with four articulating segments.

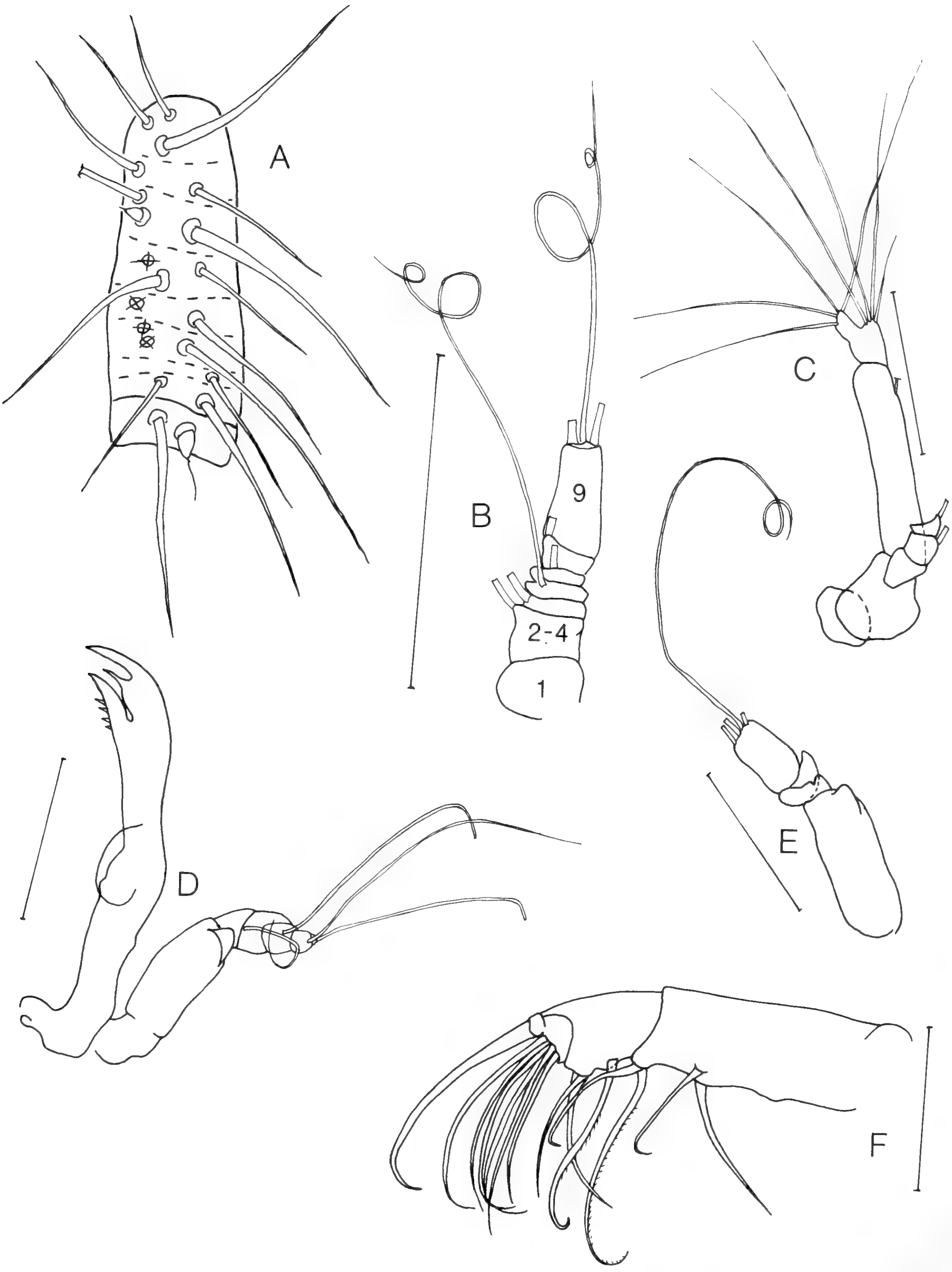

Fig. 4. *Griceus buskeyi* new genus, new species. A, proximal segmental complex plus following incompletely articulating segment of left antenna 1, ventral view, distal is down, wavy line cutoff on broken seta, circle with X is setal scar, broken lines are incomplete arthrodial membranes (scale line as for B); B, exopod of right antenna 2 with, segments 1, 2–4 and 9 indicated; C, left antenna 2, with exopod broken; D, left mandible; E, left maxilla 1; F, left maxilla 2. All scale lines are 0.01 mm.

The effect of the changes in location of the cephalic appendages may be generalized as follows: A2, Mn and Mx1 retain their ancestral positions relative to one another but as a group they have been drawn back posteriorly and laterally from the usual calanoid locations. The penultimate segment of the maxilliped may be a complex

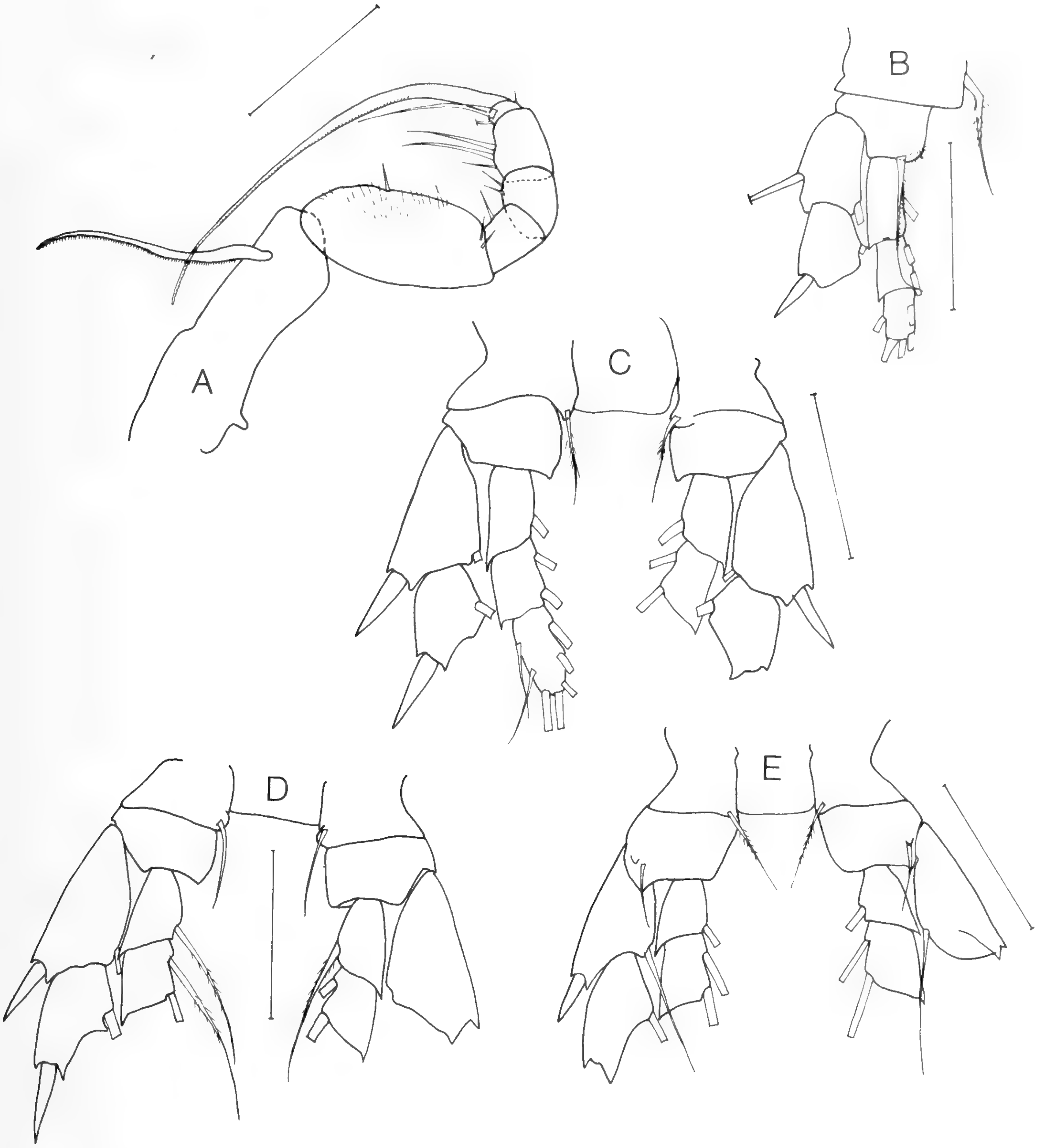

Fig. 5. *Griceus buskeyi* new genus, new species. A, left maxilliped; B, swimming leg 1, anterior; C, swimming leg 2, posterior; D, swimming leg 3, posterior; E, swimming leg 4, posterior. All scale lines are 0.01 mm.

of 2nd and 5th segments with the arthrodial membrane missing because it bears more setae than the two segments proximal to it (see Ferrari 1995, Ferrari & Dahms 1998). The endopod of the maxilliped of derived centropagoideans is poorly sclerotized and without arthrodial membranes; setal additions during development of *Acartia tonsa* Dana, 1849, *Tortanus dextrilobatus* Chen & Zhang, 1965, and *Epilabidocera longipedata* (Sato 1913) suggest these endopods are 4-segmented with one seta on proximal, antepenultimate and penultimate segments, and two setae on the distal segment. The endopod of *G. buskeyi* is well-sclerotized; there is one seta on the proximal, two setae on the antepenultimate, three setae on the penultimate and four setae on the distal segments suggesting that this 4-segmented ramus is not convergent with the centropagoideans. The ramus of maxilla 1 is interpreted as an exopod because its quadrate morphology and terminal crown of setae is similar to the exopod of many heterorhabdids and augaptilids. We know of no calanoid copepod with a maxilla 1 in which the endopod is the only ramus. Segmental homologies of leg 5 are based on the location of the terminal seta toward the lateral side of the appendage. This seta is interpreted as the terminal seta of the distal exopodal segment; the proximal segment is a fused coxa plus basis.

We have reconsidered what kinds of information the morphology of the exopod of A2 provides about the superfamily of *Griceus*. We do not follow the hypothesis of Park (1986) that the exopod of antenna 2 of species of Augaptiloidea have only nine segments, none of which are complexes, while among the remaining superfamilies there are up to 10 segments, and except for the Eucalanoidea with the 2nd always fused to the 3rd and 9th always fused to the 10th. Which of the ten segments present in the remaining superfamilies fails to form in Augaptiloidea is not indicated by Park (1986). Here, homologies of the exopod are derived from the following assumption: all segments, with the exception of the distal segment, are serial homologues bearing at most one medial seta. The female of *Rhincalanus gigas* Brady, 1883 has nine medial setae, each proximal to an arthrodial membrane, and a distal segment with a terminal and two sequentially arranged medial setae (Fig. 6A). An incomplete, distal arthrodial membrane extends in part along the anterior and posterior surfaces between the second and third medial setae, while an incomplete, distal arthrodial membrane fails to extend to the lateral surface separating the 3rd and 4th medial setae. Giesbrecht (1892: plate 11, figs. 16, 17) shows the exopod of *Eucalanus attenuatus* (Dana 1849) and *E. crassus* Giesbrecht, 1888 which can be interpreted as 11-segmented, a proximal complex of four segments represented by four medial setae, followed by six articulating segments, each with a seta, and a distal segment with a crown of three setae. We have been able to verify only a crown of three setae and nine medial setae each with at least part of a distal arthrodial membrane for these species.

Males of *Temora longicornis* (Müller, 1785) have a more common calanoid morphology (Fig. 6B). An elongate segment distally with a medial seta near its midlength is assumed to correspond to the penultimate segment which is elongate distad from the seta in this species. The distal segment has a crown of three setae corresponding to the distal segment of *R. gigas*. The 2nd articulating segment with three medial setae is assumed to be a complex of the 2nd, 3rd, and 4th segments in which the incomplete arthrodial membranes of *R. gigas* fail to form on *T. longicornis*. The five remaining articulating segments with a medial setae and distal arthrodial membrane are the 1st and 5th–8th of *R. gigas*. There are many calanoids in which the distal arthrodial membrane of three or more proximal segments fails to form; in these cases, a medial setae is assumed to represent the location of each segment. For example, in *Calanus finmarchicus* (Gunnerus, 1765) the elongate second segment shows no trace of an arthrodial membrane on its dorsal surface but four medial setae suggest this is a complex of the 2nd–5th segments; the remaining distal segments, each with a medial seta, articulate distally (Fig. 6C).

In contrast, in augaptiloidean species like *Phyllopus bidentatus* Brady, 1883 and *Heterorhabdus spinifrons* (Claus 1863), a medial seta on each of a set of proximal segments fails to form while the distal arthrodial membrane of each of those segments is present (Giesbrecht 1892: plate 18, fig. 29 and plate 20, fig. 9). Ohtsuka et al. (1994) describe arietellids with an elongate, proximal segmental complex in which both the seta and distal arthrodial membrane of a set of segments apparently fail to form. *Griceus buskeyi* has its 1st segment with a distal arthrodial membrane but no medial seta; the following segmental complex is interpreted as composed of the 2nd and 3rd segments which have neither an arthrodial membrane nor a medial seta, plus the 4th segment with a medial seta and a distal arthrodial membrane. The next four articulat-

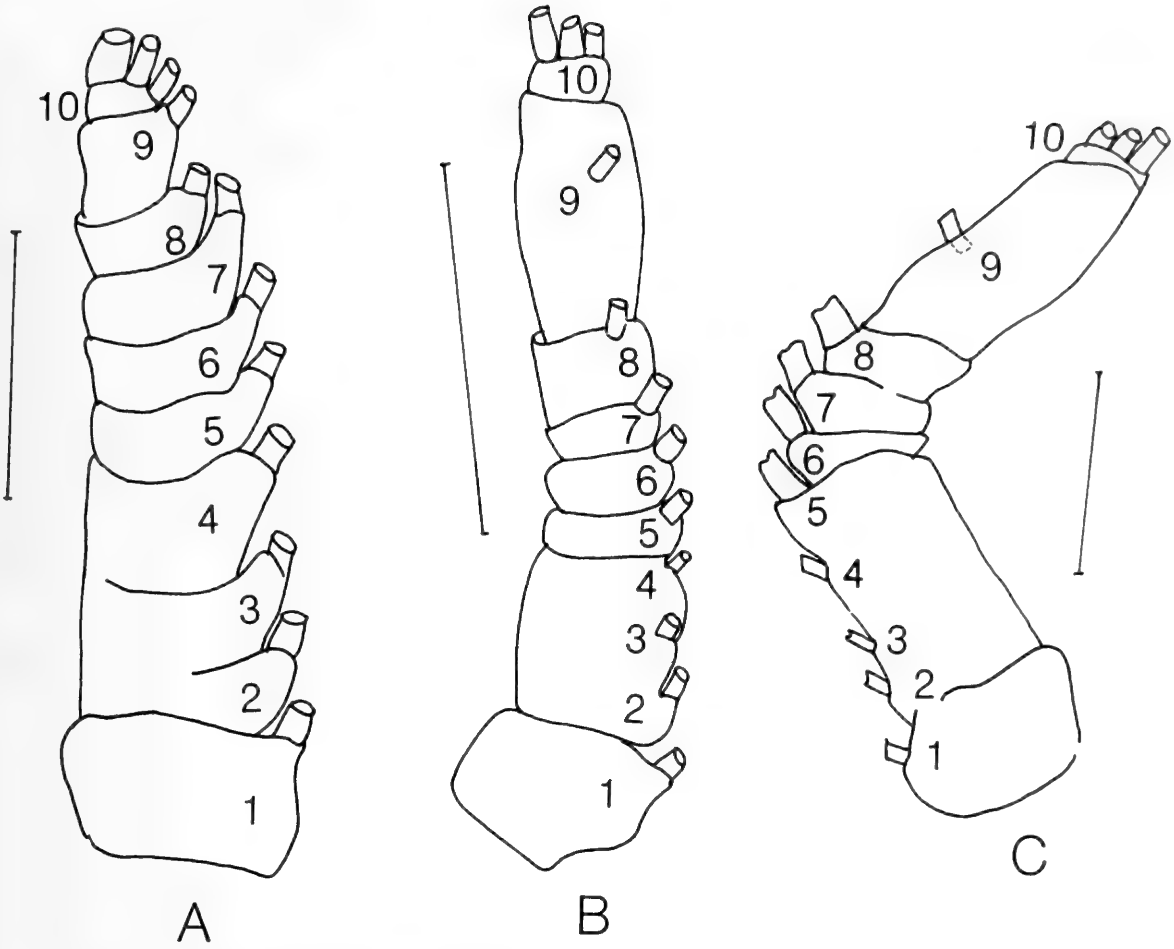

Fig. 6. *Rhincalanus gigas* antenna 2 exopod; *Temora longicornis* antenna 2 exopod; *Calanus finmarchicus* antenna 2 exopod. Presumed segments are numbered proximal to distal; scale lines for A and C are 0.01 mm; B is 0.05 mm.

ing segments each with a seta are the 5th–8th segments. The following elongate segment is an unarmed 9th segment and the 10th segment has a crown of three setae. Our interpretation assumes that all segments homologous to those of *R. gigas* are present in these calanoids. The alternate hypothesis of Park (1986) that one of the ten segments fails to form, has not been considered because we are unsure of the location on the antennal exopod that new segments are patterned, and whether there is a single location for segment patterning, like the copepod maxilliped (Ferrari & Dahms 1998), or more than one location, like the calanoid antenna 1 (Ferrari & Benforado 1998).

Loss of segments on some of the swimming legs complicates the assignment of this specimen to the correct calanoid family. However, two character states suggest that *G. buskeyi* belongs to the superfamily Augaptiloidea. Two setae on middle segment of endopod of swimming legs 3 and 4, probably an ancestral calanoid state, are present only on Epacteriscioidea, Pseudocyclopoidea, Augaptiloidea, Centropagoidea, Megacalanoidea, and some Bathypontioidea (Andronov 1974, Suárez-Morales & Iliffe 1996). We note in passing a misprint in Table 1 of Suárez-Morales & Iliffe (1996) in the number of inner setae on the terminal segment of swimming legs 3 and 4 (column E); Pseudocalanoidea (Clausocalanoidea) are unique in having four setae while the Spinocalanoidea with five setae are identical to the remaining superfamilies. The Arietellidae and Heterorhabdidae are the only families among the above six superfamilies with species in which the endopod of maxilla 1 does not develop (Ohtsuka et al. 1994, Park 2000), so an assignment to the Augaptiloidea seems reasonable.

Among the eight families and 39 genera of Augaptiloidea, a set of derived characters states have been proposed only for the family Heterorhabdidae and its genera (Park 2000), so placement of *G. buskeyi* in a family is difficult. With respect to the affinity of *G. buskeyi,* a small unarmed mandibular endopod and maxilla 1 without an endopod are character states shared only with *Paraugaptilus* Wolfenden, 1904 (Arietellidae) and a few species of *Augaptilus* Giesbrecht, 1889 (Augaptilidae). The absence of setae on the praecoxal endites of maxilla 2 suggests a relationship with *Paraugaptilus* which has only one seta on each praecoxal endite. All species of *Augaptilus* have two setae on these endites; this is a widespread and presumably ancestral state for the Augaptiloidea. Given our limited knowledge the Augaptiloidea and its families, the shared similarities of *G. buskeyi* to species of *Paraugaptilus* provides a reasonable justification for placing this new genus in the Arietellidae.

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Studies on the Crustacea of the Turks and Caicos Islands, British West Indies. IV. *Heteromysis* (*Heteromysis*) *spottei,* a new species (Peracarida: Mysidacea: Mysidae) from Pine Cay

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Abstract.—During a survey of the marine Crustacea in the vicinity of Pine Cay, Turks and Caicos Islands, an undescribed mysid, *Heteromysis spottei,* new species, was collected at depths ranging from 1 to 18 m. The new species belongs to the subgenus *Heteromysis* Băcescu and can be distinguished from the five other members of that subgenus known from the western Atlantic by the setation of the telson. In *Heteromysis spottei* the telson has spine-setae along the entire length of the lateral margins, spinules along the entire margins of the cleft, and a pair of spine-setae on each apical lobe, the outer being nearly three times longer than the inner. A key and diagnostic table to the species of the subgenus *Heteromysis* from the Northwest Atlantic is presented.

Excluding the commensal palaemonid shrimps, which have been addressed in a separate series of publications (Heard & Spotte 1991, Heard et al. 1993, Spotte et al. 1994, Spotte & Bubucis 1996, Heard & Spotte 1997), this is the fourth contribution in a series on the crustacean fauna of the Turks and Caicos Islands. The first three reports dealt with marine isopods (Kensley & Heard 1991, Schotte & Heard 1991, Schotte et al. 1991).

This report presents the description of a new species of mysid belonging to the genus *Heteromysis* Smith, 1873. The new species, which is referred to the subgenus *Heteromysis* (*Heteromysis*) Smith 1873 sensu Băcescu, 1968, was collected in water depths ranging from 1 to 18 m in the vicinity of Pine Cay.

The type material was deposited in the National Museum of Natural History (USNM), Smithsonian Institution, and the Gulf Coast Research Laboratory (GCRL). We follow the setal classification of Watling (1989) in which a seta is defined as an articulated cuticular outgrowth of the integument. The term "spine-seta" as used here refers to any seta with spine-like characteristics; a spine is defined as a non-articulated extension of the cuticle.

Heteromysis (*Heteromysis*) *spottei,* new species
Figs. 1–2

Material examined (all material from Turks and Caicos).—Holotype: adult ♀ (Length [L] 3.1 mm), USNM 282719, fringing reef off Pine Cay, live bottom/sand, depth 18 m, J. A. McLelland (coll.), suction device, 12 Nov 1989. Paratypes: adult ♂ (L3.5mm), USNM 282720; adult ♂, damaged, GCRL 1346, same collection data as holotype.—1 adult ♂, 2 ♀♀, (all damaged) Pine Cay, shallow inner reef, sand-coral rubble substratum with associated sponges and cnidarians, depth 4 m, 1 mm mesh dredge net, R. Heard, J. McLelland, P. Bubucis, & S. Spotte (colls.), 5 Nov 1988.—1♂ (damaged), Pine Cay (Rock-a-Wash Cay), depth 1 m, *Neogoniolithon* & sponge washings, R. Heard (coll.), 30 Oct 1988.—2♂♂, 1 ♀ (all damaged), same data as holotype.

Diagnosis.—Article 3 of antennular peduncle without distomedial flagellated spine-seta; thoracic endopod 3 with 3 flagellated spine-setae on medial margin of merus, medial margin of carpo-propodus without flagellated spine-setae; pleopods uniramous, reduced to simple setose plates with no modified spine-setae in either sex; endopod of uropod armed with 1 small spine-seta near statocyst; lateral margins of telson armed along entire length with 10–12 spine-setae per margin (including apical spine-setae), posterior-most lateral spine-seta 1.6–1.7 times length of preceding spine-seta, extending beyond posterior end of telson; outer apical spine-seta nearly 3 times longer than inner; cleft completely armed with 18–20 spinules.

Description.—General body form (Fig. 1A): moderately robust; carapace with anterior margin produced into pointed triangular rostrum; posterior dorsal margin emarginate, partly exposing thoracic segment 8; anterolateral lobes rounded.

Antennule peduncle (Fig. 1B): article 1 slightly shorter than article 3, with 3 plumose and 2 simple spine-setae on distolateral process, dorsomedial longitudinal ridge with 4 strong simple distal spine-setae; article 2 compressed with 2 distomedial spine-setae, 1 simple and 3 plumose spine-setae near middle of distal margin; article 3 with simple spine-seta on medial margin, 3 simple distomedial spine-setae, 3 plumose spine-setae near distolateral margin, 1 simple spine-seta on dorsolateral surface, lacking flagellated spine-seta, males with small moderately setose lobe on ventral surface.

Antenna (Fig. 1C): scale slightly shorter than peduncle, 3.0–3.2 times as long as maximum width, medial margin strongly convex, lateral margin straight, all margins setose, lacking distal article; antennal peduncle having 3 articles; article 1 inconspicuous; article 2 just over 1.5 times longer than article 3, short plumose spine-seta near distolateral border, 2 simple and 2 plumose distomedial spine-setae; article 3 with 1 plumose and 3 simple distomedial spine-setae, 3 plumose spine-setae along lateral margin.

Eyes (Fig. 1A): large, oval, directed laterally, distal part of eye stalk wider than cornea, lacking ocular tooth; cornea large, oval.

Mandibles (Fig. 1D–F): molar, incisor, and lacina mobilis as illustrated. Palp 3-segmented; article 1 small, inconspicuous; article 2 expanded, medial margin with 5–10 simple spine-setae, lateral margin with 4–5 proximal plumose spine-setae and 1 simple distolateral spine-seta; article 3 half as long as 2, medial margin with 1 plumose spine-seta, distal part armed with 1 simple and 9–10 barbed spine-setae, 1 simple spine-seta on medial surface.

Labrum and paragnaths (Fig. 1D, G): as illustrated.

Maxillule (Fig. 1H): outer lobe with 11 stout apical and 3 subapical spine-setae; inner lobe with 3 long, distally curved, serrate spine-setae, 2 plumose and 2 simple spine-setae distally, and 1 plumose and 1 simple spine-seta on distomedial margin.

Maxilla (Fig. 1I): as illustrated; exopod with 13–15 plumose spine-setae on distolateral margin.

Thoracic endopods 1–8 (Fig. 2A–G): thoracic endopods 1 and 2 as illustrated. Thoracic endopod 3, merus approximately 1.6 length of ischium and equal in length to carpo-propodus, medial margin with 3 flagellated and 3 simple spine-setae, lateral margin with 1 distal simple spine seta; medial margin of carpo-propodus with 4–5 simple spine-setae, 2 simple and 2 stout serrate spine-setae on distomedial margin; dactyl small, with long, slightly curved claw on distal end surrounded by several simple spine-setae. Thoracic endopod 4, merus about 1.5 length of ischium; carpo-propodus about ¾ length of merus, with 3 articles (distal 2 subequal, combined length slightly longer than proximal article); dactyl minute, papillate, lacking terminal claw. Thoracic endopod 5, ischium and merus sub-

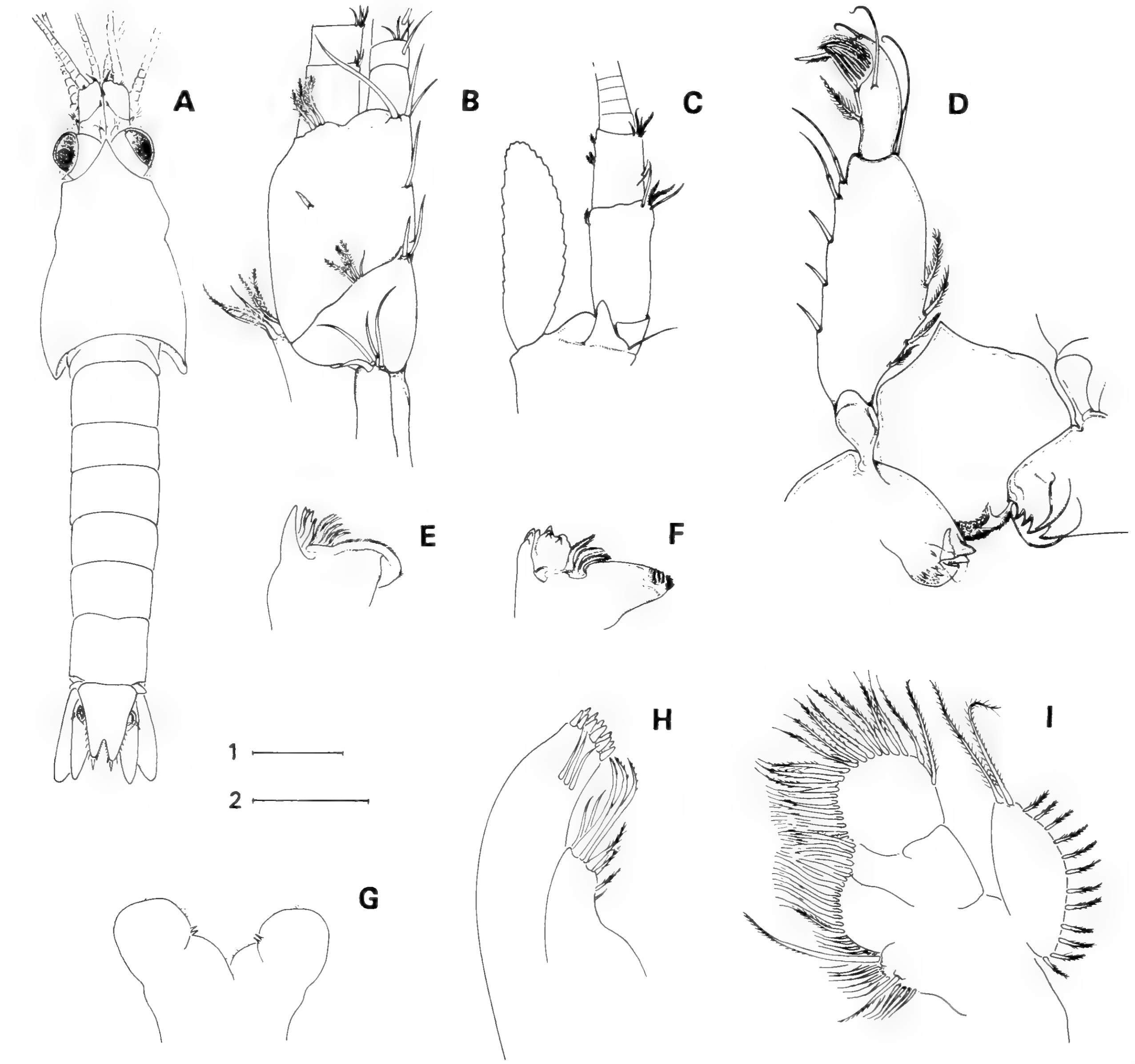

Fig. 1. *Heteromysis spottei,* new species. A, adult ♀, dorsal view; B, antennular peduncle; C, antennal peduncle and scale; D, labrium & right mandibular palp; E, F, right mandible, inner and upper aspects, respectively; G, paragnaths; H, maxillule; I, maxilla. Scale 1, A = 0.5 mm; C = 0.2 mm; B, D–F, I = 0.1 mm; A = 0.05 mm; Scale 2, G = 0.1 mm.

equal in length; carpo-propodus with 4 articles, distal 3 subequal in length, each half as long as proximal article, ultimate article with 6–7 simple spine-setae (2 sickle-shaped with strong articulated bases); dactyl small, papillate with long distal, slender claw. Thoracic endopod 6, carpo-propodus, ischium and merus subequal in length; carpo-propodus with 5 articles, distal 4 subequal in length, each about ⅔ as long as proximal article; dactyl small, papillate with distal serrate slender claw. Thoracic endopod limb 7, ischium slightly longer than merus, merus slightly longer than carpo-propodus; carpo-propodus with 3 articles, proximal distinctly longer than each of distal articles; dactyl small, papillate with distal serrate slender claw. Thoracic endopod 8 (1 damaged limb available for study), long, attenuated, at least ⅓ longer than other thoracic endopods; carpo-propodus with at least 5 articles.

Thoracic exopods: exopod 1 with 8 articles; exopods 2–8 with 9 articles.

Thoracic sternal processes: median spiniform processes on sterna 3–7 in males.

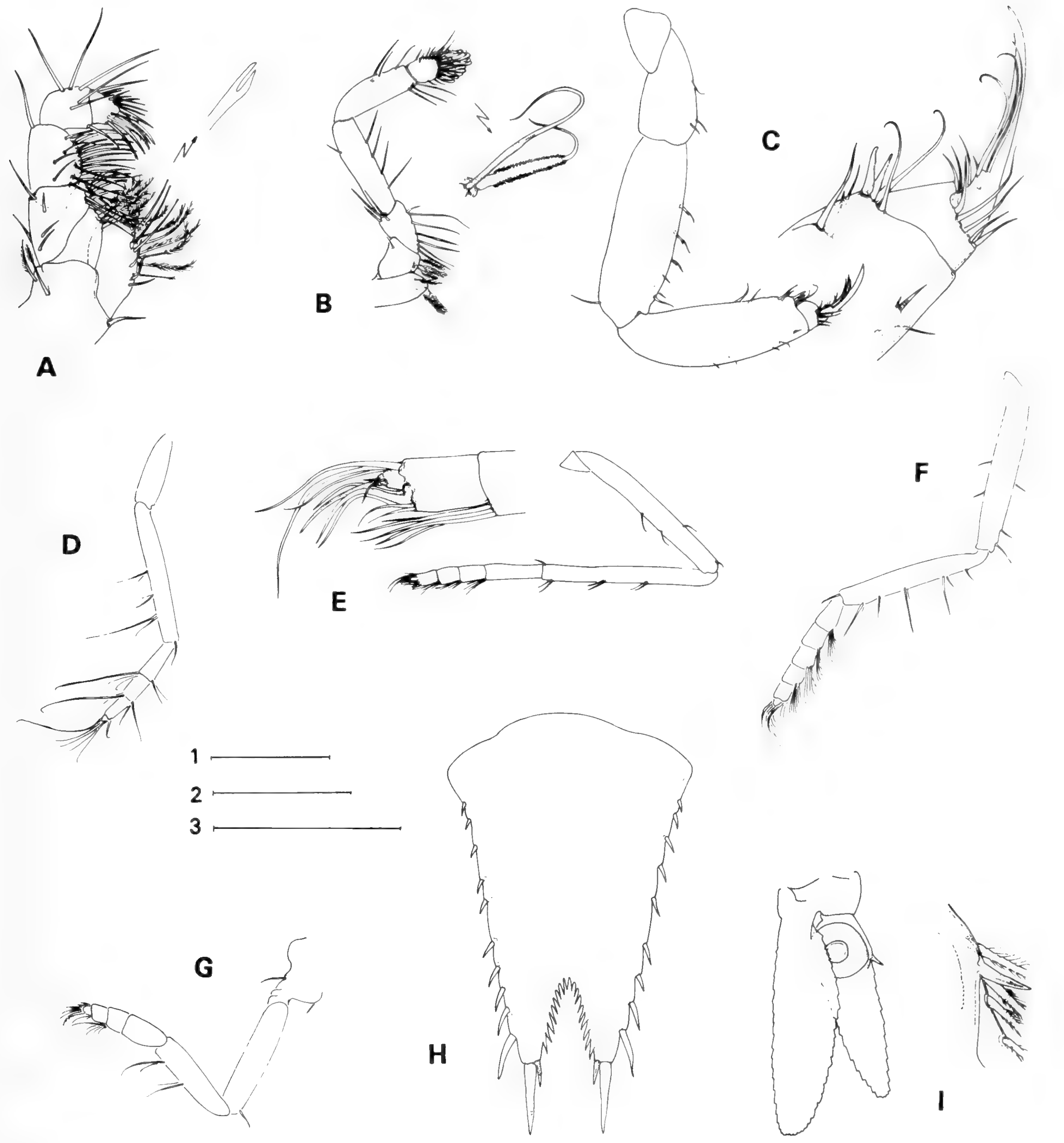

Fig. 2. *Heteromysis spottei,* new species. A–G endopods of thoracic limbs 1–7; H, telson; I, uropod. Scale 1, H = 0.1 mm; Scale 2, A = 0.1 mm, B–G = 0.2 mm; Scale 3, I = 0.2 mm.

Pleopods: without sexual dimorphism; reduced to uniramous plates with no modified spine-setae, similar in form.

Uropods (Fig. 2I): exopod about 1.2 times longer than endopod, lateral margin straight, medial margin slightly convex, all margins setose; endopod linguiform with 1 spine-seta on medial margin in region of statocyst, all margins setose.

Telson (Fig. 2H): 0.8 times length of exopod of uropod, 1.4–1.5 times as long as maximum width, lateral margins slightly concave, armed along entire length with 10–12 spine-setae per margin (apical spine-setae included), increasing in length posteriorly, most posterio-lateral spine-seta 1.6–1.7 times length of preceding spine-seta, extending beyond posterior lobes of telson; outer apical spine-seta 2.8–3.0 times longer than inner; cleft, depth 0.25 length of telson, completely armed with 18–20 small spines.

Etymology.—This species is named for

Table 1.—Common and specific adult characters of the subgenus *Heteromysis* in the northwestern Atlantic.

Character	Species					
	elegans	*formosa*	*mexicana*	*nouveli*	*mureseanui*	*spottei*
Flagellated spine-seta on antennular peduncle	absent	absent	absent	absent	absent	absent
Spine-setae on medial margin of carpo-propodus of thoracic endopod 3	simple, slender, about 10	simple, 8–9 slender, 6 stout	none	simple, 7 slender, 6 stout	simple, 9 slender; flagellated 2	simple, 6–7 slender; serrate, 2
Spine-setae on medial margin of merus of thoracic endopod 3	simple, 7	simple, 8–13	none	simple, 2	simple, 7	simple, 3; flagellated, 3
Modified male pleopods	none	none	none	?	none	none
No. spine-setae on uropodal endopod	15–25	14–19	20–23	1	0	1
Spinules in telson cleft	anterior half, 10–15	entire, 16–30	entire, 22–23	anterior half, 18	entire, 20	entire, 18–20
Lateral spine-setae on telson (apical spine setae included)	posterior half, 7–10	posterior half, 11–19	posterior half, 14–17	posterior half, 8	posterior half, 3–4	entire, 10–12
Apical telson spine-setae per lobe; outer:inner length	single	single	single	pair, 0.5	pair, 2.0	pair, 2.8–3.0
Distal article on antennal scale	present	absent	present	present	present	absent
Length:width ratio of antennal scale	3.8–4.0	2.7–2.9	2.3	2.6	3.7	3.0–3.2

Stephen Spotte in recognition of his many contributions to marine science.

Habitat.—Heteromysis spottei was collected from habitats having a variety of calcareous algae, sponges, anthozoans, and other sessile forms. It occurred in depths of less than 1 m on the Caicos Banks, 3–4 m in the back reef area, and 18 m on the outer fringing reef. Unfortunately, our collecting techniques were too general to determine if the species was associated with a specific sessile host.

Distribution.—This species is presently known only from waters immediately adjacent to Pine Cay, Turks and Caicos Islands, British West Indies.

Remarks.—The dichotomous key and Table 1 present some of the salient characters that distinguish these western Atlantic species of the subgenus *Heteromysis.*

Key to western Atlantic species of the subgenus *Heteromysis* Smith, 1873 sensu Băcescu, 1968

(species lacking flagellated spine on segment 3 of antennular peduncle and sexually dimorphic pleopods).

1. Endopod of uropod with 12 or more spines along medial margin from region of statocyst to apex 2
   –Endopod of uropod with no spines or one spine medially, near statocyst 4
2. Margins of telsonic cleft with spinules along entire length; antennal scale 3 times or less as long as maximum width 3
   –Margins of telsonic cleft with spinules only in apical part; antennal scale at least 3.5 times as long as maximum width . . . .
   . . . . . *Heteromysis elegans* Brattegard, 1974
3. Carpo-propodus of third thoracic endopod with 3 pairs of stout spine-setae on distomedial margin . . . .
   . . . . *Heteromysis formosa* S. I. Smith, 1873
   –Carpo-propodus of third thoracic endopod with no stout spine-setae on medial margin. . . . .
   Heteromysis mexicana Escobar-Briones & Soto, 1990
4. Endopod of uropod with no spine-setae medially, near statocyst . . . .
   . . . .*Heteromysis mureseanui* Băcescu, 1986
   –Endopod of uropod with 1 medial spine-seta, near statocyst 5
5. Posterior half of lateral margins of telson armed with spine-setae; margins of telsonal cleft with spinules in apical half only . . . . .
   . . . . . *Heteromysis nouveli* Brattegard, 1969
   –Lateral margins of telson armed with spine-setae along entire length; margins of telsonal cleft with spinules along entire length . . . .
   . . . . *Heteromysis spottei,* n.sp.

Heteromysis spottei appears most similar to *H. nouveli,* but differs in several aspects, especially in the setation of the telson and third thoracic endopod (see Key, Table 1). Except for *H.* (*Heteromysis*) *waitei* W. Tattersall, 1927, a South Australian species, the distinctive telson setation of *H. spottei* differs from all other described species of the subgenus *Heteromysis.* Several characters distinguish *H. spottei* from *H. waitei* including the presence of a single, instead of 3–4, spine-setae adjacent to the statocyst on the uropodal endopod and the absence of ocular teeth (see W. Tattersall 1927).

Acknowledgments

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Gynodiastylis laciniacristatus, a new species (Crustacea: Cumacea) from Australia

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Abstract.—A new species, *Gynodiastylis laciniacristatus* (Crustacea: Cumacea) is described from two disparate localities on the Australian shelf, the Bass Strait (Southeast) and the Dampier Archipelago (West), from depths of 48–85 m. The ovigerous female is completely figured. No males were collected. The new species is distinguished from all other species of *Gynodiastylis* by a large blunt process on the ischium of pereopod 4 and by the pattern of toothed ridges on the carapace. *G. mutabilis* Hale, 1946 and *G. ornata* Hale, 1946 have similar ridge patterns, however *G. laciniacristatus* has a distinct sharp corner on the anterolateral prominence of the carapace and rudimentary exopods on pereopods 3 and 4, in addition to the large blunt process on the ischium of pereopod 4.

The genus *Gynodiastylis* is known primarily from the Southern hemisphere. Hale (1946) described the great majority of the species in the genus, from the environs of Australia. A new and unusual species of *Gynodiastylis* was identified from the extensive cumacean collections of the Museum of Victoria and is described here, as part of an NSF PEET (Partnerships for Enhancing Expertise in Taxonomy) project.

Methods

Samples were collected with the WHOI epibenthic sled or a Smith-McIntyre grab. Drawings were prepared using a *camera lucida* on a Wild compound microscope. Body length was measured from the tip of the pseudorostral lobes to the posterior border of the last somite. One ovigerous female was prepared for SEM (scanning electron microscope) photography.

Family Gynodiastylidae Stebbing 1912
Gynodiastylis Calman 1911
Gynodiastylis laciniacristatus, new species
Figs. 1–5

Type material.—Holotype (NMV J45433) 1 ovigerous female, Bass Strait, Australia, 39°49.0′S, 143°24.0′E, 56 m, 20 Nov 1981. Paratype (NMV J45434) 1 ovigerous ♀, Bass Strait, Australia, 39°49.0′S, 143°24.0′E, 56 m, 20 Nov 1981. Paratypes (NMV J45435) 1 ovigerous ♀, 1 subadult ♀, Bass Strait, Australia, 39°49.0′S, 143°24.0′E, 56 m, 20 Nov 1981. Paratype (NMV J45436) 1 ovigerous ♀, Bass Strait, Australia, 38°38.2′S, 142°35.0′E, 59 m, 20 Nov 1981. Paratype (NMV J45437) 1 ovigerous ♀, Bass Strait, Australia, 39°06.3′S, 142°55.6′E, 81 m, 21 Nov 1981. Paratype (NMV J45438) 1 ovigerous ♀, Bass Strait, Australia, 40°00.0′S, 144°20.9′E, 48 m, 22 Nov 1981. Paratype (NMV J45439) 1 ovigerous ♀, Bass Strait, Australia, 39°00.2′S, 144°33.9′E, 74 m, 23 Nov 1981. Paratype (NMV J45440) 1 subadult ♀, Bass Strait, Australia, 39°13.6′S, 143°55.6′E, 85 m, 23 Nov 1981. Paratype (NMV J45441) 1 subadult ♀, Western Australia, (damaged), 20°1.00′S, 117°11.00′E, 48 m, 11 Jun 1983. Paratype (NMV J45442) 1 subadult ♀, Western Australia, 19°38.00′S, 118°6.00′E, 49 m, 13 Jun 1983.

Diagnosis.—Carapace with depression sweeping dorsally from anterior edge, anterolateral prominence produced as sharp corner, with dorsal ridge bounding prominence toothed, dorsal depression bounded by sharp lateral ridges, continuing through dorsum of pereon 5, anterior ventral margin toothed, antennal notch oblique. Pereopod 4 with large blunt process on ischium. Adult females less than 4 mm.

Description.—Ovigerous female, 3.5 mm. Carapace with dorsal depression, eyelobe present, no lenses; pseudorostral lobes 0.5 carapace length; antenna 1 visible, extending just past pseudorostral lobes. Pereonites 1–3 expanded ventrally as anteriorly directed flap, pereonites 4 and 5 directed posteriorly dorsally (Figs. 1A, 1B, 2A).

Antennule article 1 longer than articles 2 and 3 together, bearing 1 plumose and 2 simple setae proximally and 1 simple seta distally; distomedial margin with fine hair-like setae; article 2 bearing 1 simple and 1 plumose setae distally, medial margin bearing fine hair-like setae; articles 2 & 3 subequal in length, article 3 bearing 2 simple setae; main flagellum of 2 articles bearing 1 long annulate seta, 2 long simple setae, and 2 short simple setae terminally; accessory flagellum of 1 article with 2 terminal setae (Fig. 3A).

Mandible navicular, with 10 lifting setae; left side with stout lacinia mobilis, incisor quadridentate, right side with slender lacinia mobilis, incisor bidentate (Fig. 3B).

Maxillule of 2 lobes, outer broad lobe bearing double row of stout setae terminally, medial margin bearing fine hair-like setae; inner lobe bearing 2 tridentate, 1 long, 2 short setae terminally, medial margin bearing fine hair-like setae (Fig. 3C).

Maxilla of 3 lobes; broad lobe 4 times as wide as narrow lobe, medial margin bearing 9 simple setae, medial-distal corner bearing 2 plumose setae, distal margin bearing many simple setae; distal-lateral corner bearing 1 forked and 1 microserrate setae; inner narrow lobe bearing 2 microserrate and 2 simple setae apically; outer narrow lobe bearing 5 simple setae apically (Fig. 3D).

Maxilliped 1 basis as long as all other articles together, produced as large distomedial lobe, lobe bearing several short simple setae distally, lobe bearing several plumose setae, setulose on distal 0.3 only; ischium not present, merus half as long as carpus, medial margin bearing fine hair-like setae; carpus bearing 3 blade-like, 3–4 bidentate, several simple setae medially, 1 long plumose seta distolaterally; propodus as long as carpus, half as broad, bearing 2 tridentate and 2 long plumose setae distally, margins with many fine hair-like setae; dactyl half as long and half as wide as propodus, bearing 4 small simple setae terminally (Fig. 5C).

Maxilliped 2 basis as long as next 2 articles together, bearing 3 long plumose setae distally; ischium not present; merus 0.5 basis length, bearing 2 plumose setae distally; carpus slightly longer than propodus, bearing 3 plumose setae medially; propodus bearing 2 long plumose setae distally and 3 plumose setae medially; dactyl half length of propodus, bearing 4 simple setae terminally; endite bearing 5 stout annulate setae and 2 simple setae (Fig. 2B).

Maxilliped 3 basis 2 times as long as next 4 articles together, medial margin bearing 8 plumose setae, lined with short hair-like setae, single plumose seta distally, distomedial corner produced as 2 teeth, lateral margin lined with fine hair-like setae, distolateral corner bearing 4 long plumose setae; ischium 0.5 basis width, slightly longer than merus, 1 plumose setae medially, otherwise margins lined with fine hair-like setae; merus 0.5 length carpus, produced as tooth at distolateral corner and bearing 1 plumose seta, medial margin lined with fine hair-like setae and bearing 1 plumose and 1 simple setae distally; carpus bearing 1 plumose seta on distolateral corner, medial margin lined with fine hair-like setae and bearing 1 plumose and 1 simple setae; propodus subequal to dactyl, bearing 1 simple seta on distolateral corner, medial margin bearing 2 simple setae; dactyl bearing 4 simple setae terminally (Fig. 3E).

Pereopod 1 basis as long as all other ar-

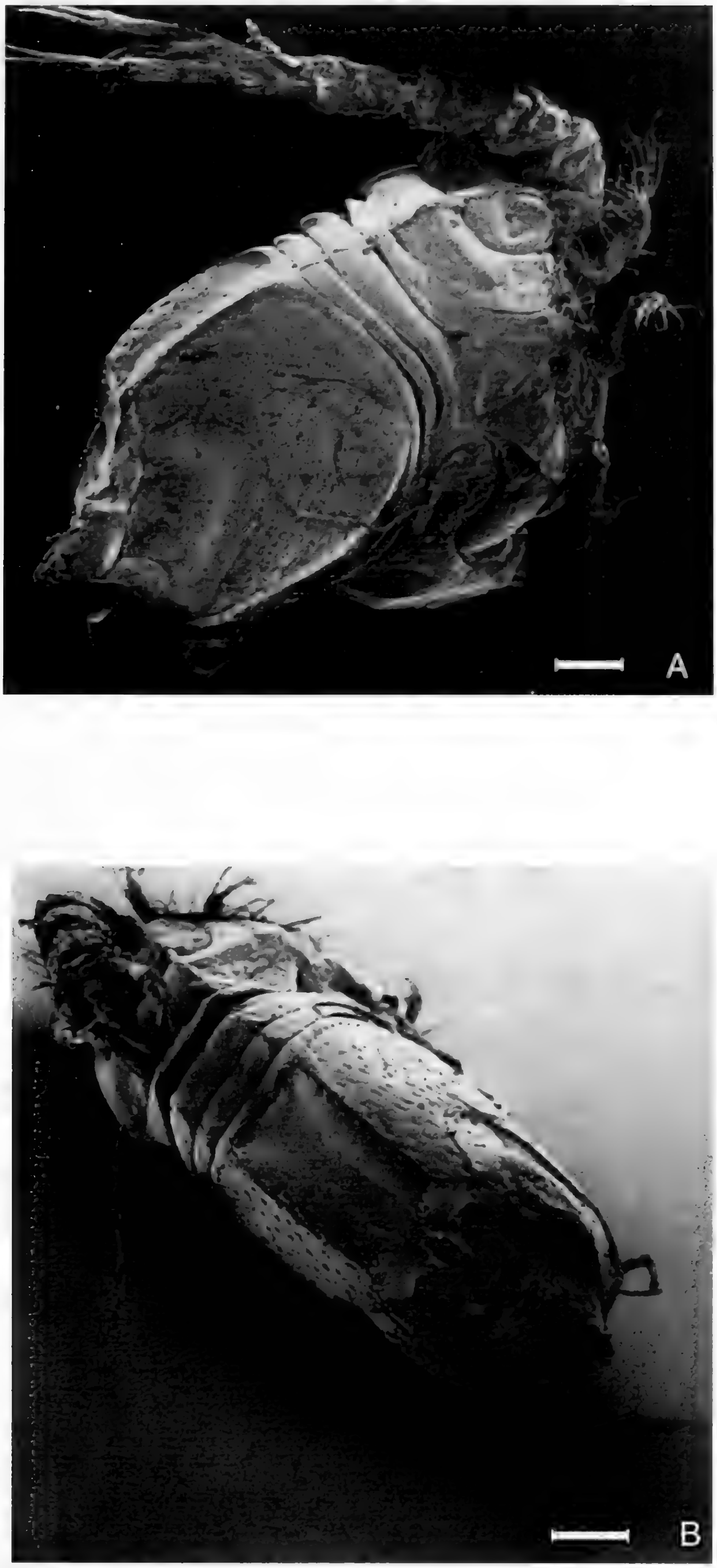

Fig. 1. *Gynodiastylis laciniacristatus,* new species. Ovigerous ♀ (not the same individual as Figs. 2–5); A, habitus; B, dorsal view. Scale bars are 200 microns in length.

ticles together, posterior margin bearing many simple and 2 plumose setae, posterodistal corner produced as 3 teeth, anterior margin bearing 1 simple seta, lined with fine hair-like setae, anterodistal corner bearing 2 plumose setae; ischium 0.5 length of merus, posterodistal corner produced as tooth; merus produced as 3 small teeth on

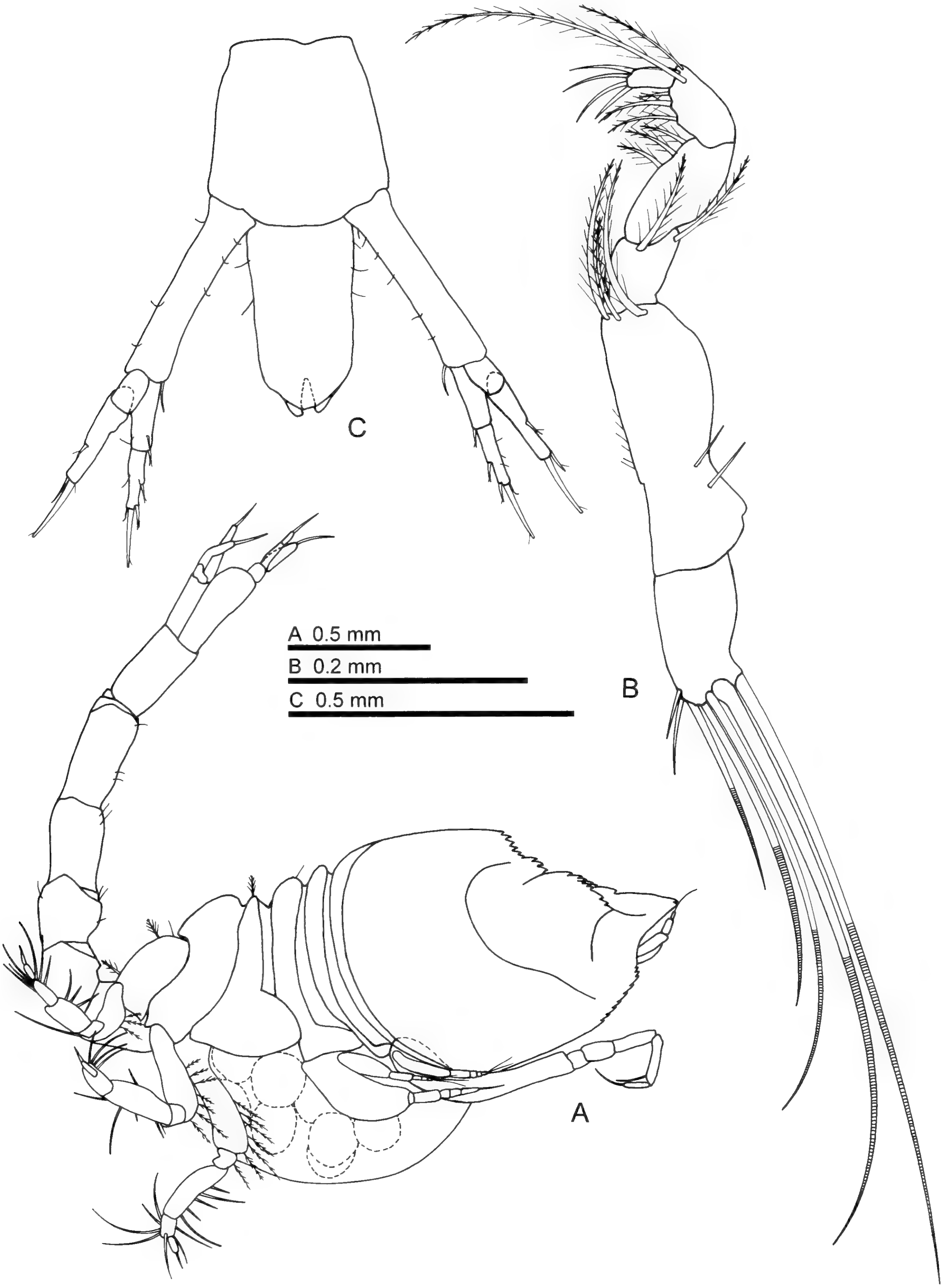

Fig. 2. *Gynodiastylis laciniacristatus,* new species. Ovigerous ♀ paratype NMV 45434; A, habitus; B, maxilliped 2; C, telson and uropods.

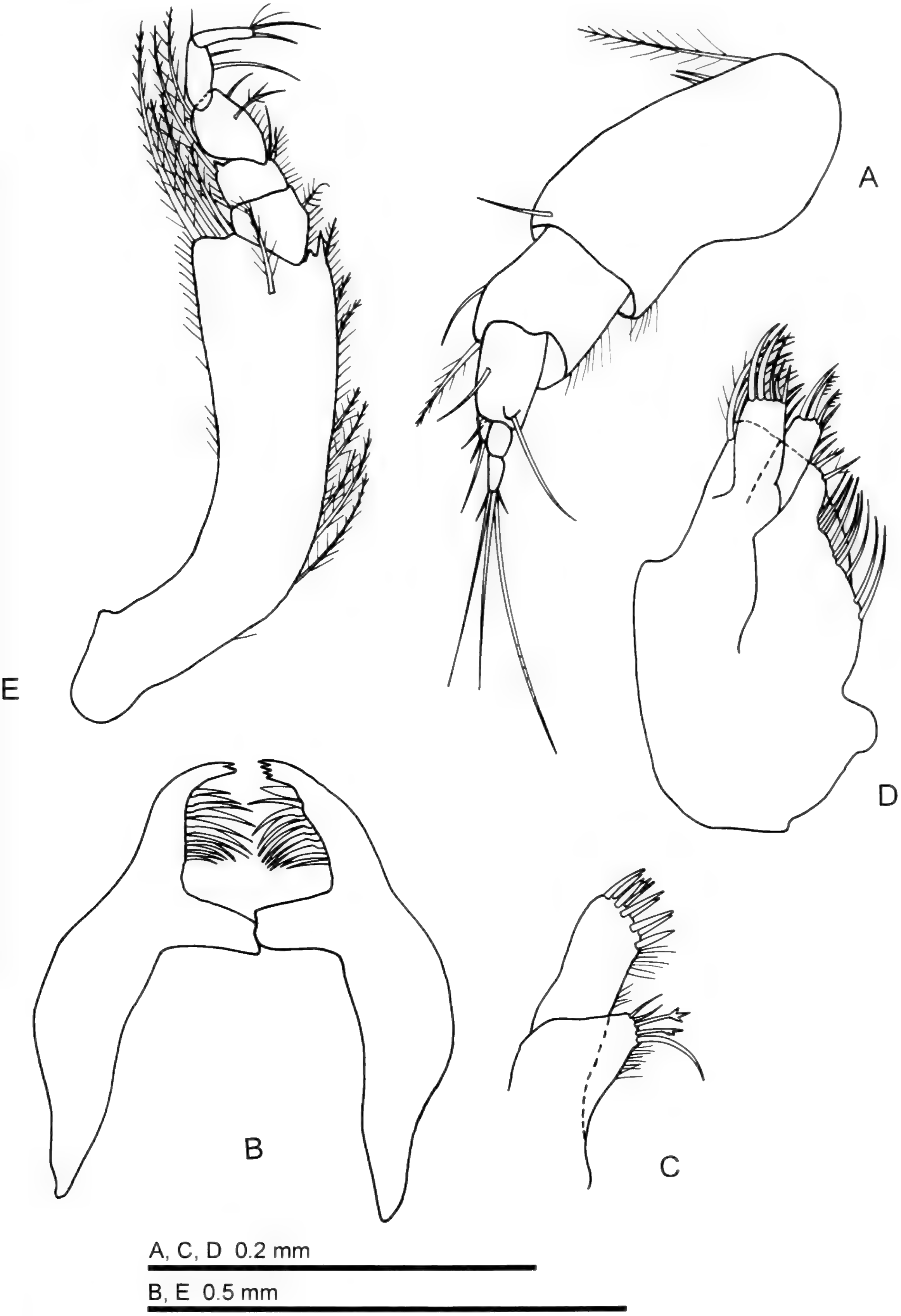

Fig. 3. *Gynodiastylis laciniacristatus*, new species. Ovigerous ♀ paratype NMV 45434; A, antennule; B, mandible; C, maxillule; D, maxilla; E, maxilliped 3.

posterior margin; carpus subequal to propodus; propodus twice dactyl length, bearing 1 long and 1 short simple setae distally, single small simple seta proximally; dactyl bearing 1 long and 1 short simple setae terminally; exopod 0.5 length basis, basal article bearing 2 simple setae, produced as small tooth distally; flagellum bearing 6 long stout plumose setae (Fig. 4A).

Pereopod 2 basis longer than all other articles together, 3 times ischium width, margins lined with many simple setae, anterior margin produced as multiple teeth; ischium reduced, unarmed; merus twice carpus length, anterior margin produced as multiple teeth, bearing 2 simple setae; carpus anterior margin produced as 2 teeth, bearing 2 simple setae; propodus subequal to carpus, unarmed; dactyl slightly longer than propodus, bearing 3 simple setae terminally; exopod subequal to basis, basal article unarmed, flagellum bearing 4 long stout plumose setae (Fig. 4B).

Pereopod 3 basis as long as next 2 articles together, anterior margin produced as multiple teeth, bearing 5 plumose, 1 annulate and 2 annulate plumose setae, posterior margin bearing 2 simple setae; ischium 0.2 length merus, bearing 1 simple seta; merus twice carpus length, bearing 2 annulate and 4 simple setae; carpus twice propodus length, bearing 6 annulate and 2 simple setae distally; propodus twice dactyl length, bearing single annulate seta distally; dactyl bearing 2 simple setae terminally; exopod biarticulate, rudimentary, bearing 1 simple seta apically (Fig. 4C).

Pereopod 4 coxa bearing several stout simple setae; basis as long as next 2 articles together, anterior margin bearing 2 plumose, 1 annulate plumose, 7 annulate, and 3 simple setae, produced as multiple teeth distally, 1 plumose seta mid article; ischium 0.3 length merus, unarmed, produced as large posteriorly directed blunt lobe; merus 3 times carpus length, bearing 7 annulate setae, produced as multiple scales, posterior margin produced as 3 teeth; carpus slightly longer than propodus, bearing 7 annulate setae, produced as 2 teeth proximally; propodus slightly longer than dactyl, bearing 2 annulate setae; dactyl bearing single stout seta with single setule; exopod biarticulate, rudimentary, bearing 1 simple seta apically (Fig. 5A).

Pereopod 5 basis as long as next 2 articles together, bearing 6 plumose, 1 annulate plumose and 1 annulate setae, produced as small blunt processes on posterior margin; ischium 0.5 length merus, bearing 1 simple seta; merus slightly longer than carpus, bearing 5 simple and 1 annulate setae, posterior margin produced as scales; carpus bearing 7 annulate setae; propodus subequal to carpus, bearing 1 annulate seta; dactyl 0.5 length propodus, bearing 1 stout and 1 slender setae terminally (Fig. 5B).

Telson equal in length to pleonite 6, postanal section negligible, unarmed (Fig. 2C).

Uropod peduncles equal in length to telson, bearing single seta at distomedial corner; rami shorter than peduncles; endopod biarticulate, article 1 bearing 1 short stout seta at distomedial corner, article 2 bearing 2 short stout setae medially, single long seta terminally; exopod biarticulate, article 1 half length article 2, unarmed, article 2 bearing 2 short setae laterally, single long stout seta terminally; all setae on rami bearing single thick setule apically (Fig. 2C).

Etymology.—*laciniacristatus* from the Latin *lacinia,* meaning jagged and *crista,* meaning ridge.

Remarks.—*Gynodiastylis laciniacristatus* is distinguished from all other *Gynodiastylis* by the large blunt process on the ischium of pereopod 4. *Gynodiastylis laciniacristatus* is superficially similar to both *G. ornata* Hale, 1946 and *G. mutabilis* Hale, 1946. However, there are obvious differences in addition to the process on pereopod 4. Neither *G. ornata* nor *G. mutabilis* have exopods on pereopods 3 and 4 of the female, while they are present in *G. laciniacristatus.* The uropod endopod in *G. mutabilis* is uniarticulate, while in *G. laciniacristatus* the uropod endopod is biarticulate. The lateral margins of the telson in

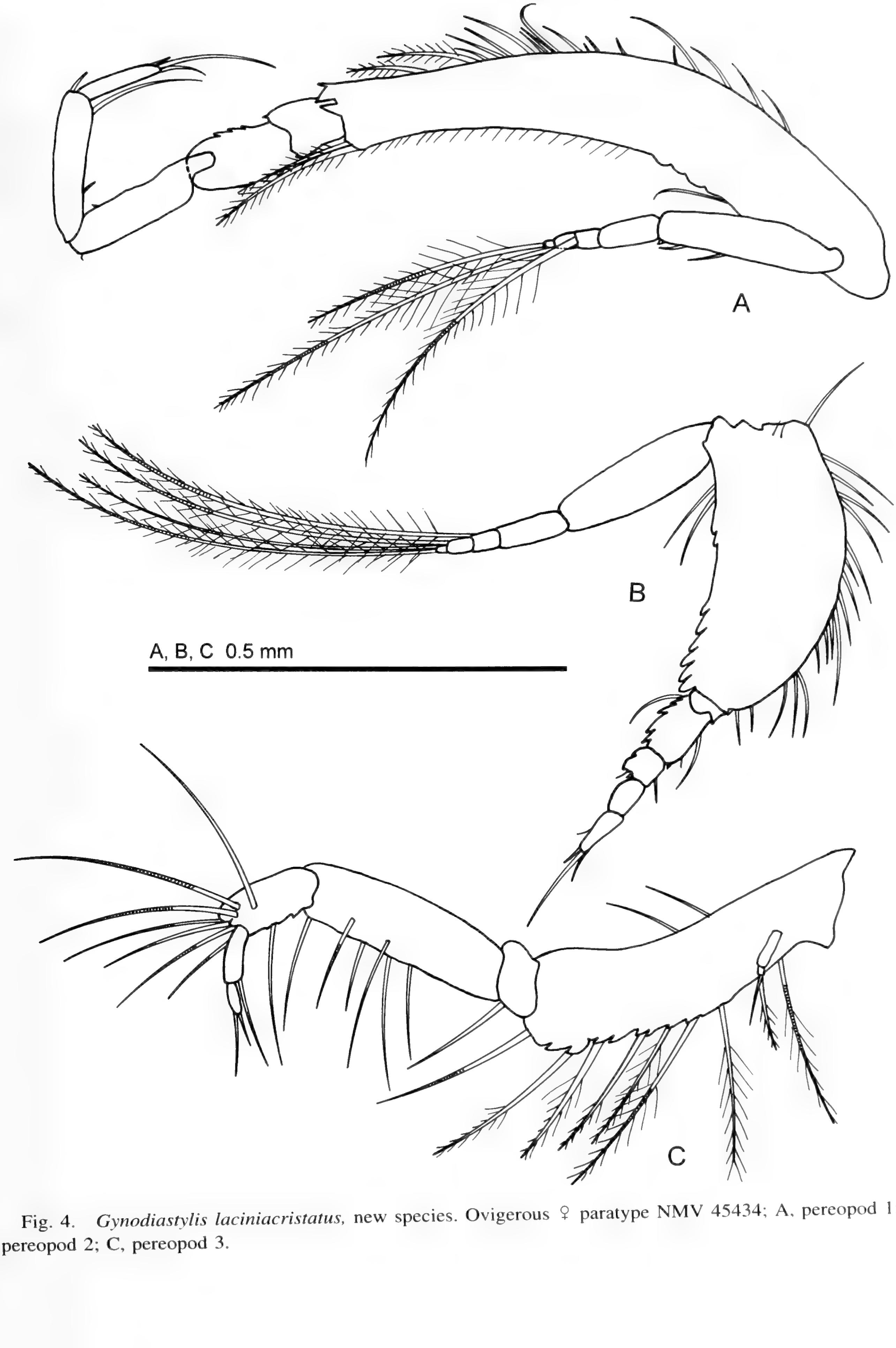

Fig. 4. *Gynodiastylis laciniacristatus,* new species. Ovigerous ♀ paratype NMV 45434; A, pereopod 1; B, pereopod 2; C, pereopod 3.

Fig. 5. *Gynodiastylis laciniacristatus,* new species. Ovigerous ♀ paratype NMV 45434; A, pereopod 4; B, pereopod 5; C, maxilliped 1.

G. mutabilis are produced as at least one pair of teeth, while in *G. laciniacristatus* the telson lateral margins are entire. The carapace of *G. laciniacristatus* has a distinct anterolateral prominence produced as a sharp corner, while *G. ornata* has no such prominence.

Acknowledgments

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Revision of the subterranean amphipod genus *Spelaeogammarus* (Bogidiellidae) from Brazil, including descriptions of three new species and considerations of their phylogeny and biogeography

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Abstract.—Three new subterranean amphipods of the genus *Spelaeogammarus* da Silva Brum, 1975, are described from eastern Brazil, bringing the total number of species in the genus to four. Based on the examination of type-material of *Spelaeogammarus bahiensis,* a comparative diagnosis of all four species of *Spelaeogammarus,* including the new species *Spelaeogammarus spinilacertus, Spelaeogammarus trajanoae,* and *Spelaeogammarus santanensis,* is given. A diagnosis for the genus is also provided. The occurrence of these species in caves that are separated from each other in discontinuous karst areas is biogeographically significant for the family Bogidiellidae in continental South America.

Exploration of caves in eastern Brazil in the early 1970s resulted in the discovery of the new bogidiellid genus and species *Spelaeogammarus bahiensis* (da Silva Brum, 1975). The specimens were collected from a cave near Curaçá, capital of the district Matamuté, in the state of Bahia. Subsequently, between 1989 and 1993, many additional specimens from various caves in Bahia were collected by Brazilian speleologists and sent to us for identification. Because these specimens differed morphologically from the description of *Spelaeogammarus bahiensis,* we borrowed paratypes of this species from the Museu Nacional in Rio de Janeiro, for a comparison with the new material. The paratypes enabled us to identify and describe three new species and also to diagnose the genus *Spelaeogammarus.* In addition, a key to the four species of the genus is provided as well as a table detailing morphological differences.

The holotypes of the new species are deposited in the Museu Nacional in Rio de Janeiro (MNRJ), Brazil, as indicated.

Genus *Spelaeogammarus* da Silva Brum, 1975

Spelaeogammarus da Silva Brum, 1975: 125–128.

Type species (by monotypy): *Spelaeogammarus bahiensis* da Silva Brum, 1975.

Diagnosis.—Eyes absent. Body smooth, unpigmented. Coxal plates 1–2 small, wider than long; plates 3–6 longer than wide, overlapping. Antenna 1 about 45–50% of body length, primary flagellum longer than peduncle, with 16–20 segments. Accessory flagellum with 4–5 segments. Antenna 2 flagellum bearing 7–10 segments. Mandibular palp 3-segmented. Maxilla 1 with symmetrical, 2-segmented palp; inner plate with 3 plumose setae; outer plate bearing 6–7 serrate spines. Inner plate of maxilliped bearing apically 2 bifid (y-shaped) spines; outer plate with 3 or 4 blade-like spines apically and subapically. Propodus of gnathopod 1 larger than that of gnathopod 2. Dactyls of both gnathopods distinctly serrate along inner margins. Pereopods without any trace of lenticular organs; pereopods 5–7

Table 1.—Major morphological differences of the four species of the genus *Spelaeogammarus*.

Character	*S. spinilacertus*	*S. trajanoae*	*S. santanensis*	*S. bahiensis*
Accessory flagellum	4 segments	4 segments	5 segments	4 segments
Antenna 2 flagellum	7 segments	7 segments	8–10 segments	7 segments
Maxilla 1: outer lobe	6 serrate spines + 1 plumose seta	6 serrate spines + 1 plumose seta	7 serrate spines	7 serrate spines
Maxilliped: apical margin of inner lobe	4 plumose setae	4 plumose setae	2 plumose setae	no plumose setae
Gnathopod 1	propod a littler larger than basis	propod a littler larger than basis	propod much larger than basis	propod a littler larger than basis
Gnathopod 1: post. margin of basis	6–8 setae (some double)	9–10 setae (all single)	~20 setae (all single)	7–9 setae (all single)
Gnathopod 1: ant. margin of basis	2–4 spines + 1 short seta	5–9 short setae	4 short setae	3–5 short setae
Gnathopod 2: post. margin of basis	9–10 setae	8–9 setae	21–23 setae	~9 setae
Coxal plate 5	1 spine + 9 setae	1 spine + 17–18 setae	1 spine + 12 setae	1 spine + 20–21 setae
Coxal plate 6	1 spine, no setae	1 spine, no setae	1 spine + 1 seta	1 spine + 20–21 setae
Pleopods: inner ramus	4–5 setae	5–7 setae	7–8 setae	~7 setae
Uropod 3: outer ramus	~20 bifurcate setae	~20 bifurcate setae	~8 bifurcate setae	missing
Telson: spines per lobe	2 apical + 3–4 subapical	3 apical + 2–3 subapical	1 apical + 3 subapical	2 apical + 3–4 subapical

bases broad, propodus and/or carpus with long, bifurcate setae. Pleopods and uropods unmodified. Pleopods biramous, with 3-segmented outer ramus and 1-segmented inner ramus, rami subequal in length. Uropods biramous: peduncle of uropod 1 with 3 or 4 large basiofacial (ventrolateral) spines; uropod 3 with subequal, 1-segmented rami, outer ramus bearing a row of long, bifurcate setae along medial margin. Telson typically longer than wide, apex with shallow excavation, bearing apical and subapical spines. Coxal gills present on pereopods 4–6. Oostegites linear and elongate, on pereopods 2–5. No sexual dimorphism in any characters.

Key to the species of *Spelaeogammarus* (based on males and females)

1\. Accessory flagellum of antenna 1 with 4 segments; flagellum of antenna 2 with 7 segments; propodus of gnathopod 1 slightly larger than basis 2

Accessory flagellum of antenna 1 with 5 segments; flagellum of antenna 2 with 8–10 segments; propodus of gnathopod 1 much larger than basis . . . . *S. santanensis*

2\. Coxal plate 6 bearing 1 spine, setae absent; outer plate of maxilla 1 with 6 serrate spines and 1 plumose seta; inner plate of maxilliped with 4 plumose setae 3

Coxal plate 6 bearing 1 spine and about 20 setae; outer plate of maxilla 1 with 7 serrate spines; inner plate of maxilliped without plumose setae . . . . *S. bahiensis*

3\. Anterior margin of basis of gnathopod 1 with 5–9 short setae; coxal plate 5 bearing 1 spine and 17–18 setae . . . . *S. trajanoae*

Anterior margin of basis of gnathopod 1 with 2–4 spines (or longer setae) and 1 short seta; coxal plate 5 bearing 1 spine and about 9 setae . . . . *S. spinilacertus*

Spelaeogammarus spinilacertus, new species

Figs. 1–5, 6c

Material examined.—Estado do Bahia, Brazil: holotype male (6.1 mm) and 1 paratype male (7.5 mm) from Baixa do Salitre Cave, Iraquara, collected by J. A. Cardoso, Sep 1993; 4 paratypes (3 females, 1 male) from Baixa do Salitre Cave, collected by L. Mendes & E. Rubbioli, 24 May, 1997; allotype female (8.1 mm) and 2 paratypes (1 male, 1 female), from Jaburu Cave, Iraquara, collected by J. A. Cardoso, Sep 1993.

The holotype and allotype are dissected and mounted on microscope slides in Faure's medium. Holotype (MNRJ 13340) and allotype are deposited in the Museu Nacional. The remaining 7 paratypes are retained in the research collection of the second author.

Diagnosis.—*Spelaeogammarus spinilacertus* is easily distinguished from other species in the genus by 2–4 spines or setae of corresponding length on the distoanterior margin of basis of gnathopod 1. Largest male 10.5 mm, largest female 10 mm.

Description.—Antenna 1 (Fig. 2a) about 45–50% of body length. Peduncular segments 1–3 gradually decreasing in length; peduncular segment 1 with 3–4 spines; peduncular segment 2 with 2–3 short spines; peduncular segment 3 bearing 0–2 spines. Primary flagellum longer than peduncle, with 17–20 segments; aesthetascs on most segments; accessory flagellum with 4 segments, terminal segment vestigial.

Antenna 2 (Fig. 2b) about 85% length of antenna 1. Peduncular segment 4 longer than peduncular segment 5; peduncular segment 5 with 3–4 ventral and 2–4 medial spines. Flagellum with 7 segments, 1st segment twice as long as average length of segments 2–6.

Upper lip (Fig. 2c) as long as broad, trapezoidal, with few apical setules.

Mandible (Fig. 2h, i): Palp 3-segmented, with 3–4 terminal setae; 2nd segment bearing 2 apical and 2–3 subapical setae. Molar rounded and well developed, with 1 long lateral seta. Both incisor and lacinia mobilis on left mandible with 5 irregular, rounded cusps (Fig. 2h); 3 long and 3 short plumose spines between lacinia and molar. Right mandible (Fig. 2i): lacinia apically serrated, consisting of irregularly pointed denticles; 2 long and 2 short plumose spines between lacinia and molar.

Lower lip (Fig. 2d) bearing setules on outer lobes, outer and mandibular lobes with rounded corners.

Maxilla 1 (Fig. 2e): Palp 2-segmented, with 5–6 apical setae and few lateral setules. Outer plate with 6 serrate spines and 1 plumose spine; inner plate with 3 plumose setae.

Maxilla 2 (Fig. 2f): Outer plate apically with 1–2 comb-like setae, ±15 medium-sized plumose setae and 2 large plumose spines (slightly subapical); medial margin with few fine setules; apical margin of inner plate bearing ±18 long comb-like setae and ±5 short naked setae (seta/spine types in Fig. 2g).

Maxilliped (Fig. 2j, 6c): Segment 1 of palp with 1–2 medial setae; segment 2 bearing 12–13 medial setae; dactyl long and slender, bearing a row of marginal setules. Inner plates apparently fused along medial margins.

Gnathopod 1 (Fig. 3a): Posterior margin of basis with 6–8 long setae (some doubly inserted); anterior margin bearing 2–4 spines plus 1 short seta. Carpus with 8 setae on posterior lobe (4–6 comb-like and 2–3 naked). Propodus ovate, almost twice as long as broad, larger than gnathopod 2 propodus; palm uneven, serrate with minute setules at corner (Fig. 3b); palmar margin bearing 7–8 normal spines and 15–19 short bifid spines on lateral margin; medial margin with 6 short setae, 1 normal angular spine, and 4–6 oblique subangular spines (1–2 relatively long). Dactyl about 70% length of propodus; inner margin with distinct row of denticles (Fig. 3c).

Gnathopod 2 (Fig. 3d): Posterior margin of basis bearing 9–10 long setae. Carpus posteriorly with fine setules and 7 sets of setae (1–5 setae per set). Propodus ovate, almost twice as long as broad; palm oblique, with 5–6 corner spines (Fig. 3e), 11–14 short lateral bifid spines, and 7–8 short medial setae; palmar margin finely serrate at whole margin, with minute setules at corner. Dactyl about 50% length of propodus; inner margin with distinct row of denticles.

Pereopods 3 and 4 subequal (Fig. 4a). Basis without spines, anterodistal margin even (pereopod 4 basis with 0–1 spine plus 1 seta at anterodistal margin). Posterior margin of carpus bearing 4–5 spines. Propodus with 8–9 spines along posterior margin and 2 apical spines. Dactyl about 24% length of propodus (Fig. 4b).

Pereopod 5 (Fig. 4c): Basis with 10–11 spines at posterior margin (distal and proximal group of spines separated by a gap); anterior margin bearing 13–15 spines; anterior lateral surface with 6 short setae; 10–11 short setae at posterior margin and posterior lateral surface. Ischium with 1 spine and 3 setae. Anterior margin of carpus with a row of long, bifurcate setae (Fig. 4f) and 6–12 spines (some doubly inserted). Propodus anteriorly with a row of long, bifurcate setae, occurring progressively shorter distally, with slightly thicker bases; lateral margin with 17–19 spines (some doubly inserted); proximal part with 3–4 spines. Dactyl 14–20% length of propodus.

Pereopod 6 subequal to pereopod 5 but slightly longer.

Pereopod 7 (Fig. 4d): Basis ovate, bearing 8 spines on anterior margin and 7–9 spines on posterior margin. Ischium with 2 spines. Merus with 3 spines on posterior margin and 5 spines at anterior margin (1 singly and 2 doubly inserted). Carpus with 13 spines, occurring in 6–7 sets (with 1–3 spines per set) on anterior margin, 4 spines (2 doubly inserted) plus 4 setae on posterior margin, and 10–11 terminal spines. Propodus bearing 12 slender spines on anterior margin and rows of long, bifurcate setae along posterior and anterior margins (Fig. 4f). Dactyl about 27% length of propodus.

Pereopods 1–7 without any trace of lenticular organs; pereopods 5–7 with broad bases.

Coxal gills ovate, present on pereopods 4–6.

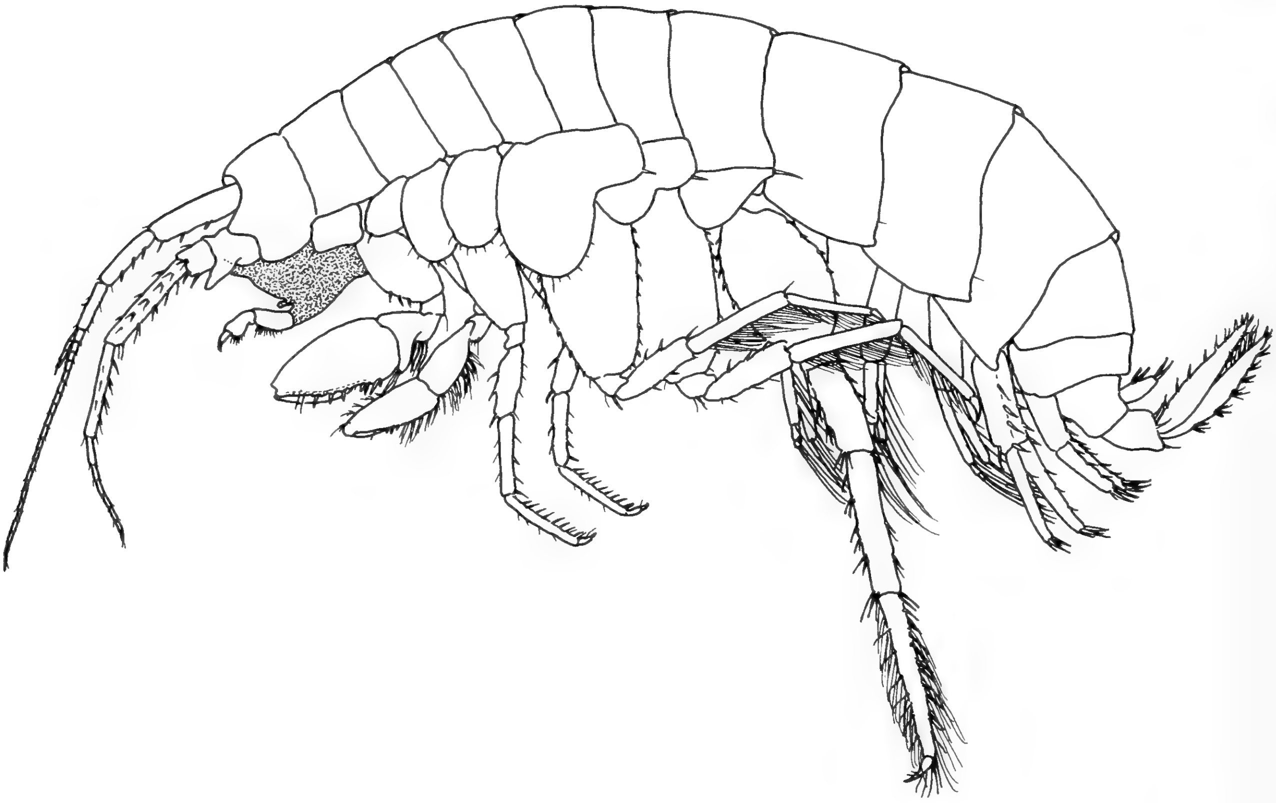


Fig. 1. *Spelaeogammarus spinilacertus* n. sp., allotype female (8.1 mm) from Jaburu Cave, Estado do Bahia, Brazil.

Coxal plates 1 and 2 (Fig. 3f, g) about equal in size, subrectangular to ovate in shape, wider than long; plates 3–6 longer than wide, overlapping; plates 3 and 4 about the same size, plate 5 largest; plate 5 and 6 with distinct anterodistal lobes (Fig. 4c, g); plate 7 (Fig. 4e) subtriangular to irregular in shape, with single long spine at tapered posterior corner.

Oostegites linear and elongate, on pereopods 2–5.

Pleopods 1–3 morphologically alike (Fig. 5a), decreasing slightly in size posteriorly, with subequal outer and inner rami. Outer rami 3-segmented, with 2 terminal plumose setae per segment; segment 1 bearing 6–10 lateral plumose setae and 5–8 medial plumose setae. Inner rami 1-segmented, with 4–5 medial plumose setae.

Epimeral (pleonal) plates subquadrate, with small, subacute posterior margins, bearing 1 setule each (Fig. 4h).

Uropod 1 (Fig. 5b): Rami subequal in length, slightly shorter than peduncle. Peduncle with 3 spines on dorsolateral, dorsomedial, ventrolateral (basofacial), and apical margin, respectively. Outer ramus bearing 3–4 dorsolateral and 4 apical spines. Inner ramus with 5 apical and 4–5 dorsolateral spines, the latter occurring as 3–4 singly and 1–2 doubly inserted.

Uropod 2 (Fig. 5c): Peduncle bearing 1 dorsomedial spine, 2 dorsolateral spines, and 2 apical spines. Outer ramus slightly shorter than inner ramus, as long as peduncle, bearing 2–3 spines dorsolaterally and 4 spines apically. Inner ramus with 5 dorsolateral and 4–5 apical spines.

Uropod 3 (Fig. 5d) with subequal, lanceolate rami, both 1-segmented. Peduncle about 46% length of rami, with 2 apical spines, 1 subapical spine, and 1 small dorsoproximal spine. Outer ramus bearing 3 apical spines, 6 sets of spines (with 2–3 spines per set) along lateral margin, and about 20 bifurcate long setae along medial margin (Fig. 5e). Inner ramus with 3 apical spines; lateral margin with 5 spines; medial margin bearing 9 spines (some doubly inserted).

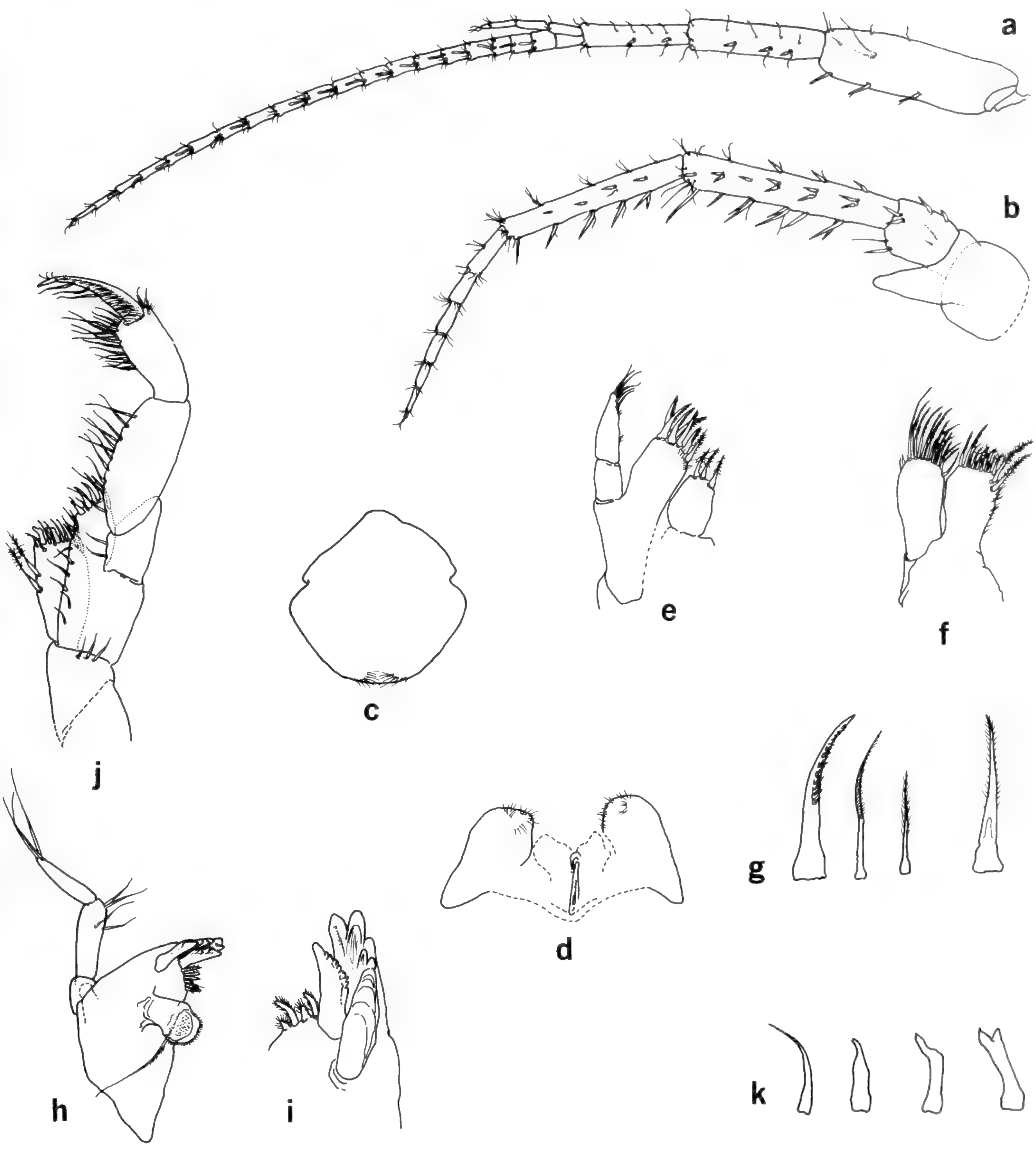


Fig. 2. *Spelaeogammarus spinilacertus* n. sp., allotype female: a) antenna 1, b) antenna 2, c) upper lip, d) lower lip, e) maxilla 1, f) maxilla 2, g) spine and seta types (on maxilla 1 and 2, maxilliped, and gnathopod 1 and 2), from left: serrate spine, comb-like seta, plumose seta, and plumose spine, h) left mandible, i) right incisor and lacinia mobilis, j) maxilliped, k) spine types of maxilliped outer plate (far left 2) and inner plate (far right 2).

Telson (Fig. 5f) width about 84% of length, with shallow excavation (10% of length); each side bearing 3 setae, 2 apical and 2 (sometimes 3) subapical spines.

Etymology.—The epithet *spinilacertus* is a noun in apposition, alluding to the presence of spines on the anterior margin of the basis of gnathopod 1. It is formed by combining *spini,* from Latin meaning thorn or spine, with *lacertus,* from Latin meaning upper arm (~basis).

Remarks.—Two of the three specimens

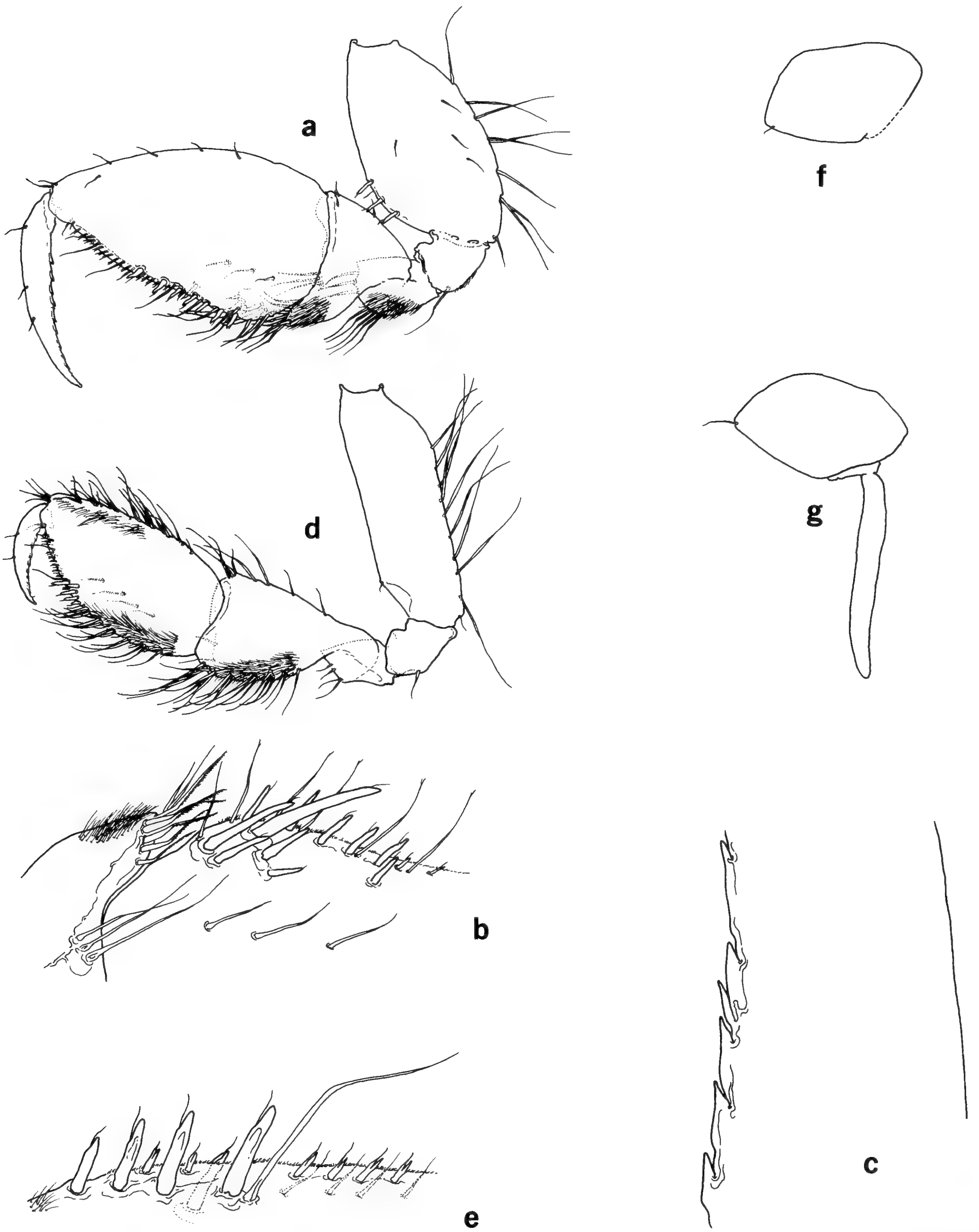


Fig. 3. *Spelaeogammarus spinilacertus* n. sp., holotype male: a) left gnathopod 1, b) detail of right gnathopod 1, c) detail of right gnathopod 1 dactyl, d) left gnathopod 2, e) detail of left gnathopod 2; allotype female: f) coxal plate of gnathopod 1, g) coxal plate of gnathopod 2.

from Jaburu cave showed variation in some characters, one of which is diagnostic for the species: instead of 2–4 spines, the basis of the female gnathopod 1 had 2–3 setae along the anterodistal margin (compare Fig. 3a with Fig. 7a and c). These setae had the same length as the spines they replaced and could be clearly distinguished from corre-

Fig. 4. *Spelaeogammarus spinilacertus* n. sp., allotype female: a) left pereopod 4, b) right pereopod 4 dactyl, c) left pereopod 5, d) right pereopod 7, e) coxal plate of right pereopod 7, f) bifurcate seta (on carpus and propodus of pereopod 5–7), g) coxal plate of left pereopod 6, h) epimeral plates.

sponding setae in *S. santanensis* and *S. trajanoae* (described below). Furthermore, both specimens (10 mm male and 7 mm female) had 3 subapical spines on each lobe of the telson. The male from the Jaburu sample also showed morphological variability in its appendages, e.g., the bases of both gnathopods and pereopods 3–6 were relatively narrow and elongate; similarly, the propods of both gnathopods appeared relatively longer and larger, with a conspicuously sinusoid palmar margin.

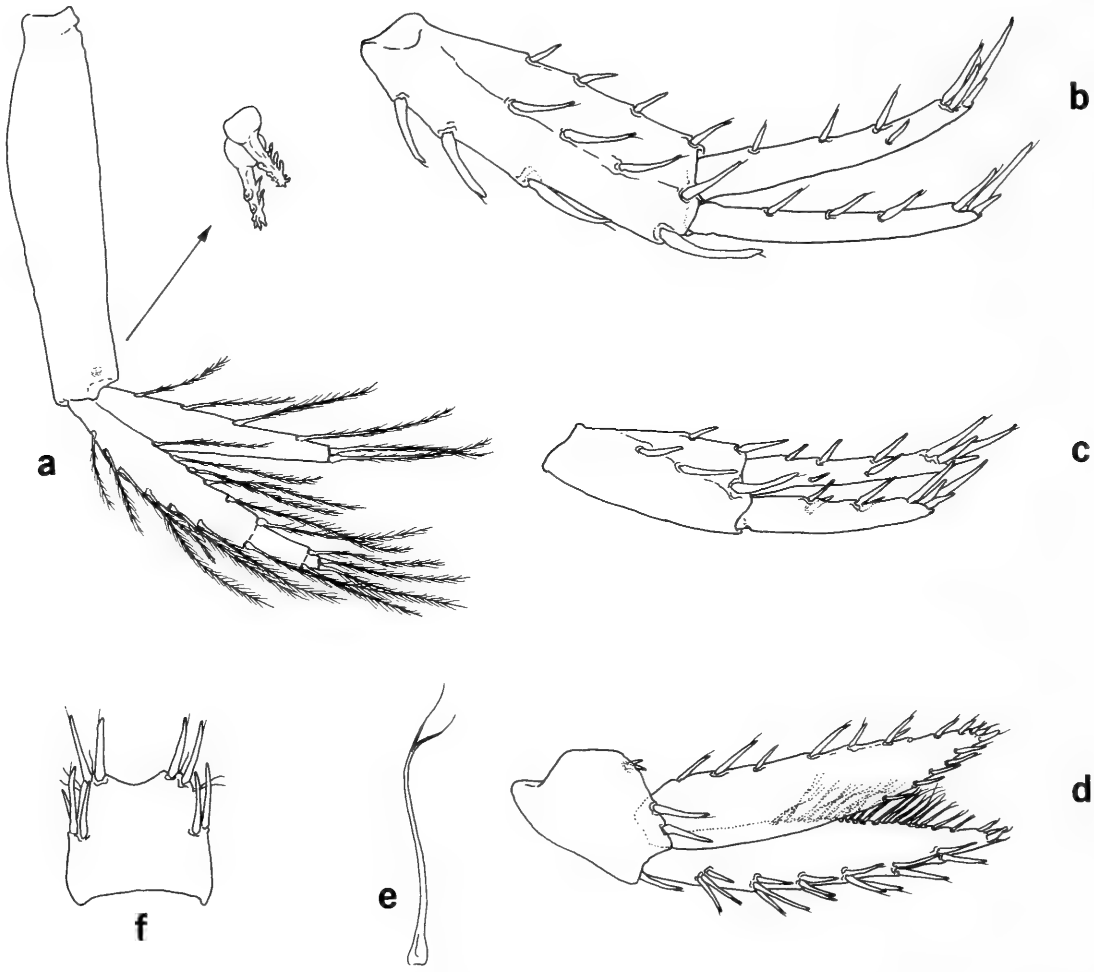


Fig. 5. *Spelaeogammarus spinilacertus* n. sp., holotype male: a) left pleopod 3, b) left uropod 1, c) left uropod 2, d) left uropod 3, e) bifurcate seta of outer ramus of uropod 3, f) telson.

Spelaeogammarus trajanoae, new species

Figs. 6b, i, 7c, d, 8a, b

Material examined.—Campo Formoso, Estado do Bahia, Brazil: holotype female (10.4 mm) and 5 paratypes (2 males, 3 females) from Toca do Pitu Cave (=Gruta do Pitu?), collected by A. Auler & M. Martins, Sep 1989; 1 male and 1 female paratype from Toca do Pitu Cave, collected by E. Rubbioli, Jan 1992; 3 paratypes (1 female, 2 juveniles) from Buraco do Teodoro Cave, collected by J. A. Cardoso (no date given); 1 female paratype from Toca do Gonçalo Cave, collected by P. Gernhard, 4 Jul, 1997; 1 fragmented specimen from Convento Cave, collected by S. Larizotti, 1986 (?).

The holotype is dissected and mounted on microscope slides in Faure's medium. Holotype (MNRJ 13341) and 2 paratypes from the type locality are deposited in the Museu Nacional. The allotype and the remaining paratypes are retained in the collection of the second author.

Diagnosis.—*Spelaeogammarus trajanoae* is morphologically closely allied with *S. spinilacertus* but can be distinguished from that species by 5–9 short setae instead of spines or spine-length setae on the distoanterior margin of the basis of gnathopod 1 and coxal plate 5 with approximately 18 setae plus 1 spine on margins instead of 9 setae plus 1 spine. Largest males 10.0 mm, largest female 10.5 mm. *S. trajanoae* is moreover distinguished from *S. spinilacertus* as indicated in the following description.

Description.—Antenna 1: Peduncular segment 1 with 5–7 spines; peduncular segment 2 with 3–4 short spines; peduncular segment 3 bearing 2 spines.

Lower lip (Fig. 6i) bearing setules on medial margin of outer lobes.

Maxilliped: Segment 2 with ±17 setae along medial margin. Inner and outer plate shown in Fig. 6b.

Gnathopod 1 (Fig. 7c): Posterior margin of basis bearing 9–10 singly inserted, long setae; anterior margin with 5–9 short setae. No setules on posterior margin of ischium. Carpus bearing 6–9 setae on pointed posterior lobe (4–6 comb-like and 2–3 naked). Palm of propodus even; lateral margin with 5–7 normal spines and 16–17 short bifid spines; medial margin with 6–8 short and 6 long setae.

Gnathopod 2: Posterior margin of basis with 8–9 long setae. Carpus posteriorly with 5–6 rows of setae (1–5 setae per row). Propodus with 6–8 rows of setae (1–3 setae per row) at proximoposterior margin; palmar margin with 3–4 lateral corner spines, 16–17 short lateral bifid spines, and 8–9 short medial setae.

Pereopods 3 and 4 (Fig. 8a): Basis bearing 1 spine at posterodistal margin; anterodistal margin sinusoid, with 1 spine and 1 seta (pereopod 3) or 2 spines and 1 seta (pereopod 4). Carpus bearing 6–7 spines posteriorly. Propodus with 13–15 spines along posterior margin.

Pereopod 5: Coxal plate with 17–18 marginal setae on anterior lobe. Anterior margin of basis bearing 10–12 spines; 15 short setae on both posterior and anterior lateral surfaces. Dactyl about 22% length of propodus.

Pereopod 6: Ischium with 2 spines and 1–2 setae. Dactyl about 26% of propodus length.

Pereopod 7: Basis with 11 spines on anterior margin and 10 spines on posterior margin. Merus with 3 sets of doubly inserted spines at posterior margin and 3 sets of spines at anterior margin (with 3–4 spines per set).

Pleopods: Outer ramus with 8–10 lateral plumose setae and 8–9 medial plumose setae on first segment. Inner ramus bearing 5–7 medial plumose setae.

Epimeral plates (Fig. 7d) with produced, bluntly rounded distoposterior corners.

Uropod 1: Peduncle with 3–4 spines on dorsolateral margin, 4–5 spines on dorsomedial margin. Inner ramus with 4–5 marginal spines, occurring as 4 dorsomedial and 0–1 dorsolateral spines.

Uropod 2: Peduncle with 1–2 dorsomedial spines, 2–3 dorsolateral spines.

Uropod 3: Outer ramus bearing 3–5 apical spines, 4–6 rows of spines (with 1–3 spines per row) along lateral margin. Inner ramus bearing 10–11 rows of spines (with 5 singly and 5 doubly inserted) at medial margin.

Telson (Fig. 8b) width about 81% of length, with u-shaped apical excavation (19% of length); each side with 3 apical setae, 2 apical spines, and 3–4 subapical spines.

Etymology.—The species is named in honor of Professor Dr. Eleonora Trajano of the University of São Paulo, who has made important contributions to Brazilian biospeleology.

Remarks.—Out of a total of 12 specimens examined, 2 individuals were found with 2 and 3 subapical spines on each telsonic lobe, respectively. The majority (10 specimens) had 4 subapical spines on one lobe and 3 subapical spines on the other lobe.

Spelaeogammarus santanensis, new species

Figs. 6a, e–g, 7a, b, 8c–e

Material examined.—Padre Cave, Santana, Estado do Bahia, Brazil: holotype male (13.6 mm), 3 male and 3 female paratypes (11.5–13.6 mm), and 1 juvenile paratype (10.6 mm), collected by F. Chaimowicz, July 1987.

The holotype is dissected and mounted on microscope slides in Faure's medium. Holotype (MNRJ 13342) and 2 paratypes are deposited in the Museu Nacional. The remaining paratypes are retained in the collection of the second author.

Diagnosis.—A comparatively large cavernicolous species, easily distinguished

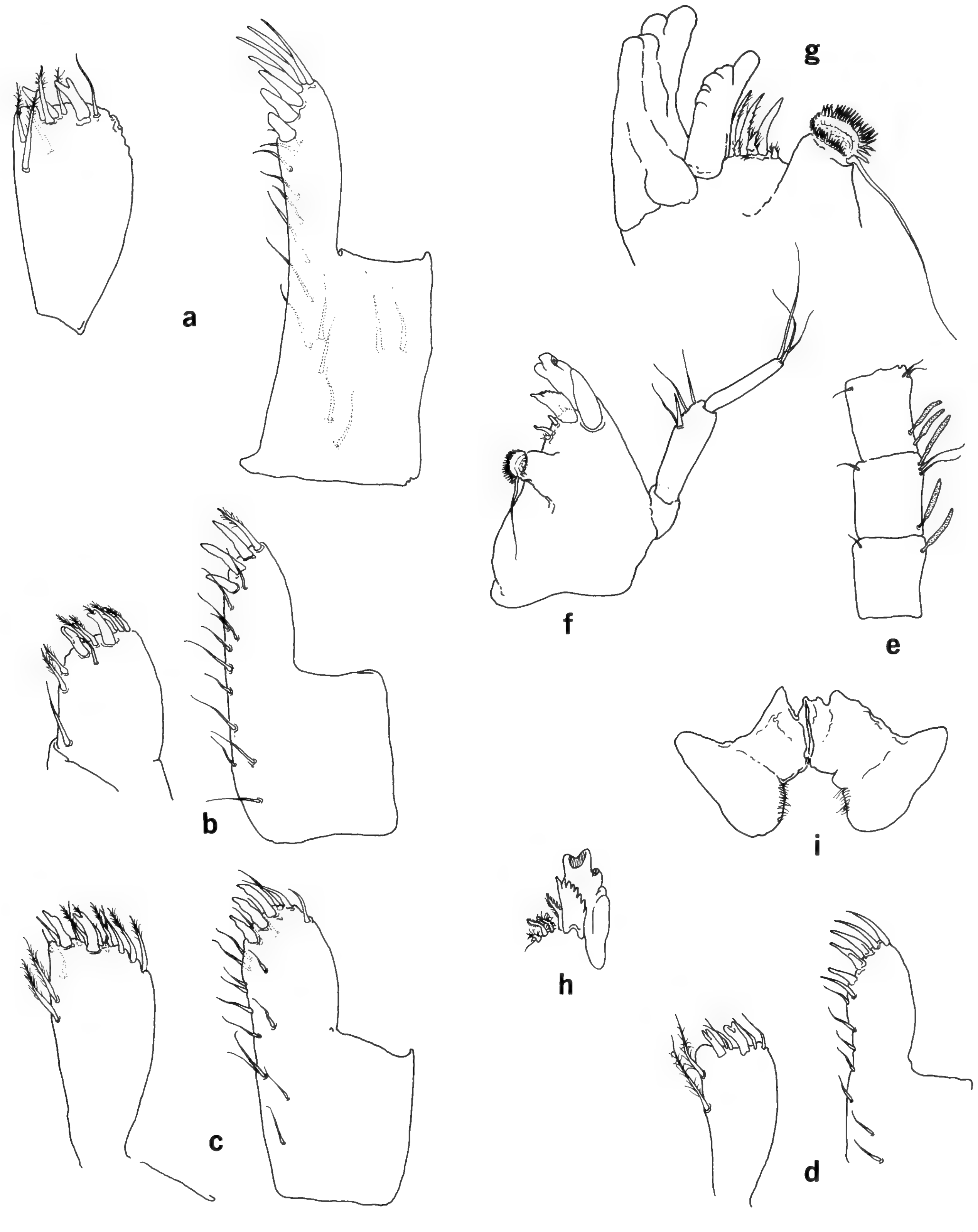


Fig. 6. *Spelaeogammarus santanensis* n. sp., holotype male: a) inner and outer plate of maxilliped, e) detail of antenna 1, f) left mandible, g) detail of right mandible; *S. trajanoae* n. sp., paratype female (10.36 mm): b) inner and outer plate of maxilliped, i) lower lip; *S. spinilacertus* n. sp., holotype male: c) inner and outer plate of maxilliped; *S. bahiensis* paratype (8 mm juvenile): d) inner and outer plate of maxilliped, h) left incisor and lacinia mobilis.

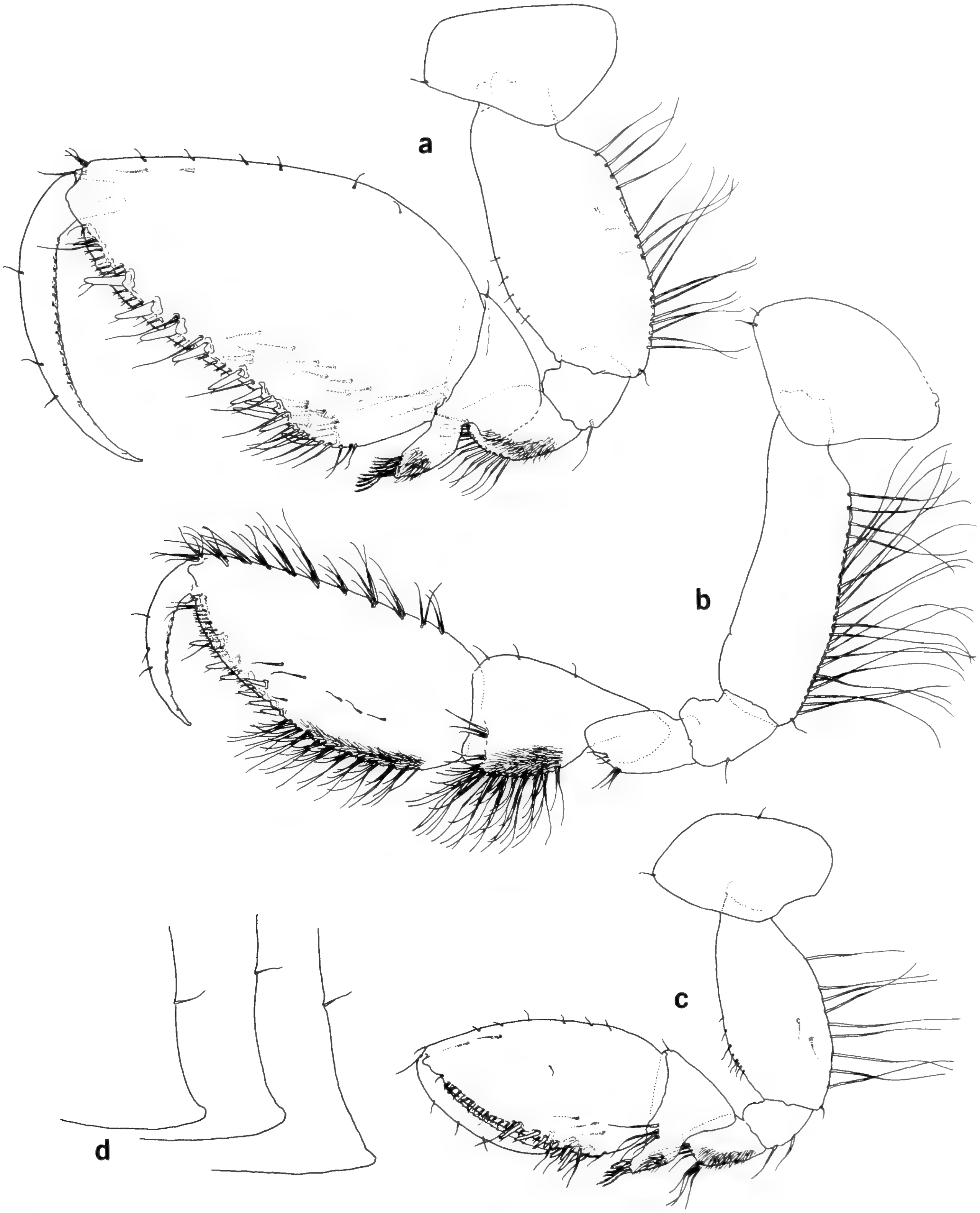


Fig. 7. *Spelaeogammarus santanensis* n. sp., holotype male: a) left gnathopod 1, b) right gnathopod 2; *S. trajanoae* n. sp., paratype female (10.36 mm): c) left gnathopod 1, d) epimeral plates.

from other species in the genus by having: 5-segmented accessory flagellum; 20–23 setae on posterior margins of the bases of gnathopods 1 and 2; propodus of gnathopod 1 proportionally larger. Largest male 13.6 mm, largest female 10.5 mm. *S. santanensis* is furthermore distinguished from *S. spinilacertus* according to the following description.

Description.—Antenna 1 about 40–45% length of body. Primary flagellum bearing 20–21 segments, some of which with mul-

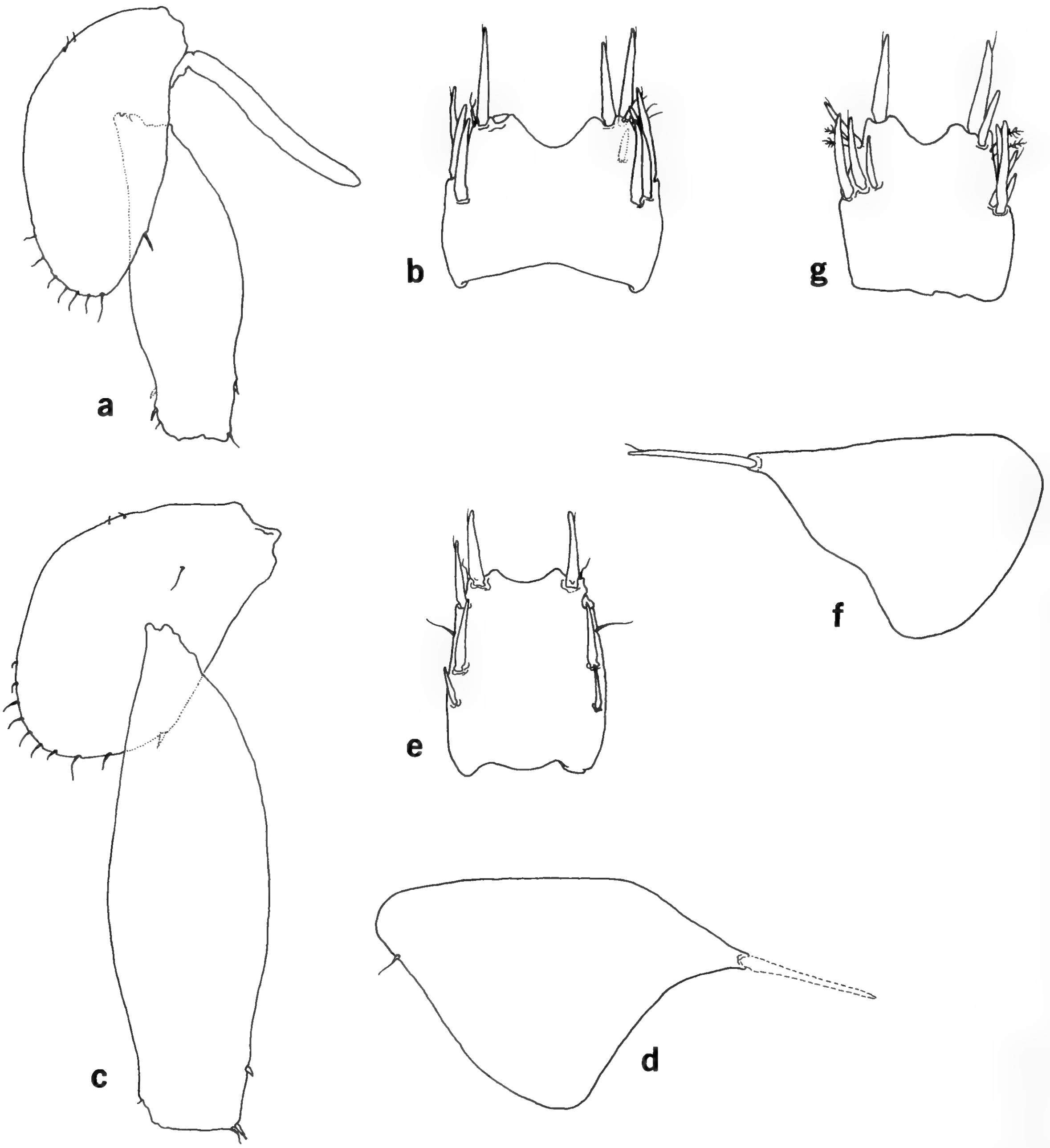


Fig. 8. *Spelaeogammarus trajanoae* n. sp., paratype female (10.36 mm): a) left pereopod 3, b) holotype female: telson; *S. santanensis* n. sp., holotype male: c) right pereopod 3, d) coxal plate of pereopod 7, e) telson; *S. bahiensis,* paratype (8 mm juvenile): f) coxal plate of pereopod 7, g) telson.

tiple inserted aesthetascs (Fig. 6e). Peduncular segment 1 with 5–6 spines; peduncular segment 3 with 2 ventromedial spines. Accessory flagellum 5-segmented.

Antenna 2 slightly shorter than antenna 1. Peduncular segment 5 with 5 ventral spines. Flagellum as long as peduncular segment 5, with 8–10 segments.

Mandible (Fig. 6f, g): Palp with 3 terminal setae. Palp segment 2 of left mandible with 3 setae and 1 spine; 3 short and 1(–2?) long plumose spines between lacinia and molar. Palp segment 2 of right mandible with 4 setae and 2 spines.

Lower lip with few thin setules on medial margin of outer and inner lobes; corner of outer lobes with slightly pointed corners.

Maxilla 1: Palp with 8–9 apical and subapical setae and a few lateral setules. Outer plate with 7 serrate spines apically.

Maxilla 2: Outer plate apically with 0–1 comb-like setae, ±21 plumose setae, and 1–2 plumose spines (slightly subapical). Inner plate bearing ±22 long comb-like setae and several short naked setae (two of which on medial margin).

Maxilliped: Palp segment 1 with 2 medial and 2 proximomedial setae; segment 2 with ±25 medial setae; segment 3 bearing ±17 medial and 3 dorsomedial setae. Dactyl with 8 setae on outer margin. Inner and outer plate shown in Fig. 6a.

Gnathopod 1 (Fig. 7a): Posterior margin of basis bearing 20 long, singly inserted setae; anterior margin with 4 setae. Carpus with distinctly pointed posterior lobe, which bears 13–14 plumose setae. Propodus bearing 7–8 setae on medial surface; palmar margin sinusoid, with 10 short medial setae, 4 long lateral setae, 8–9 normal lateral spines, 19–20 short bifid lateral spines, 1 normal angular spine medially, 2–3 oblique subangular spines (1–2 relatively long), ±13 subangular lateral setae, and 6–7 subangular medial setae. Inner margin of dactyl with row of blunt denticles.

Gnathopod 2 (Fig. 7b): Posterior margin of basis bearing 21–23 long setae. Carpus posteriorly with 8–9 rows of setae and 5 short setae distolaterally. Propodus twice as long as broad; palm with 6 lateral spines and 1 medial spine, 18 short lateral bifid spines, 1 long lateral seta, and 12 short medial setae; palmar margin with blunt serration of whole margin, distinct serration and minute cilia at corner. Dactyl about 53% length of propodus, inner margin with row of blunt denticles.

Pereopod 3: Basis (Fig. 8c) with 2 spines at posteriodistal margin. Carpus bearing 5–6 spines posteriorly and 2–3 spines plus 1–2 setae anteriorly. Propodus with 11–12 spines along posterior margin (some doubly inserted) and 2 spines plus 4 setae apically. Dactyl about 25% length of propodus.

Pereopod 4 subequal to pereopod 3, except for the following differences: coxal plate with 1 spine and 8 setae along distal margin, 2 setae at proximal margin, and 3 setae on lateral surface. Basis with 2–4 spines at posterodistal margin.

Pereopod 5: Coxal plate with 12 setae on anterior lobe and 2 setae on lateral surface. Basis bearing 12 spines on anterior margin; anterior and posterior lateral surface with 4 short setae respectively. Ischium with 4 setae. Anterior margin of carpus with 5–6 sets of spines (2–3 singly and 2–3 doubly inserted). Lateral margin of propodus with 13 spines (5–6 doubly inserted). Dactyl about 18% length of propodus, bearing 1 plumose seta posteriorly.

Pereopod 6 subequal to pereopod 5 except for the following characters: coxal plate with 1 spine and 1 seta on anterior lobe. Basis without setae on posterolateral surface; anterolateral surface with 2–6 setae; posterior margin bearing 14 spines (pereopod 5: 11 spines). Merus posteriorly with 3 spines and anteriorly with 3–4 spines plus 3–4 setae (see *S. spinilacertus* for pereopod 5). Anterior margin of carpus with 8 spines (3 doubly inserted). Dactyl about 20% length of propodus, bearing 1 plumose seta and 1 spine posteriorly.

Pereopod 7: Coxal plate (Fig. 8d) irregular in shape. Basis with 10–11 spines on anterior margin. Ischium bearing 1 spine and 1–2 setae. Merus with 6 spines (3 doubly inserted) on anterior margin. Carpus with 3 sets of spines (with 3–4 spines per set) on anterior margin and 4 sets of spines (with 1–3 spines per set) on posterior margin. Anterior margin of propodus additionally with 10 sets of 1–3 slender spines. Dactyl about 21% length of propodus, with 1 plumose seta at posterior margin.

Pleopods: Outer rami bearing 12–13 lateral plumose setae and 7–8 medial plumose setae. Inner rami with 7–8 medial plumose setae.

Epimeral plates subquadrate, with small, subacute posterior margins, bearing 1 setule each.

Uropod 1: Peduncle with 4 spines on dorsolateral, 4 on dorsomedial, 3 on ventrolateral, and 3 on apical margin, respectively. Inner ramus with 7 dorsolateral spines (3–4 dorsomedial and 1–2 dorsolateral spines).

Uropod 2: Outer ramus bearing 4 dorsolateral spines (doubly inserted).

Uropod 3: Outer ramus bearing 2 spines

and 1 seta apically, 5 sets of spines (with 1–3 spines per set) along lateral margin; medial margin with ±8 bifurcate setae proximally and ±6 slender setae distally. Medial margin of inner ramus with 8 sets of singly and doubly inserted spines.

Telson (Fig. 8e) width about 76% of length; apex with shallow excavation (5% of length); each lobe bearing 1 spine plus 1 seta apically and 3 spines plus 1 seta subapically.

Etymology.—The proposed epithet *Santanensis* is a toponym, referring to the capital city Santana, which is situated near the type-locality.

Remarks.—In marked contrast to the 3 other species of the genus, the preserved specimens of *S. santanensis* appeared whitish and almost transparent. Specimens of *S. spinilacertus* and *S. trajanoae* were yellowish-grey, whereas *S. bahiensis* showed a dark, brownish tone. Since these variations appeared to be interspecific (i.e., consistent for species from different localities) it is possible that they were caused by structural differences of the exoskeletons.

Spelaeogammarus bahiensis da Silva Brum, 1975

Figs. 6d, h, 7f, g

Material examined.—Patamute Cave (type locality), Curaça, Distrito de Matamuté, Estado do Bahia, Brazil: 1 male paratype, 11.1 mm, and 1 juvenile paratype, 8 mm (Museu Nacional catalogue no. MN 5725), collected by P. Magalháes, 1972–1973 (?).

Diagnosis.—*Spelaeogammarus bahiensis* is morphologically more similar to *S. spinilacertus* and *S. trajanoae* than to *S. santanensis* but differs from the former two species in having 7 serrate spines on the outer plate of maxilla 1, 20–21 setae on coxal plate 5, and the presence of dorsal setules on pereonite 7 (1 setule), pleonites 1–3 (2–10 setules), and uronites 1–2 (1–7 setules). In addition, it is distinguished from *S. spinilacertus* by short setae instead of spines on the anterior margin of the basis of gnathopod 1. Male specimen 11.1 mm in length. Corresponding to the original description by da Silva Brum (1975) with the additions and modifications given below.

Redescription.—Antenna 1: Peduncular segment 1–3 gradually decreasing in length; peduncular segment 1 with 6 ventral spines. Aesthetascs on most segments of primary flagellum (as long as segments); accessory flagellum with 4 segments, terminal segment vestigial.

Antenna 2: Peduncular segment 3 with 3–4 spines. Flagellum with 7 segments.

Mandible: Left lacinia mobilis distinctly toothed. Long and short plumose spines between lacinia and molar more dissimilar than in other species (Fig. 6h).

Maxilla 1: Palp without lateral setules. Outer lobe with 7 apical spines (3 different types) and distinct row of setules at medial margin, subapically.

Maxilliped: Dactyl bearing 3–4 relatively long setae along inner margin. Inner plate bearing apically 2 bifid (y-shaped) spines; outer plate with 3 blade-like spines subapically and 2 strong setae apically (Fig. 6d).

Gnathopod 1: Posterior margin of basis with 7–9 long setae (all singly inserted); anterior margin bearing 3–5 short setae. Carpus with rectangular posterior lobe, bearing 3–5 long, sickle-shaped, naked setae, 3–6 comb-like setae, and 3–4 long, naked setae. Palmar margin of propodus bearing 5–9 normal spines and 13–18 short bifid spines on the lateral margin; medial margin with 8–10 short setae, 1 normal angular spine, and 3–5 corner spines (1–2 relatively long). Dactyl with 9–10 denticles, each with 1 short seta.

Gnathopod 2 basically like that of *S. spinilacertus.* Palp with 2 normal spines and 4 spines at corner. Dactyl with 6–7 denticles.

Pereopods 3 and 4 subequal. Pereopod 3 basis with 1 distoanterior spine, and 1 distoposterior seta. Pereopod 4 basis with 1–2 distoanterior spines and 1 seta plus 1 spine at distoposterior margin; dactyl with 1 spine similar to *S. santanensis.*

Pereopods 5–7 missing in specimens examined.

Pleopods basically like those of *S. spinilacertus.* Segment 1 bearing 7–8 lateral plumose setae and 5–6 medial plumose setae. Inner ramus with 7 plumose setae on medial margin.

Coxal plates 3–4 with 9–10 setae and 1 spine; plates 5–6 identical, bearing 20–21 setae and 1 spine, respectively; plate 7 (Fig. 8f) irregular, slightly lobed.

Uropod 1: Peduncle with 4 spines on dorsolateral, dorsomedial, and ventrolateral margins, respectively, and 2 on apical margin. Outer ramus with up to 5 apical spines. All spines on inner ramus singly inserted.

Uropod 2: Peduncle bearing 1–2 dorsomedial, 1–2 dorsolateral, and 2 apical spines.

Uropod 3 missing in specimens examined.

Telson (Fig. 8g) width about 80% of length; each lobe bearing 2 setae, 2 apical and 3–4 subapical spines.

Discussion

The four species described above are recorded from eight caves in a series of discontinuous karst areas that extend over a linear distance of ca. 1200 km from north to south in eastern Brazil (Fig. 9). The records for each species per karst area are as follows: *S. santanensis*—1 cave, *S. bahiensis*—1 cave, *S. spinilacertus*—2 caves, and *S. trajanoae*—4 caves. Each species is obviously restricted to one or more caves in a separate karst area. These areas are disjunct and apparently physically isolated from each other. The greatest distance between caves with two species is roughly 650 km (*S. bahiensis* and *S. santanensis*), whereas the shortest distance is only about 135 km (*S. bahiensis* and *S. spinilacertus*). Caves situated within a single, continuous karst area that are inhabited by the same species are never more than ca. 100 km apart.

Both the elongate coxal plates and aequiramus pleopods found in the genus *Spelaeogammarus* are characters usually considered plesiomorphic for the family Bogidiellidae (Stock 1981, Barnard & Barnard 1983). Apart from *Spelaeogammarus,* coxal plates that are longer than wide are known only for the genus *Artesia* Holsinger, 1980 (*in* Holsinger & Longley 1980), and this genus, like *Spelaeogammarus,* also has pleopods with aequiramus inner rami. However, they are 5-segmented in *Artesia* and only 1-segmented in *Spelaeogammarus. Artesia* can also be distinguished from *Spelaeogammarus* by 1-segmented accessory flagellum, fewer flagellar segments in both antennae, 1-segmented palp of maxilla 2, 6-segmented pleopodal exopodite, unlobed coxal plates 5 and 6, and the telson, which is deeply cleft and bears 4–6 apical spines on each lobe. Equally long rami are also found in *Aequigidiella* Botosaneanu & Stock, 1989, *Kerguelenicola* Ruffo, 1974, and *Parabogidiella* Holsinger, 1980 (*in* Holsinger & Longley 1980). However, in these three genera the coxal plates are typically wider than long. Moreover, *Aequigidiella* differs from *Spelaeogammarus* by sexually dimorphic inner rami and spines of the second uropods of the male and a telson that is much longer than wide. Although to date only one specimen of the genus *Kerguelenicola* is known, there are several characters that distinguish it from *Spelaeogammarus:* 1-segmented accessory flagellum, distinct shape of and lack of armature on the telson, large mandibular molar, and reduced number of spines and setae on the outer and inner lobes of maxilla 1. *Parabogidiella* differs from *Spelaeogammarus* by 1-segmented accessory flagellum, 5-segmented flagellum of antenna 2, 1-segmented palp of maxilla 2, characteristically elongated pereopod 7, 5 pairs of coxal gills, and armature of the telson.

The most closely related bogidiellid taxon to *Spelaeogammarus* described to date may be *Bogidiella gammariformis* Sket (1985) from a cave in Equador. This species

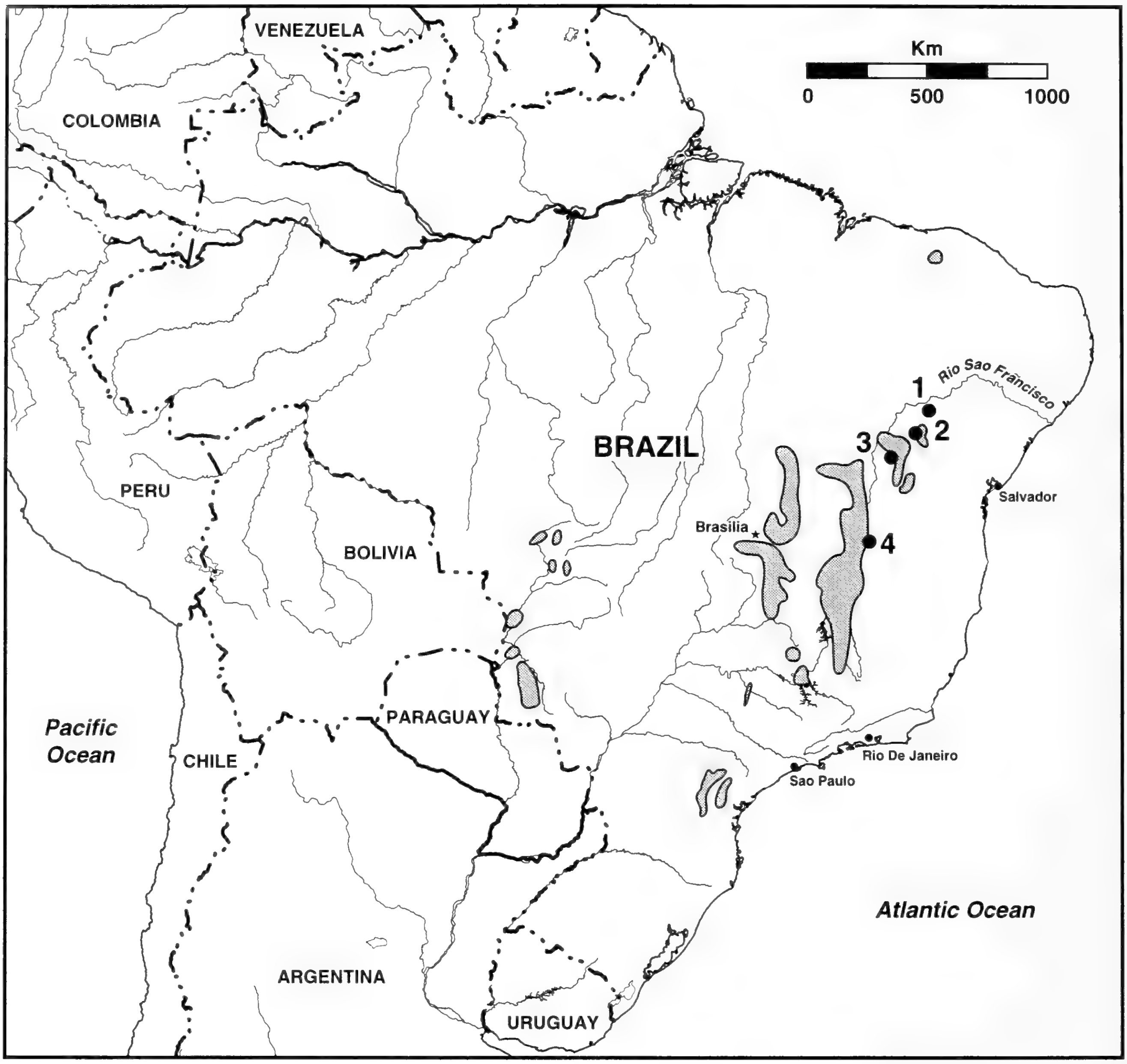


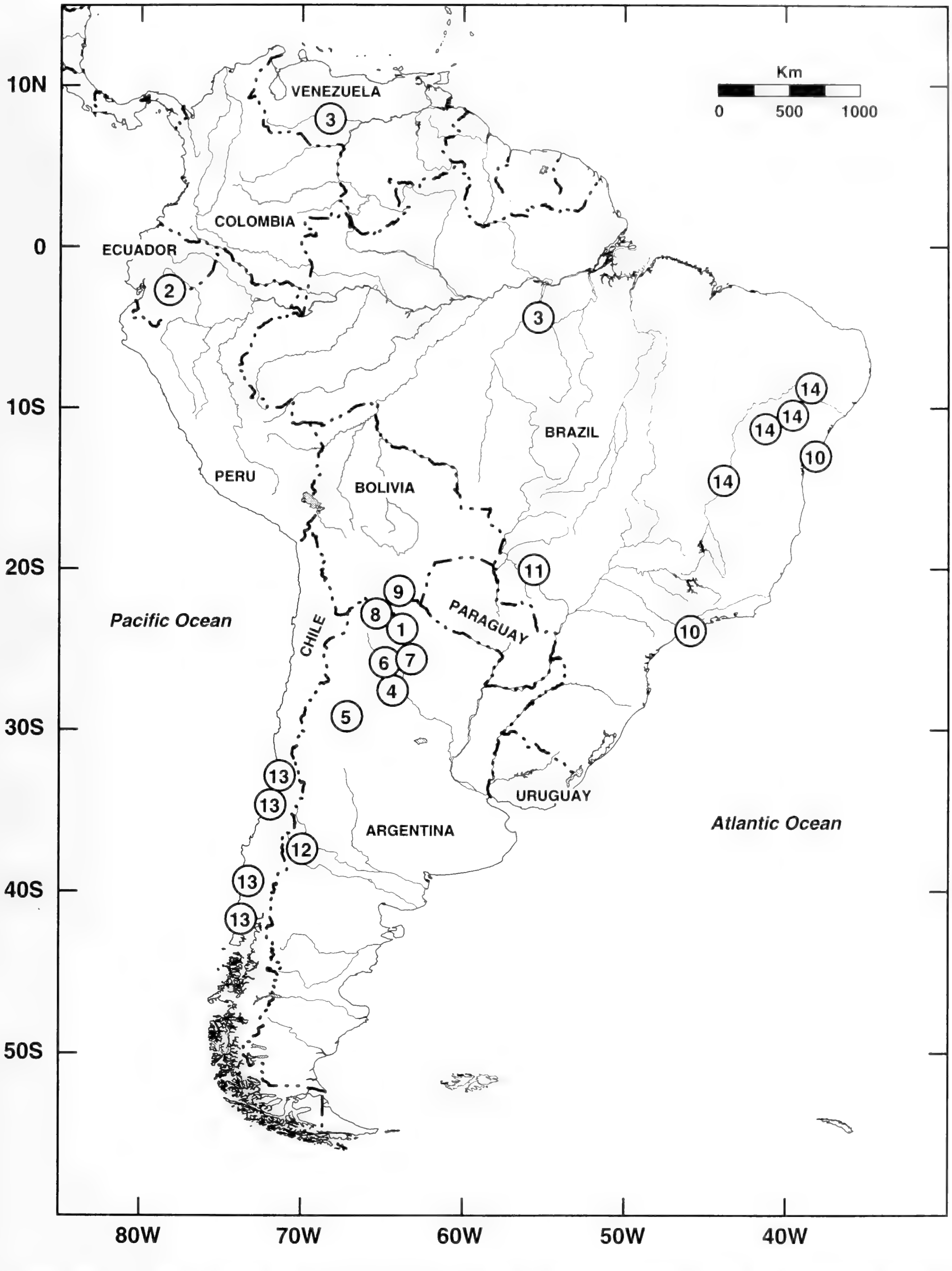
Fig. 9. Distribution of species of *Spelaeogammarus* in eastern Brazil: 1) *S. bahiensis* (1 cave); 2) *S. trajanoae* (4 caves); 3) *S. spinilacertus* (2 caves); 4) *S. santanensis* (1 cave). Shading indicates principal cave and/or karst areas. Map adapted from Trajano & Sanchez (1994).

features some interesting characters that might be interpreted as intermediate states between the relatively primitive *Spelaeogammarus* and the more derived *Bogidiella* s. str. For example, *B. gammariformis* has enlarged, bilobed coxal plates 5 and 6, which are longer than wide, therefore showing a strong resemblance to the coxae of *Spelaeogammarus*. The inner rami of the pleopods of *B. gammariformis* are also 1-segmented, but show the same reduction as in most other species of *Bogidiella* s. str. (i.e., shorter than segment 1 of the outer ramus).

The concentration of the four morphologically closely similar species of *Spelaeo-*

→

Fig. 10. Distribution of bogidiellid genera in continental South America: 1) *Bogidiella cooki* Grosso & Ringuelet, 1979; 2) *B. gammariformis* Sket, 1985; 3) *B. neotropica* Ruffo, 1952; 4) *B. (Dycticogidiella) ringueleti* Grosso & Fernandez, 1988; 5) *B. (Dyct.) talampayensis* Grosso & Claps, 1985; 6) *B. (Mesochthongidiella)*



tucumanensis Grosso & Fernandez, 1985; 7) *B. (Stygogidiella) hormocollensis* Grosso & Fernandez, 1988; 8) *B. (Styg.) lavillai* Grosso & Claps, 1984; 9) *Eobogidiella purmamarcensis* Karaman, 1982; 10) *Marigidiella brasiliensis* Stock, 1981; 11) *Megagidiella azul* Koenemann & Holsinger, 1999; 12) *Patagongidiella danieli* Grosso & Fernandez, 1993 and *P. mauryi* Grosso & Fernandez, 1993 (sympatric species); 13) *Pseudingolfiella chilensis* Noodt, 1965; 14) *Spelaeogammarus bahiensis* da Silva Brum, 1975, *S. santanensis* n. sp., *S. spinilacertus* n. sp., and *S. trajanoae* n. sp.

gammarus in a series of disjunct caves is unique for South America (see Fig. 10). Particularly interesting are the relatively subtle morphological differences between the four species that, in turn, appear to be correlated with the interspecific spatial distance as well as the abundance of species per area: *S. spinilacertus* and *S. trajanoae* occur in the central part of the range of *Spelaeogammarus* and show the highest morphological resemblance. In contrast are the more obvious differences between the relatively large *S. santanensis* and the smaller *S. bahiensis,* which occur on opposite ends of the generic range.

In South America there is a second concentration of species in northern Argentina, which occur exclusively in hyporheic (?) habitats along the Rio Grande (see Fig. 10). This cluster is also strictly endemic but it has a higher generic diversity, with six species in two genera and three subgenera, possibly reflecting the time of divergence from a very old freshwater precursor and the subsequent radiation into a region of isolated inland habitats. However, the distribution pattern of *Spelaeogammarus* seems to indicate quite a different historical scenario, inasmuch as the species of this genus show an exceptionally close morphological relationship with each other when compared with all other South American bogidiellids. If we assume, for the sake of argument, the same evolutionary rate for all South American bogidiellids, the cluster of species belonging to *Spelaeogammarus* appears to have originated from a common ancestor far more recently as opposed to other bogidiellids in South American freshwater habitats.

The morphological appearance of the four species as well as their distribution over a relatively wide range of disjunct karst "islands" characterize *Spelaeogammarus* as a distinct genus within the family Bogidiellidae. The apparent isolation of these species may well reflect a sequence of allopatric (geographic) speciation events over a relatively short period of time.

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Eudendrium bathyalis, a new species of hydroid (Hydrozoa: Anthomedusae: Eudendriidae) from Bermuda

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Abstract.—*Eudendrium bathyalis,* a new species, is described from relatively deep-water (283 m) on the offshore slope of the oceanic island of Bermuda. Its distinctive characters are the small size of the colony, the cnidome, comprising two sizes of microbasic euryteles and the unreduced female blastostyle, bearing eggs supported by long peduncles.

The shallow-water hydroids of Bermuda were recently revised in a series of studies by Calder (1988, 1991, 1997). These reports complemented several earlier studies on the fauna of the region (viz. Allman 1888, Congdon 1907, Ritchie 1909, Bennitt 1922, among others).

Combining records from these studies with collections of hydroids from deeper waters (Calder 1996, 1998), a total of 110 species has been reported from this small oceanic island. The relatively large number of species from a small geographic area likely reflects the extensive sampling undertaken in the area, from the intertidal zone to abyssal bottoms, including bays, grassbeds, caves, reefs, ponds, mangroves, and pelagic seaweeds.

Within the Eudendriidae, four species belonging to the two known genera of the family (*Myrionema amboinense* Pictet, 1893, *Eudendrium bermudense* Calder, 1988, *Eudendrium capillare* Alder, 1856, and *Eudendrium carneum* Clarke, 1882) are known from Bermuda.

These four species appear to be widespread in the warm western Atlantic. Another species recorded from the Caribbean region is *Eudendrium ramosum* (Linnaeus 1758) (Wedler 1975, for Colombia; Wedler & Larson 1986, for Puerto Rico); this species is also present in the fauna of Bermuda (pers. obs.). Other species of *Eudendrium* have also been described or reported for the region (Allman 1877, Fraser 1944). These species are poorly known taxonomically, being characterized on gross morphology alone; in some cases, hydranths were lacking, and no information exists on their complement of nematocysts.

The purpose of this report is to describe a new species of *Eudendrium,* collected by submersible from bathyal waters on the slope of the Bermuda Pedestal.

Methods

Material was collected by submersible (SDL-1) on 3 Mar 1997, depth 283 m, from the Bermuda Pedestal. The study area is discussed more fully elsewhere (Calder 1998). The holotype was examined, measured, and drawn under microscope and stereomicroscope, both with camara lucida. The cnidome terminology follows Weill (1934) and Mariscal (1974), and measures of nematocysts were made on non-discharged capsules. The L/W ratio (Kubota 1976) and S/C ratio (Watson 1987) are also provided. Other study methods for Eudendriidae are from Marques (1995) and Marques & Migotto (1998).

Systematics

Genus *Eudendrium* Ehrenberg, 1834

Eudendrium bathyalis, new species

Fig. 1

Examined material.—Holotype, one female colony, Bermuda Pedestal 32°16.6′N 64°44.3′W, 283 m, 3 Mar 1997, on a sponge, ROMIZ B3034.

Description.—Colonies dioecious, fragile, up to 18 mm in height; main stems slightly fascicled basally or up to the half of the colony, sometimes formed only by a couple of tubes, fascicled region up to 0.18 mm in diameter. Hydrocauli arising from stolonal hydrorhiza growing over a sponge; branches few, irregular, occurring over entire hydrocaulus, branches up to third order, in radiate planes; pedicels arising from main stem or branches of first and second order. Perisarc of main stem weakly developed, single tubes 0.08–0.10 mm in diameter, unfascicled region with scarce annulations, in sets of 2–3 rings. Branches with 2–5 rings at origin, 0.06–0.08 mm in diameter. Pedicels obscurely annulated at origin, with 2–4 rings, very delicate, 0.05–0.06 mm in diameter.

Hydranths 0.10–0.25 mm in height, 0.10–0.29 mm in diameter (measured in the body region just below the tentacles), with a distinct deep groove in the aboral region; hypostome large; tentacles 18–24 in number, occurring in a whorl below hypostome.

Gonophores styloids, arising from body of hydranth. Immature styloids placed in a circle around body of hydranth. Female blastostyles styloids without a characteristic spadix over a single egg. Tentacles and hypostome not reduced during ontogeny of female gonophores. Eggs almost circular, maturity undeterminable, encapsulated by a thin gelatinous layer, linked by long peduncles to body of hydranth, distal part of peduncle broadened for egg support. Eggs 3–5 in number, 0.14–0.15 mm in diameter. Male gonophores not observed.

Nematocysts of one category, heterotrichous microbasic euryteles in two size classes.

Small microbasic euryteles (not seen discharged), 6.0–6.3 by 2.8–3.2 μm, L/W = 1:2.0–2.1, oval, abundant; distributed over hydranth body, hypostome, peduncle coenosarc of female gonophore, and tentacles.

Large microbasic euryteles (seen discharged), 22.1–23.4 by 8.2–8.9 μm, L/W = 1:2.6–2.7, bean-shaped; shaft crossing about from 0.5 to 0.75 of the whole length of undischarged capsule, discharged shaft heavily armed, ca. 19.8 μm in length, proportion S/C = 1.4; nematocysts distributed over hydranth body (sometimes common), egg peduncle (rare), and coenosarc (not seen on hypostome).

Etymology.—*bathyalis,* adj. from Greek *bathys* = deep, in allusion to the bathyal depth from which material of this species was collected.

Remarks.—The distinctive character of this species is the pedunculated gonophore, which we presumed would be a female one. A similar female gonophore has only been observed in *Eudendrium vervoorti* Marques & Migotto, 1998, a recently described species based on scarce material, without hydrorhiza and covered by debris, from the coast of the Netherlands. In *E. vervoorti,* the gonophores apparently arose from the hydranth body, without a conspicuous spadix; some other gonophores (presumably older ones) are linked to the body of hydranth or to the pedicel by long stalks (Marques & Migotto 1998). Another similar feature between both species is the extremely delicate branches (widths barely greater than 0.1 mm), but this character is also shared by several other species of the genus [e.g., *Eudendrium album* Nutting, 1896, *Eudendrium fragile* Motz-Kossowska, 1905, *Eudendrium generale* von Lendenfeld, 1885, *Eudendrium tottoni* Stechow, 1932 (=*Eudendrium antarcticum* Totton, 1930, see Stechow 1932) and *Eu-*

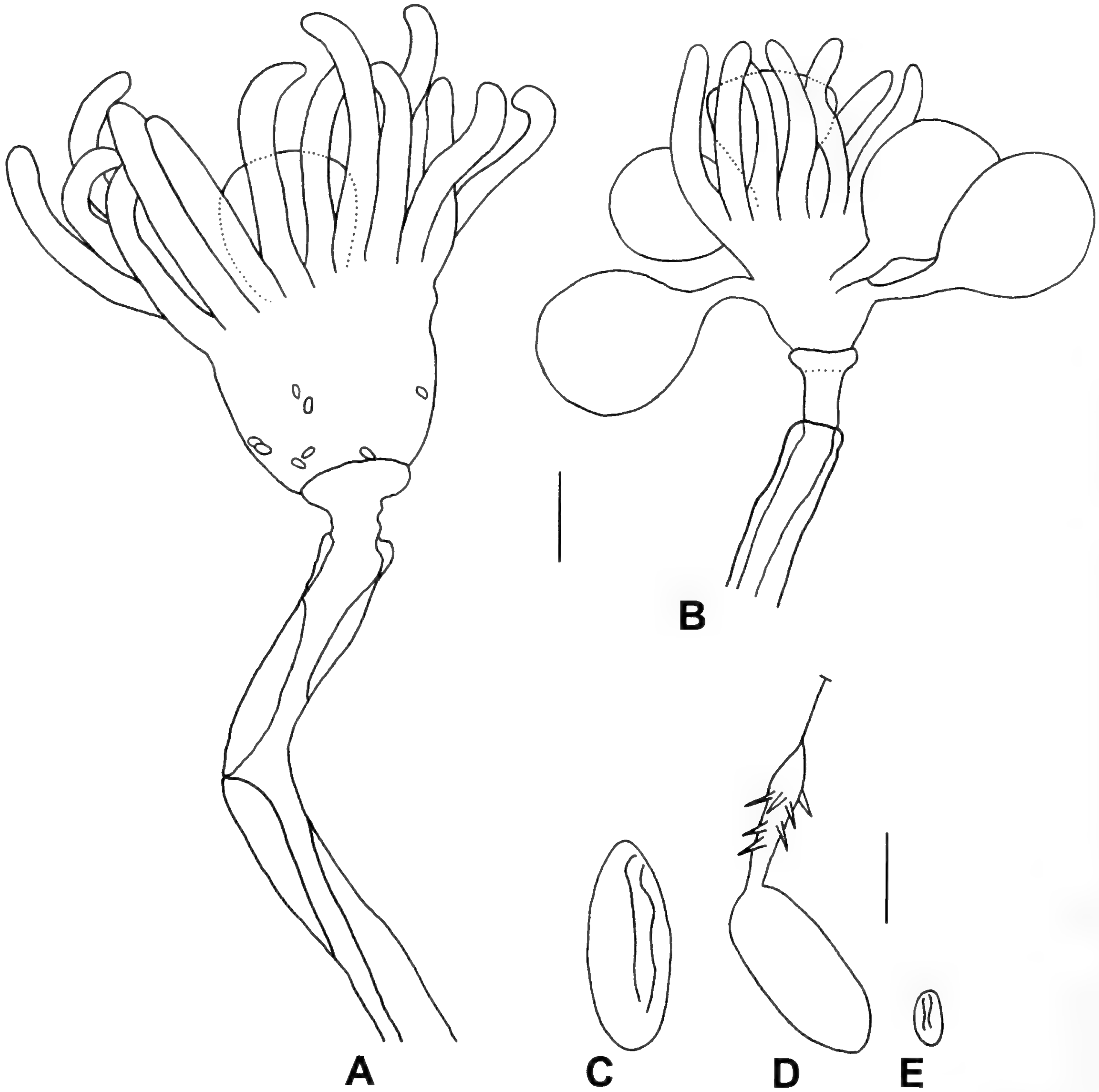

Fig. 1. *Eudendrium bathyalis,* new species; all from holotype ROMIZ B3034. A, hydranth with the distribution of the large microbasic euryteles represented over the body; B, female blastostyle; C, capsule of the large microbasic eurytele; D, discharged large microbasic eurytele; E, capsule of the small microbasic euryteles. Scale bar, A–B = 0.1 mm; C–E = 10 μm.

dendrium motzkossowskae Picard, 1951], but none of those has a female gonophore as in *E. vervoorti* and *E. bathyalis.*

The cnidome is the distinctive character between *E. vervoorti* and *E. bathyalis.* The Netherlands species has only small microbasic euryteles and the species from Bermuda has both small and large nematocysts. The material from Bermuda is slightly fascicled, but as the Netherlands material is represented only by a small fragment, even without hydrorhiza (Marques & Migotto 1998), this difference could be only an artifact.

Key to the species of Eudendriidae recorded from Bermuda

1a. More than 40 tentacles arranged in two whorls, presence of abundant zooxanthellae .... *Myrionema amboinense*

1b. Usually fewer than 35 tentacles arranged in a unique whorl, zooxanthellae absent 2

2a. Nematocysts of only one size class, microbasic eurytele type .... *Eudendrium capillare*
2b. Nematocysts in two size classes 3
3a. Cnidome including small and large microbasic euryteles 4
3b. Cnidome including small microbasic euryteles and large nematocysts different from microbasic euryteles 5
4a. Female gonophore encircled by unbranched spadix .... *Eudendrium ramosum*
4b. Female gonophore supported by long peduncles, no characteristic spadix .... *Eudendrium bathyalis,* new species
5a. Large nematocysts heterotrichous anisorhiza, female immature spadix bifid .... *Eudendrium carneum*
5b. Large nematocysts macrobasic euryteles, female immature spadix unbranched .... *Eudendrium bermudense*

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Cnidae of two species of Discosomatidae (Cnidaria: Anthozoa: Corallimorpharia) from Brazil

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Abstract.—The cnidae of *Discosoma carlgreni* (Watzl, 1922) and *Discosoma sanctithomae* (Duchassaing & Michelotti, 1860) are described and illustrated. Five types (sensu Schmidt 1969, 1974) were observed: spirocysts, b-rhabdoids, p-rhabdoids D, holotrichs I and holotrichs II. An unusual variety of holotrich occurred in the tentacles and column that had not been reported previously. These species are distinguished based on the distribution and size of the types of cnidae. The importance of qualitative studies of corallimorpharians cnidae is discussed.

This paper investigates the diversity of cnidae that occur in the corallimorpharians *Discosoma carlgreni* (Watzl, 1922) and *D. sanctithomae* (Duchassaing & Michelotti, 1860) from Brazil, as well as their taxonomic value.

The diagnostic value of cnidae in different structures of cnidarians has been examined by several authors (e.g., Weill 1934, Russell 1938, Carlgren 1949, Cutress 1955, Schmidt 1972, 1974, Mariscal 1974, den Hartog 1980, Fautin 1986, England 1991, Williams 1996, Pires 1997, Östman & Hydman 1997).

Corallimorpharia is a relatively small order of skeletonless Anthozoa, morphologically intermediate between sea anemones and corals. Many authors consider them most closely related to corals (e.g., Duerden 1904, Stephenson 1921, Schmidt 1974, den Hartog 1980, Fautin & Lowenstein 1992, Chen et al. 1996, Pinto & Belém 1997, Pires & Castro 1997). Contributions to the systematics of the Discosomatidae, based on morphological and anatomical characters, have been made by several authors (e.g., Duchassaing & Michelotti 1864, Duerden 1900, Stephenson 1921, Carlgren 1940, 1949, Corrêa 1964, Schmidt 1972, 1974, den Hartog 1980, Schlenz & Belém 1982). The revision of the Caribbean shallow-water Corallimorpharia, as set forth by den Hartog (1980), provided a comprehensive review of the morphology, anatomy, histology and classification of this group. den Hartog (1980) rearranged the family Discosomatidae Duchassaing & Michelotti, 1864 on the basis of an array of material from the Caribbean. He united the five genera of Actinodiscidae (Carlgren, 1949) in the genus *Discosoma* Rüppell & Leuckart, 1828. den Hartog (1980) concluded that the order Corallimorpharia does not fundamentally differ from corals and should be included as a separate sub-order in the Scleractinia.

The cnidom of the Discosomatidae was previously studied by Watzl (1922), Carlgren (1927, 1949), Corrêa (1964), den Hartog (1980) and Schlenz & Belém (1982), but these studies were not sufficiently detailed to provide a good understanding of the cnidae in this group.

Materials and Methods

Specimens of *Discosoma carlgreni* (Fig. 1A) and *D. sanctithomae* (Fig. 1B) were collected from 1990 to 1993 and deposited in the Cnidaria collection of the Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ). For this study, 57 specimens of *D. carlgreni* and 42 specimens of *D. sanctithomae* were examined. Both species were also acquired by exchange with Mexico and Cuba in order to carry out a comparative study. Specimens of *D. carlgreni* were found at the South Coast of the state of Espírito Santo and Bahia. So far, *D. sanctithomae* has been found only in Abrolhos Archipelago, between the channel of Redonda and Siriba Islands (see Appendix for details).

Material was collected by snorkel and SCUBA diving at depths between 1 m and 16 m, using a hammer and chisel. Living animals were placed in plastic sacks with water from their site of collection and transported on ice. Specimens were anesthetized by slowly adding 1:1 solution of 8% $MgCl_2$ and sea water. After anesthetization, they were fixed in 4% formalin. Cnidae were studied in squash preparations of living and preserved specimens. A fragment of tissue was squashed and spread on a slide. Five structures were examined: discal tentacle, marginal tentacle, column, stomodaeum and mesenterial filament. Measurements were made only on undischarged capsules. At least 40 length/width measurements were made of each nematocyst type in each structure examined. Measurements were made with light microscopy at magnifications up to 1250× with differential interference contrast optics (Nomarski), using an eyepiece micrometer. Drawings were made with a camera lucida. Cnidae were classified according to the nomenclatures of Weill (1934, later modified by Carlgren 1940), Schmidt (1969, 1972, 1974) and den Hartog (1980).

Results

Five types of cnidae were observed: spirocysts, b-rhabdoids, p-rhabdoids D, holotrich I and holotrich II. The cnidae were classified as follows.

Spirocysts (Figs. 3A, 6E).—Elongate and thin-walled capsule with a long tube coiled in numerous spirals, tubule without spines.

Remarks.—This variety was sparse but typical of the marginal tentacles of both species. The capsules reached up to 18 μm in length and 3.1 μm in width. Eight undischarged capsules in each species were observed. They were not included in Table 1 due to their sparseness.

B-rhabdoids.—Varied in shape and size, capsules generally oval in aspect. The thread of the b-rhabdoids is always armed with spines, not having a clear difference between the width of the proximal part of the tubule and that of the distal portion. We observed two morphological varieties of b-rhabdoids in undischarged capsules:

B-rhabdoids^1 (Figs. 2B, 3C, 4B, 6F, 7B, Table 1).—Capsule oval to cylindrical in shape, of refractive contrast. In the undischarged state, the basal portion of the tubule is shorter and thinner than that of b-rhadoids^2, up to 0.33 of the length of the capsule. Sometimes the basal part appears slightly curved, the tubule being arranged in few irregular coils.

Remarks.—The undischarged capsules from the column may be occasionally confused with holotrich II, due to little refractive contrast.

B-rhabdoids^2 (Figs. 2A, 3B, 4A, Table 1).—Capsule transparent, elongate, very small and of refractive contrast. Its basal portion is short, refractive and clear.

P-rhabdoids D.—Characterized by a notably wide tubule ending with a funnel-shaped "V" with two distinct parts: large basal shaft and tapered distal tubule. The thread is long, bearing spines. We observed two morphological varieties of p-rhabdoids D in undischarged capsules:

P-rhabdoids D^1 (Figs. 2C, D, 3D, 4C, D,

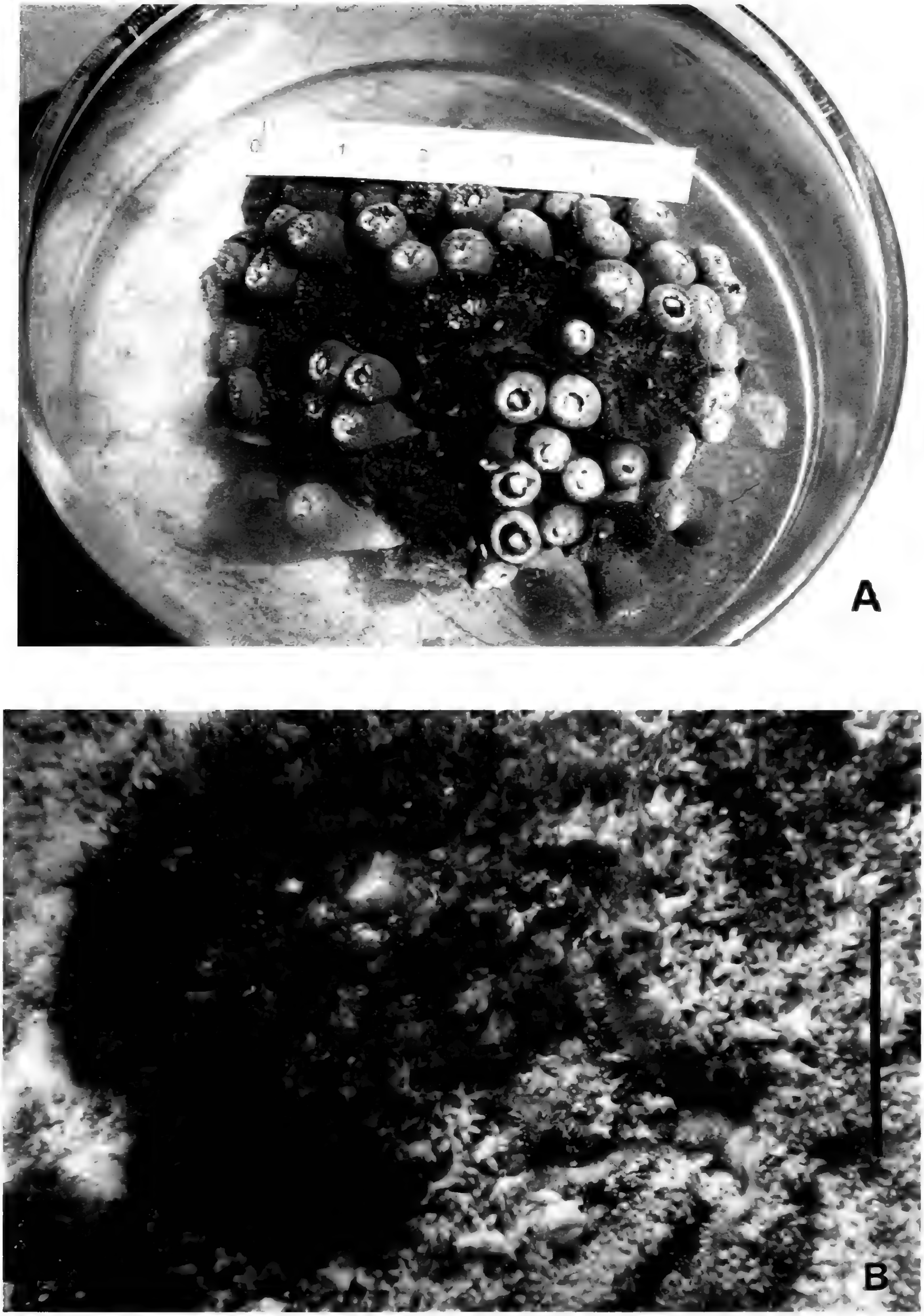

Fig. 1. A, *Discosoma carlgreni.* Specimens collected among *Zoanthus* sp. at Santa Cruz, Aracruz, ES. Scale: 5 cm. B, *D. sanctithomae.* Aggregation from study site at Abrolhos Archipelago, between the channel of Redonda and Siriba Islands. Scale: 2 cm.

G, 5B, C, 6A, B, G, H, 7A, H; 8A, B, Table 1).—Capsule cylindrical, slightly curved, of refractive contrast. The shaft has obvious turns of spines that are up to 0.5 of the capsule length.

Remarks.—This variety was rather common and also occurred in all structures examined in both species. It also occurred in two size classes in the discal tentacles, column and mesenterial filaments. In the filaments of *D. sanctithomae* some transparent thin-walled capsules, with rich contrast in the shaft, were observed (Fig. 8B).

P-rhabdoids D^2 (Fig. 7D, Table 1).—Relatively large elongate capsule, cylindrical, slightly curved and of refractive contrast. Shaft with clear turns of spines can reach up to 0.5 length of the undischarged capsule. A long tubule is irregularly arranged inside the capsule.

Holotrichs—We observed two morphological varieties of holotrich in both species:

Holotrichs I (Figs. 2E, G, 3F, G, 4F, H, I, 5A, D, 6C, D, I, K, 7E, F, G, I, 8C, D, Table. 1).—Capsules of various sizes, filled with a tubule having a long figure eight form, of rich contrast in several turns (Figs. 2G, 6K). In the discharged state, the tubule contains conspicuous spines of equal size distributed along almost its entire length, except for a short, naked basal portion. The distal end of the tubule presents an abrupt tapered distal tip, completely devoid of spines and measuring up to 30 μm (Figs. 2G, 6D).

Remarks.—The distal end of the tubule of these nematocysts was previously described by den Hartog (1980) as a terminal tubule. The terminal tubule can be seen only when the tubule is totally discharged. Holotrichs I, which are common, occurred in two size classes throughout all structures examined, except for the presence of only small capsules in the column of *D. carlgreni* (Fig. 4F, Table 1). This type ranges in size from the small (e.g., in marginal tentacles—25–34 by 9.4–18 μm) to large (e.g., in filaments—76.9–168.1 by 25–75 μm). According to den Hartog (1980), these nematocysts are the most voluminous anthozoan cnidae, reaching up to 250 by 80 μm. We also observed a particular shape of the holotrichs I in the stomodaeum. They varied from oblong to cylindrical (Figs. 4I; 7G).

Holotrichs II (Figs. 3E, 6J, Table 1).—Sharply distinguished from holotrich I in capsule shape and in having small spines with little contrast. The capsule is opaque, cylindrical, with coiled tubule in small turns, filling the entire undischarged capsule. The spines are smaller than those of holotrichs I and of little contrast and difficult to view with light microscopy.

Remarks.—These were exclusive to the marginal tentacles in both species. An unusual variety of this category is smaller and cylindrical, with a tubule filling the whole capsule and with spines smaller than those of the typical holotrich II. These capsules seem to differ from the holotrich II, except for their shape, with spines so reduced that they appear like spots distributed inside the capsule with irregularly coiled small turns. Presently, we consider it a holotrich II, occurring in the discal tentacles and in the column of *D. carlgreni* (Figs. 2F, 4E); in the column of *D. sanctithomae,* they were large (Fig. 7C). This variety has never been reported from the discal tentacles and column in the Discosomatidae.

Discussion

We identified seven types of cnidae in the Discosomatidae. The presence of spirocysts in this group was discussed by Carlgren (1949) and den Hartog (1980). Carlgren (1949) recorded the sparseness of spirocysts in the Discosomatidae, claiming that they were found in the tentacles. den Hartog (1980:36) characterized the family by the absence of spirocysts and stated "not only are spirocysts absent in the tentacles of Discosomatidae, other ectodermal cnidae too are very scarse . . . the tentacles . . . are non-retractile, non-motile . . . are either re-

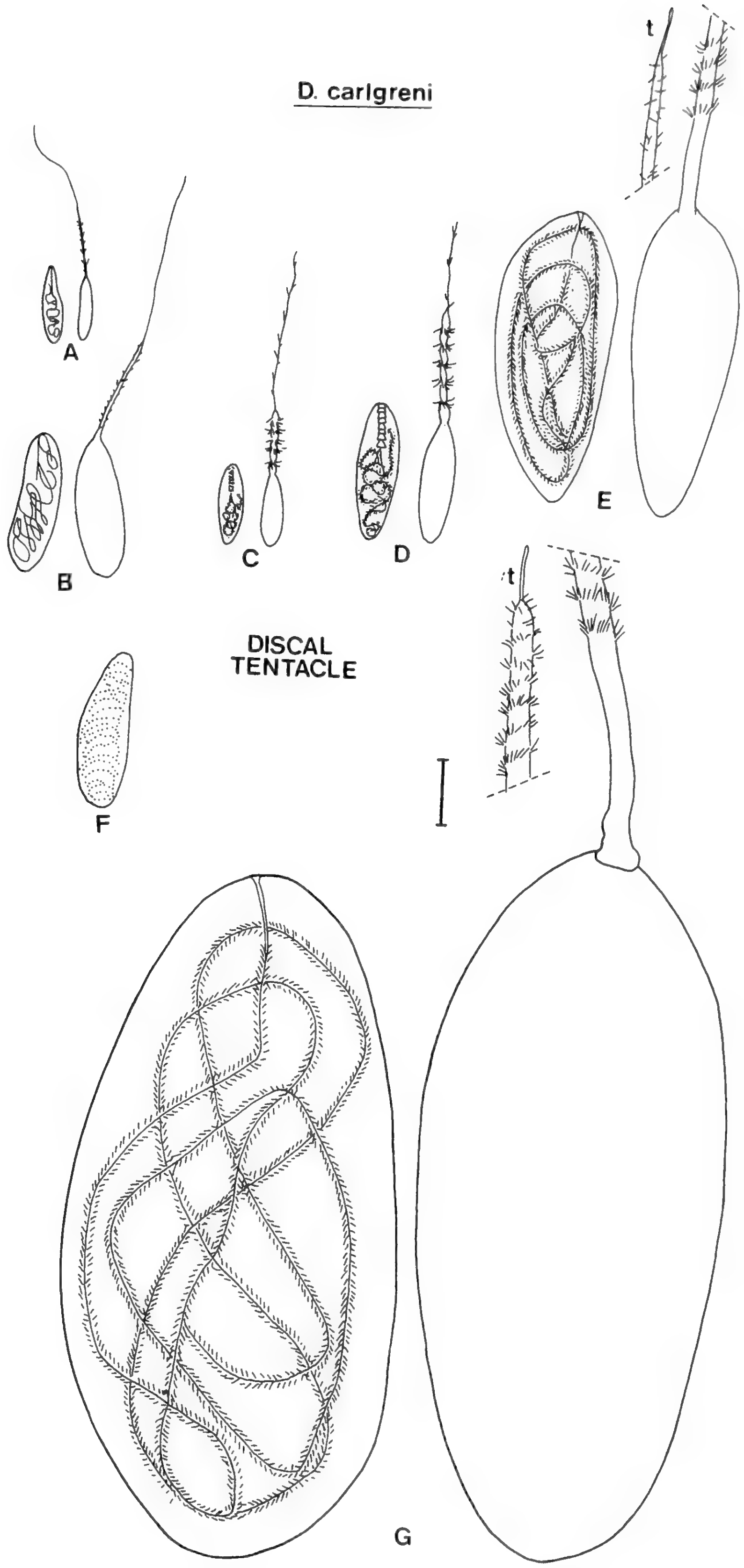

Fig. 2. Cnidome of *Discosoma carlgreni,* Discal tentacles. A, b-rhabdoids^2; B, b-rhabdoids^1; C, D, p-rhabdoids D^1; E, G, holotrichs I; F, holotrichs II. Abbreviation: t = terminal tubule. Scale: 10 μm.

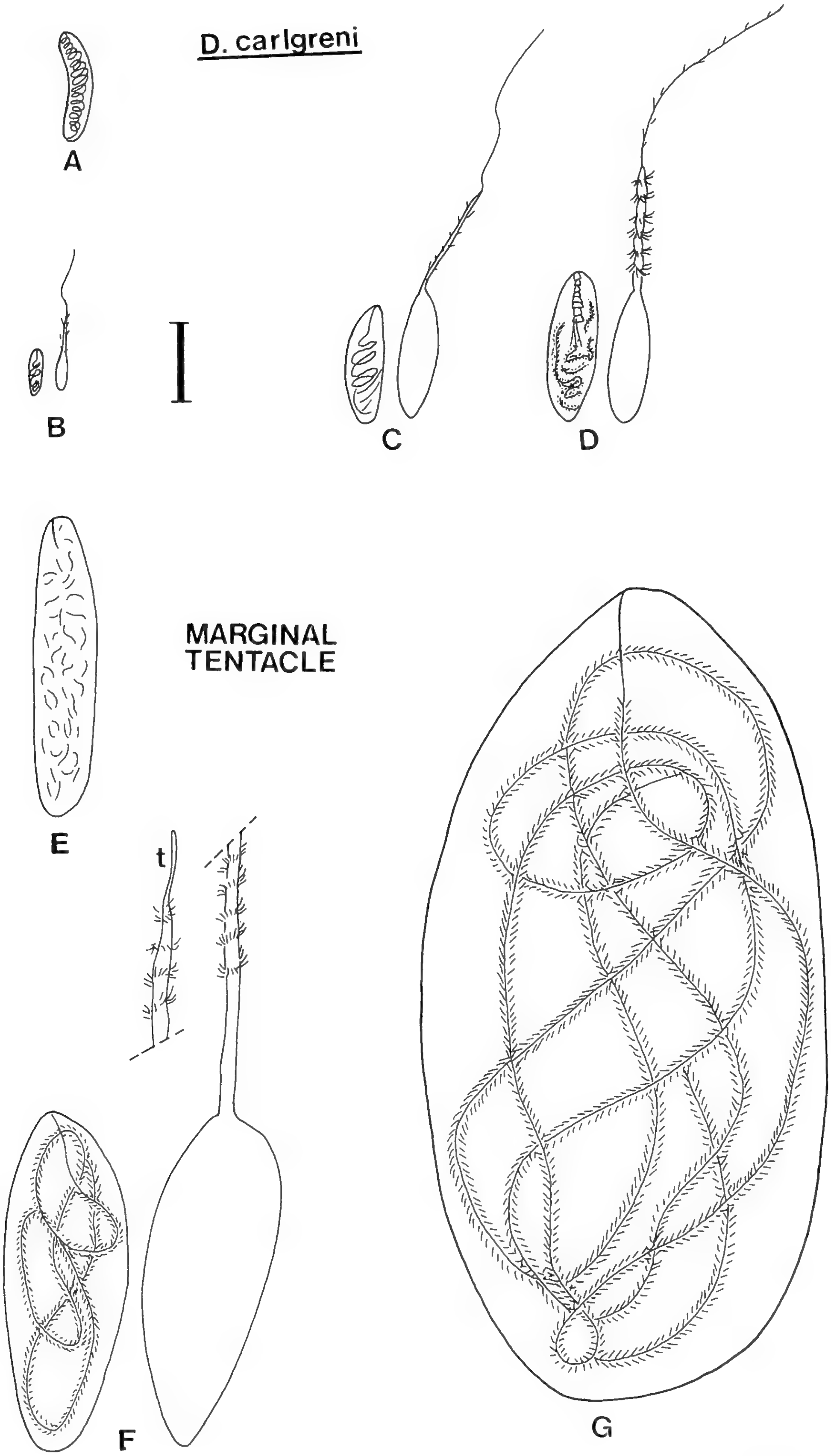

Fig. 3. Cnidome of *Discosoma carlgreni,* Marginal tentacles. A, spirocysts; B, b-rhabdoids^2; C, b-rhabdoids^1; D, p-rhabdoids D^1; E, holotrichs II; F, G, holotrichs I. Abbreviation: t = terminal tubule. Scale: 10 μm.

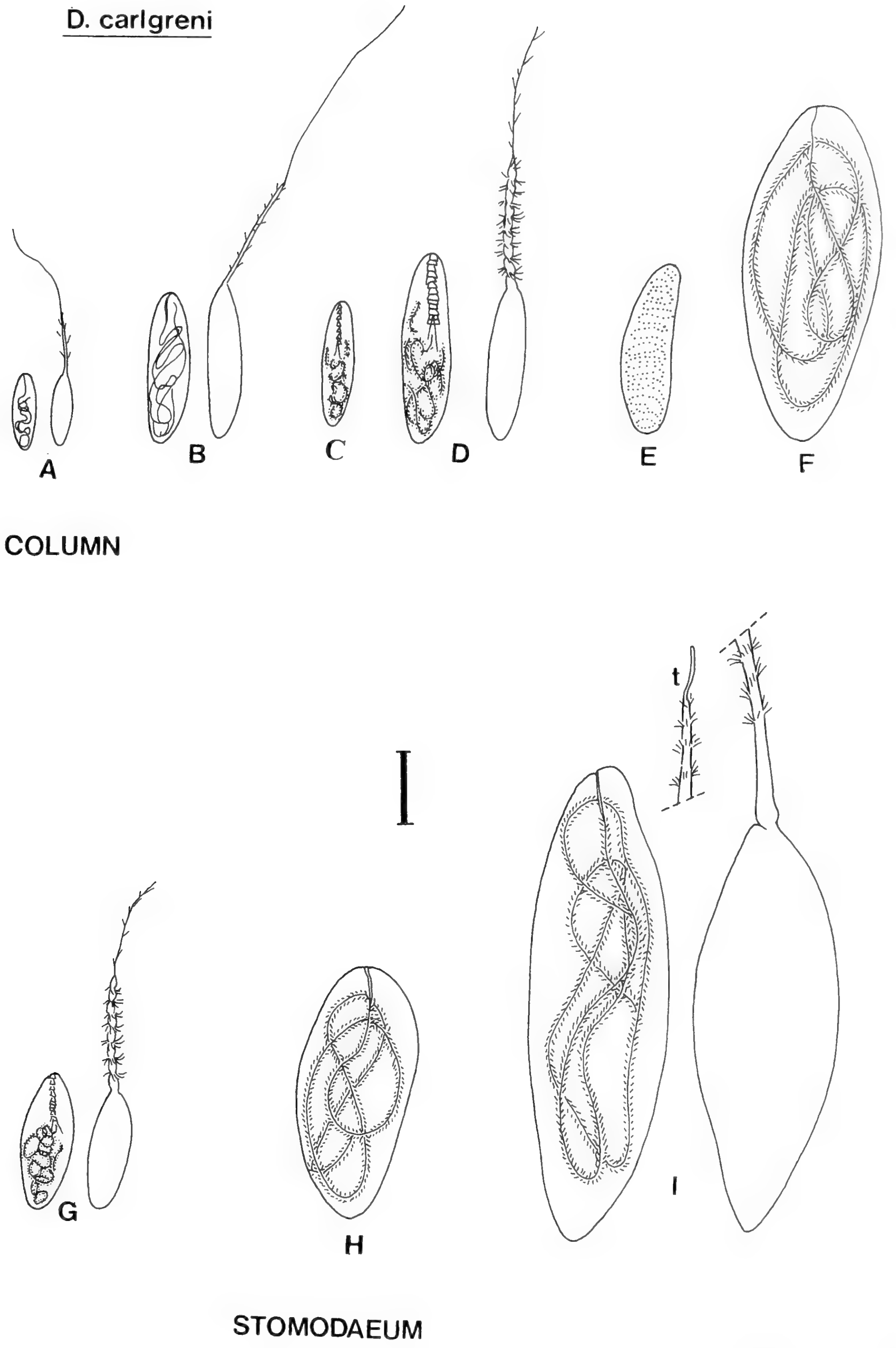

Fig. 4. Cnidome of *Discosoma carlgreni,* Column A–F; Stomodaeum G–I. A, b-rhabdoids^2; B, b-rhabdoids^1; C, D, G, p-rhabdoids D^1; E, holotrichs II; F, H, I, holotrichs I. Abbreviation: t = terminal tubule. Scale: 10 μm.

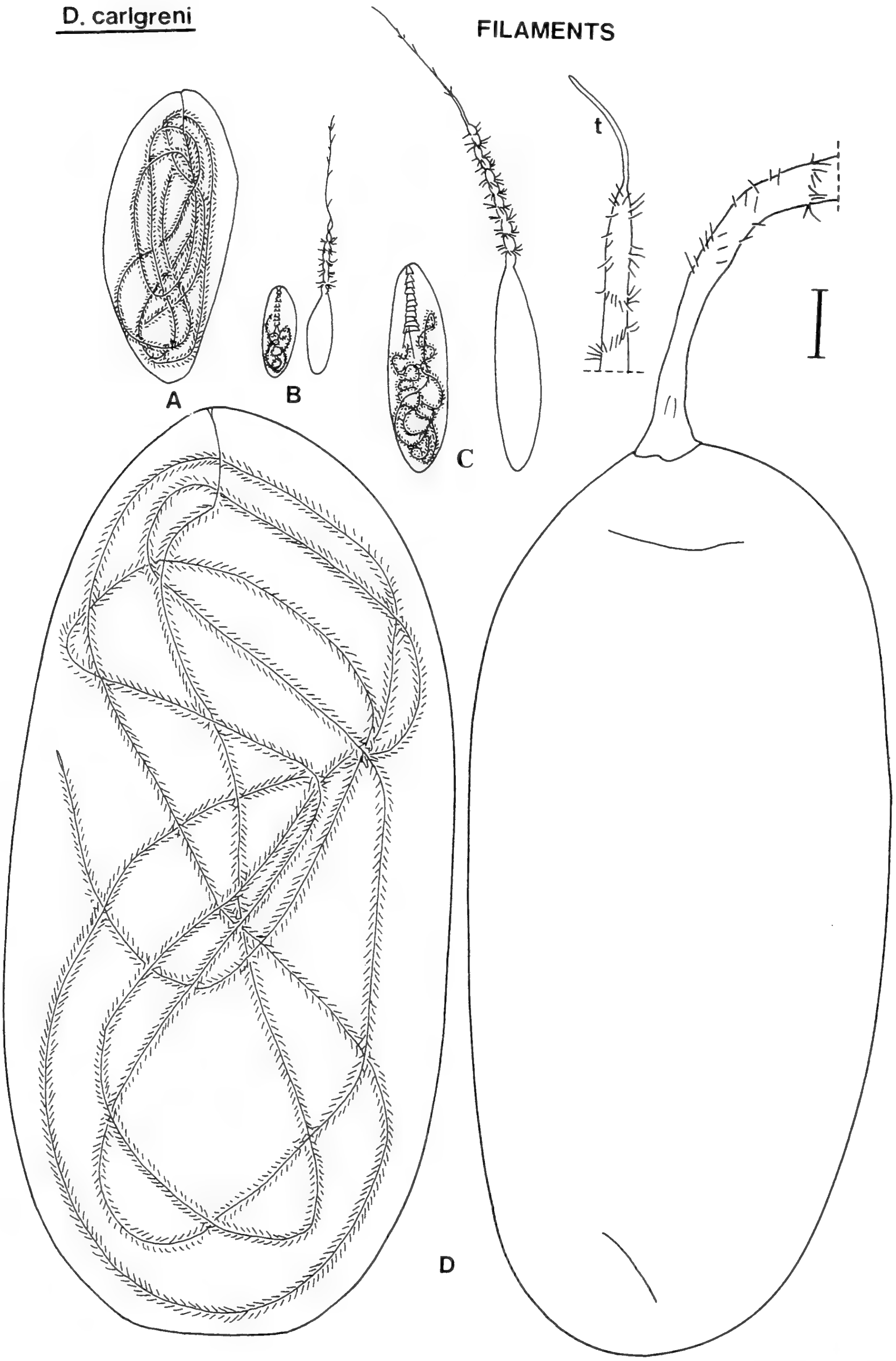

Fig. 5. Cnidome of *Discosoma carlgreni,* Filaments. A, D, holotrichs I; B, C, p-rhabdoids D^1. Abbreviation: t = terminal tubule. Scale: 10 μm.

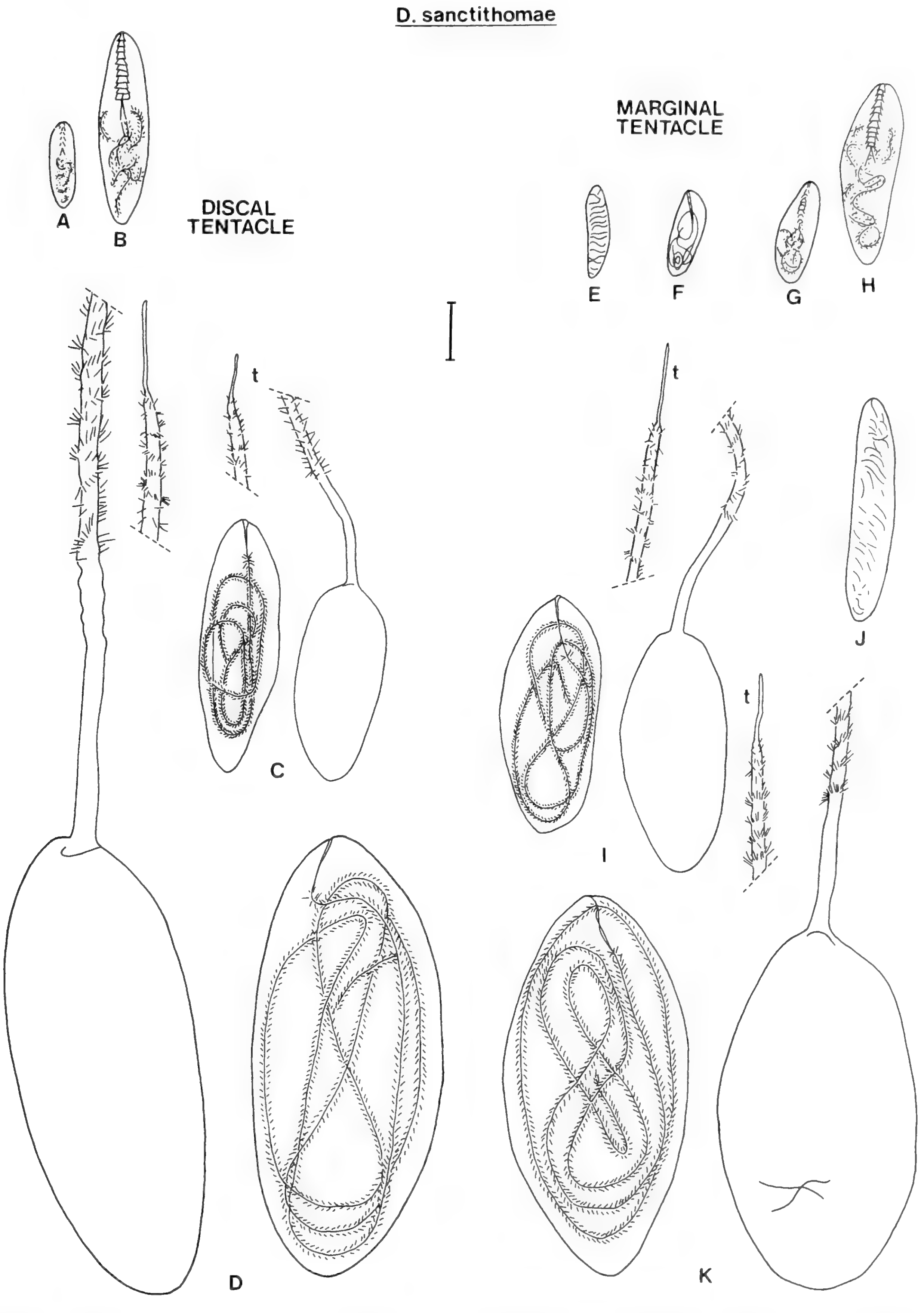

Fig. 6. Cnidome of *Discosoma sanctithomae,* Discal tentacles A–D, Marginal tentacles E–K. A, B, G, H, p-rhabdoids D[1]; C, D, I, K, holotrichs I; E, spirocysts; F, b-rhabdoids[1]; J, holotrichs II. Abbreviation: t = terminal tubule. Scale: 10 μm.

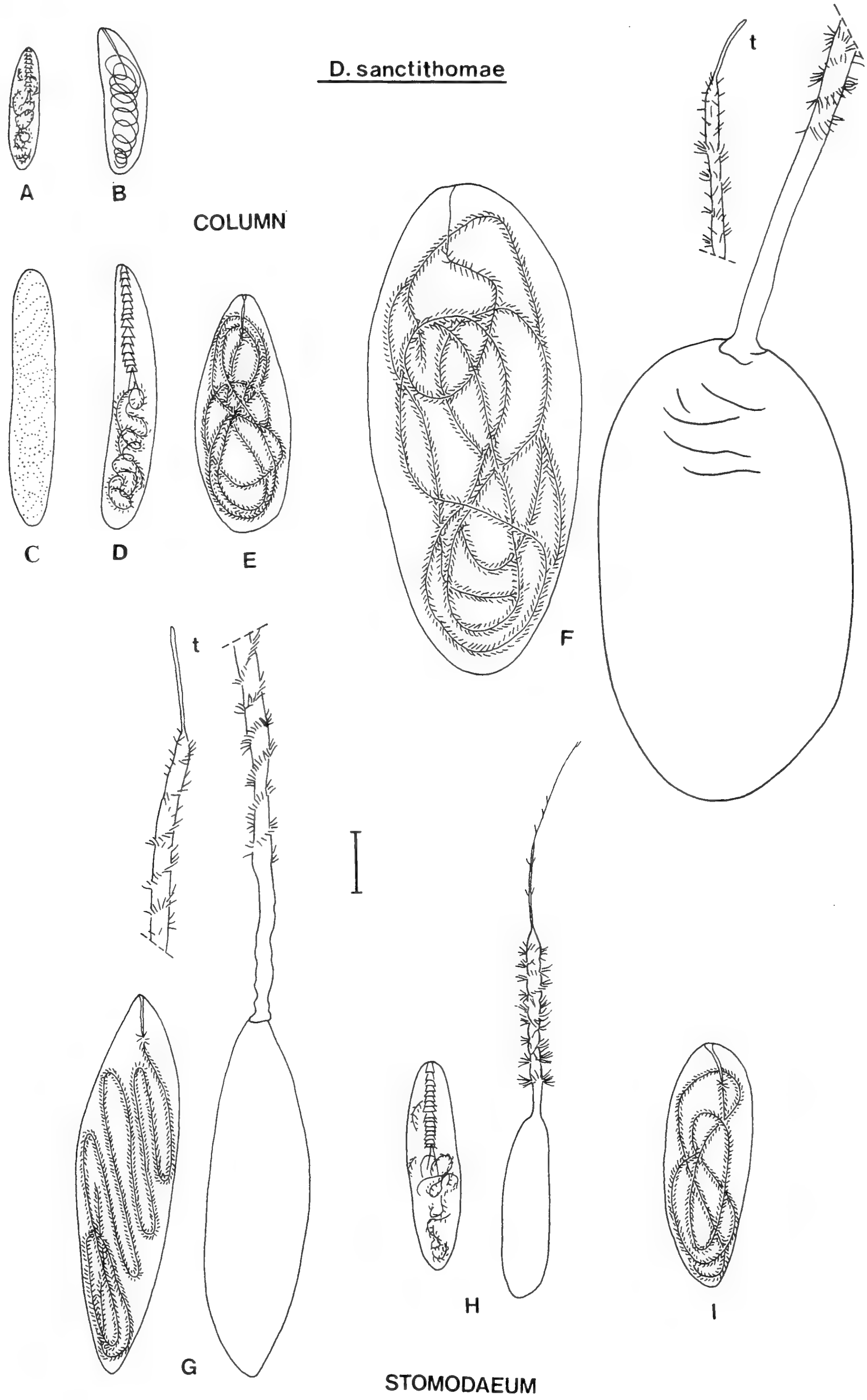

Fig. 7. Cnidome of *Discosoma sanctithomae,* Column A–F, Stomodaeum G–I. A, H, p-rhabdoids D[1]; B, b-rhabdoids[1]; C, holotrichs II; D, p-rhabdoids D[2]; E–G, I, holotrichs I. Abbreviation: t = terminal tubule. Scale: 10 μm.

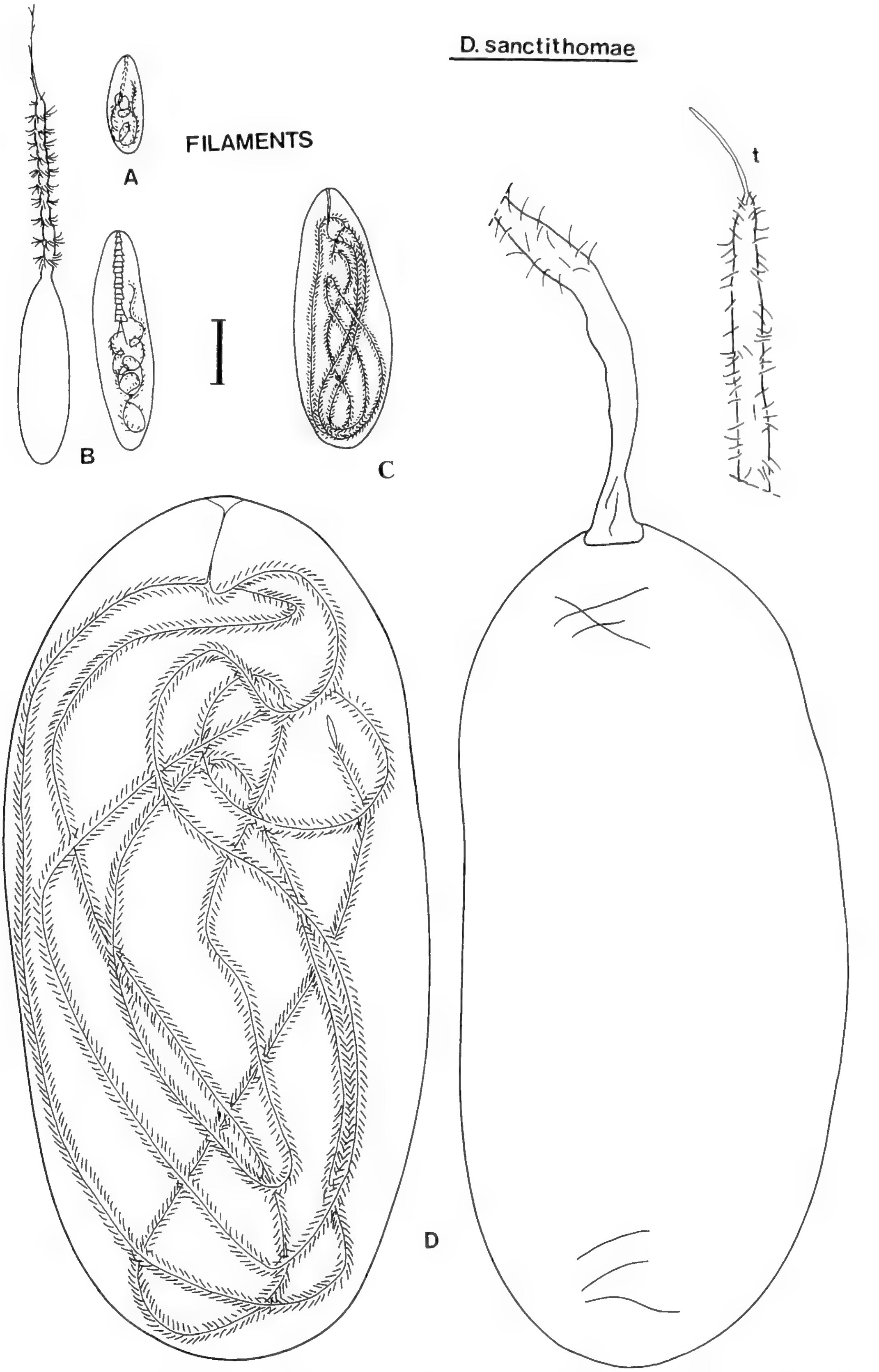

Fig. 8. Cnidome of *Discosoma sanctithomae*, Filaments. A, B, p-rhabdoids D^1; C, D, holotrichs I. Abbreviation: t = terminal tubule. Scale: 10 μm.

Table 1.—Distribution measurements of cnidae. Sp = species, A = *Discosoma carlgreni,* B = *D. sanctithomae. n* = number of capsules measured, F = figure.

Structure Cnidae type	Sp	Average and range of length and width of nematocyst capsules		*n*	F
		Length	Width		
Discal tentacles					
b-rhabdoids^1	A	14.4 (12.5–17.5)	4.7 (1.9–6.3)	41	2B
b-rhabdoids^2	A	9.5 (7.5–11.3)	1.8 (1.3–3.0)	41	2A
p-rhabdoids D^1	A	12.9 (8.8–17.5)	3.5 (1.9–5.6)	66	2C
		25.4 (18.8–30.6)	6.6 (5.6–8.8)	54	2D
	B	13.3 (10.6–17)	3.5 (2.5–5.0)	40	6A
		33.2 (20–46.9)	7.7 (4.4–11.3)	50	6B
holotrichs I	A	37.2 (28–41.3)	13.3 (6.9–18.1)	76	2E
		72.1 (45–123.1)	31.2 (18.1–55.6)	45	2G
	B	34 (26.9–43.8)	14.8 (11.3–20)	83	6C
		69 (57.5–85)	32.4 (21.9–45.8)	92	6D
holotrichs II	A	16.5 (11.3–21.9)	4.9 (3.1–6.9)	42	2F
Marginal tentacles					
b-rhabdoids^1	A	15.5 (12.2–23.8)	4.9 (3.8–6.9)	65	3C
	B	15.6 (11.3–20)	4.0 (2.5–5.6)	72	6F
b-rhabdoids^2	A	8.9 (6.3–10.9)	1.9 (0.9–3.1)	40	3B
p-rhabdoids D^1	A	13.2 (8.8–16.3)	4.2 (1.9–6.9)	79	3D
	B	13.5 (10–20)	3.8 (2.5–5.6)	50	6G
		33.7 (23.1–49)	8.0 (5.6–11.9)	45	6H
holotrichs I	A	35.6 (27.5–40.6)	12.7 (9.6–20.6)	65	3F
		82.2 (50.6–125)	34.2 (20.6–49.4)	60	3G
	B	31.6 (25–34.4)	13.6 (9.4–18.1)	52	6I
		68.0 (54.4–83.1)	30.0 (17.5–40.3)	77	6K
holotrichs II	A	29.7 (8.8–43.8)	5.4 (2.5–10.6)	159	3E
	B	24.8 (13.1–37)	5.1 (3.1–13.8)	110	6J
Column					
b-rhabdoids^1	A	15.7 (13.1–20)	5.5 (3.8–6.3)	63	4B
	B	19.6 (16.3–25)	5.5 (3.8–7.5)	50	7B
b-rhabdoids^2	A	9.6 (5.6–12.5)	2.0 (1.3–3.8)	40	4A
p-rhabdoids D^1	A	13.9 (10-17.5)	4.6 (2.5–5.3)	60	4C
		24.1 (19.1–28.8)	6.9 (6.2–8.1)	40	4D
	B	14.5 (10–20.6)	4.0 (2.5–6.3)	45	7A
p-rhabdoids D^2	B	41.1 (25–58.8)	8.2 (4.4–13.1)	64	7D
holotrichs I	A	34.6 (30.6–37.5)	12.7 (7.3–16.3)	50	4F
	B	34.1 (28.1–38.1)	15.4 (11.3–18.8)	58	7E
		76.1 (61.9–94.4)	34 (25–42.5)	53	7F
holotrichs II	A	20 (13.8–19)	6.3 (3.8–9.4)	65	4E
	B	33.7 (26.3–40.6)	4.0 (2.5–6.3)	40	7C
Stomodaeum					
p-rhabdoids D^1	A	13.5 (8.8–19)	3.9 (1.9–6.3)	50	4G
	B	17.9 (10.6–32.5)	4.7 (2.5–9.4)	52	7H
holotrichs I	A	37.3 (32.5–40.6)	14.1 (10.6–17.5)	55	4H
		54.6 (45.6–70)	18.1 (10.9–22.5)	65	4I
	B	33.7 (25.6–40)	13.3 (5.6–18.8)	57	7I
		58.8 (44.4–78.8)	18.9 (11.9–35.6)	65	7G
Filaments					
p-rhabdoids D^1	A	18.2 (11.9–23.7)	4.9 (4.5–8.8)	63	5B
		27 (25–33.1)	6.9 (5.0–10)	79	5C
	B	14.6 (8.8–20)	3.6 (1.9–6.3)	40	8A
		31.5 (24.4–38.1)	8.2 (5.0–15)	78	8B

Table 1.—Continued.

Structure Cnidae type	Sp	Average and range of length and width of nematocyst capsules		*n*	F
		Length	Width		
holotrichs I	A	36.9 (26.2–53.8)	13.6 (7.5–18.8)	50	5A
		117.6 (90.6–175.2)	49 (31.2–72)	69	5D
	B	31.8 (23.8–37.5)	13.1 (5.0–18.1)	69	8C
		146.5 (76.9–168.1)	60.3 (25–75)	73	8D

duced to insignificant, wartlike protuberances or developed into vesicle-like structures . . .” den Hartog (1980) pointed out the difficulty of accepting that these tentacles were functional catching devices because the Discosomatidade have been associated with zooxanthellae that provide nutrition to the animals. However, several Actiniaria, such as *Stichodactyla haddoni* (Saville-Kent, 1893) and *Stichodactyla duerdeni* (Carlgren, 1900), with a large number of spirocysts, have similar tentacles and zooxanthellae. In this study, we found spirocysts in the marginal tentacles of both species, thus confirming Carlgren’s finding.

Although den Hartog (1980) accepted Schmidt’s system (1972, 1974) of terminology for corallimorpharian cnidae, he preferred to adopt Stephenson’s system of classification. den Hartog (1980) considered Schmidt’s b- and p-rhabdoids (=b and p-mastigophores sensu Carlgren, 1940) as synonyms of spirulae and penicilli sensu Stephenson (1928), respectively. Therefore, he recorded four types of cnidae for the Discosomatidae: spirulae, penicilli D, penicilli E and homotrich. In agreement with Belém & Schlenz (1982), we adopted Schmidt’s classification because it provides descriptions and illustrations of the different types of corallimorpharian nematocysts, based on many specimens.

The comparative study carried out with specimens of *Discosoma carlgreni* from Mexico and *D. sanctithomae* from Cuba has confirmed that they are conspecific with the Brazilian species, respectively.

The varieties of b-rhabdoids^{1} and b-rhabdoids^{2} qualitatively separate *Discosoma carlgreni* from the *D. sanctithomae.* The first variety occurred particularly in the tentacles as well as in the column of both species, except in the discal tentacles of *D. sanctithomae.* Such absence was also verified by den Hartog (1980). The b-rhabdoids^{2} occurred particularly in the tentacles and column of *D. carlgreni.* Schlenz & Belém (1982) recorded two size-classes of b-rhabdoids in the stomodaeum of *D. carlgreni,* neither of them observed by den Hartog (1980) nor in this study.

The p-rhabdoids D^{1} were easily seen in all structures of the body. The distribution and occurrence of these nematocysts seemed uniform in both species, except for the presence of only one small size class in the marginal tentacles of *D. carlgreni* as well as in the column of *D. sanctithomae.*

Contrary to the view of den Hartog (1980) concerning the total absence of p-rhabdoid D in the stomodaeum in Corallimorpharia, we observed a variety p-rhabdoid D^{1} in this structure in both species. These nematocysts were rather common, also being larger in *Discosoma sanctithomae.* Our results are in agreement with those of Corrêa (1964), who observed the microbasic p-mastigophore (=p-rhabdoid D sensu Schmidt) in the stomodaeum of *D. sanctithomae.* We also observed the variety p-rhabdoid D^{2} in the column of *D. sanctithomae.* None of the previous works have registered this variety before.

Another feature which distinguishes *Discosoma sanctithomae* from *D. carlgreni* is the size of holotrich I. In the column of *D. sanctithomae,* both large and small ones occur, whereas in *D. carlgreni* they are small.

We noticed in all discharged capsules of holotrich I, an abruptly tapered distal tube called terminal tube by den Hartog (1980). This terminal portion is flat, hardly refractive and spineless, being also observed by Schlenz & Belém (1982). This portion can be observed in squash preparations, though sometimes it is not fully discharged so the terminal tube of most remains unevaginated. The presence of this tube was previously recognized in the macrobasic p-mastigophores [=holotrich sensu Schmidt (1974) and penicilli E sensu den Hartog (1980)] by Cutress (1955:134). In his words: "these nematocysts have a shaft which is more than three times the length of the capsule and which is abruptly reduced to a thread . . .". Cutress (1955), therefore, suggested that corallimorpharian holotrichs should be termed macrobasic p-mastigophores. Nevertheless, some authors (e.g., Werner 1965, Mariscal 1974) did not accept Cutress' proposal. An alternative and independently derived system, using Stephenson's term penicilli E, was provided by den Hartog (1980). Schmidt (1972, 1974) identified a large holotrich I, commonly occurring in the filaments, stomodaeum and tentacles in the Corallimorpharia, as well as in the Scleractinia, as having the most distinctive spines possessed by anthozoan nematocysts. As indicated by Schmidt (1972, 1974), this type presented a gradual tapering of the tubule.

Studying the cnidae of four species of Brazilian Mussidae, Pires & Pitombo (1992) observed a holotrich I in the mesenterial filaments. However, they did not record in this type the abrupt end of the tube as a vestigial thread. In short, Pires & Pitombo (1992) observed a gradual tapering of the tubule, as mentioned by Schmidt (1974).

den Hartog et al. (1993), who studied the corallimorpharians from the CANCAP expedition, found penicilli E, especially in the filaments, as well as in the tentacles, of five species of Corallimorphidae. However, they did not observe the terminal tube in discharged capsules of penicilli E from the filaments of *Corynactis* sp. den Hartog et al. (1993) added that the previous observations on this type by Cutress (1955) and especially by den Hartog (1980) needed confirmation, considering the fact that the penicilli E were based on few occasions.

In spite of the divergence among terminologies adopted in previous works, we still consider the type holotrich I sensu Schmidt (1972, 1974) the best term to be employed in this paper. To avoid further misunderstanding, the holotrichs I found in Discosomatidae here has an abrupt tapered and spineless distal tip into a terminal tubule (the reason that den Hartog (1980) considered them as penicilli E).

The holotrichs II of the marginal tentacles of *Discosoma carlgreni* are in variably larger than those of *D. sanctithomae.* This nematocyst was also found by den Hartog (1980). According to den Hartog (1980) and Belém & Schlenz (1982), this type occurs only in the marginal tentacles. Nevertheless, an unusual variety of holotrich, observed in the column and discal tentacles, showed size differences, especially in the column of *D. sanctithomae.* This variety had never been found before. We tentatively classify it as Schmidt's holotrich II; further studies of its ultrastructure will provide a more comprehensive description.

The results of this study demonstrate the importance of the nematocysts in distinguishing *Discosoma carlgreni* from *D. sanctithomae.* The varieties of b-rhabdoids and p-rhabdoids D allow us to separate the species.

Acknowledgments

We are grateful to Dr. E. Schlenz and Dr. F. L. da Silveira (Universidade de São Paulo, São Paulo) for their helpful comments to the manuscript. Thanks to Dr. A. Herrera (Instituto de Oceanologia, Academia de Ciencias de Cuba, ACC), Dr. E. Jordán (Universidade Nacional Autonoma de México), Dr. F. M. Amaral (Universidade Federal Rural de Pernambuco) and Dr. F. B. Pitombo (Universidade Federal Rural do Rio de Janeiro) for providing some of the samples used in this study. We also owe thanks to Dr. F. Pitombo for the photograph of Figure 2B. Thanks to Parque Nacional Marinhos dos Abrolhos who provided facilities and assistance during the collection of specimens. We wish to thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brazil for financial support. Part of this study was also supported by FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo), by a grant to the first author (no 98/3222-2). Finally, we also grateful to Dr. Daphne Fautin (University of Kansas) and an anonymous reviewer who made invaluable suggestions that improved the manuscript.

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Appendix

List of specimens from the Museu Nacional do Rio de Janeiro Cnidaria collection used for this study.

Discosoma carlgreni (Watzl, 1922)

MNRJ. 1796—Brazil, Espírito, Santo Santa Cruz (19°49′08″S and 40°16′43″W), Aracruz, Estação de Biologia Marinha, coll. S. M. Pinto, F. B. Pitombo & F. M. Amaral, 8 Aug 1990, 14 specimens, det. S. M. Pinto Aug 1990.

MNRJ. 1866 and 1867—Brazil, Espírito Santo, Santa Cruz (19°49′08″S and 40°16′43″W), Aracruz, Estação de Biologia Marinha, coll. M. J. C. Belém & E. Schlenz, 8 Sep 1991, 14 specimens, det. M. J. C. Belém & E. Schlenz Sep 1991.

MNRJ. 1868—Brazil, Espírito Santo, Guarapari (20°40′16″S and 40°28′5″W), Três Praias, coll. M. J. C. Belém & E. Schlenz, 5 Sep 1991, 1 specimen, det. S. M. Pinto Sep 1991.

MNRJ. 1878—Brazil, Espírito Santo, Santa Cruz (19°49′08″S and 40°16′43″W), Aracruz, Estação de Biologia Marinha, coll. M. J. C. Belém, E. Schlenz & C. C. Ratto, 8 Sep 1991, 1 specimen, det. M. J. C. Belém Aug 1991.

MNRJ. 2075—Brazil, Bahia, Abrolhos Archipelago (17°20′–18°10′S and 38°35′–39°20′W), Siriba Island, coll. F. B. Pitombo & C. G. Fonseca, 15 Dec 1992, 5 specimens, det. S. M. Pinto Dec 1992.

MNRJ. 2250—Brazil, Bahia, Abrolhos Archipelago (17°20′–18°10′S and 38°35′–39°20′W), Siriba Island, coll. F. B. Pitombo & C. C. Ratto, 19 Dec 1993, 9 specimens, det. S. M. Pinto Dec 1993.

MNRJ. 2259—Brazil, Bahia, Abrolhos Archipelago (17°20′–18°10′S and 38°35′–39°20′W), Chapeirão, coll. F. B. Pitombo, 23 Dec 1993, 13 specimens, det. S. M. Pinto Dec 1993.

MNRJ. 1540—México, Puerto Morelos, Quintana Roo, coll. E. Jordan Dahlgren & F. D. Amaral, 24 Oct 1989, 1 specimen, det. S. M. Pinto Dec 1989.

Discosoma sanctithomae (Duchassaing & Michelotti, 1860)

MNRJ. 2076—Brazil, Bahia, Abrolhos Archipelago (17°20′–18°10′S and 38°35′–39°20′W), Siriba island, coll. F. B. Pitombo & C. G. Fonseca, 15 Dec 1992, 22 specimens, det. S. M. Pinto Dec 1992.

MNRJ. 2251 and 2252—Brazil, Bahia, Abrolhos Archipelago (17°20′–18°10′S and 38°35′–39°20′W), Siriba island, coll. F. B. Pitombo & C. C. Ratto, 19 Dec 1993, 20 specimens, det. S. M. Pinto Dec 1993.

MNRJ. 2109—Cuba, La Habana, Playa, Playa Jaimanitas, coll. A. Herrera, 26 Aug 1992, 4 specimens, det. M. J. C. Belém Feb 1994.

MNRJ. 2110—Cuba, Recife de Punta del Este, Isla de Juventud, coll. A Herrera, 26 Aug 1992, 4 specimens, det. M. J. C. Belém Dec 1992.

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Additions to the cancellariid (Mollusca: Neogastropoda) fauna of South Africa

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Abstract.—Four new species of Cancellariidae are described from the continental shelf and upper continental slope off eastern South Africa. *Admetula afra* is distinguished from all congeners by its combination of small adult size (<11 mm), rounded shoulder, evenly reticulate sculpture, and distinct varix at the juncture of protoconch and teleoconch. *Trigonostoma kilburni* differs from all other *Trigonostoma* in its distinctive shell outline, unornamented peripheral keel, rounded rather than tabulate shoulder, and very narrow umbilicus. *Nipponaphera wallacei* differs from *N. paucicostata* (Sowerby, 1894), its geographically closest congener from the Arabian Sea area, in being umbilicate and in having a more rounded shoulder, and more numerous and finer spiral cords. Its frequent association with the turbinid *Bolma andersoni* suggests that it may be an ectoparasite of this species. *Zeadmete verheckeni* is most similar to *Zeadmete subantarctica* Powell, 1933, from off New Zealand, from which it can be distinguished by its lower spire and weaker surface sculpture. Among the South African taxa, *Z. verheckeni* most closely resembles "*Cancellaria*" *eutrios* Barnard, 1959, from which it is easily distinguished by its tabulate shoulder and lower spire. The geographic and bathymetric ranges of *Admetula epula* Petit & Harasewych, 1991, a species previously known only from "ex pisces" material, have been expanded based on live-collected specimens.

The Cancellariidae comprises a family of diverse and highly specialized, suctorial neogastropods that inhabit soft bottom, subtidal to bathyal habitats throughout tropical and temperate seas. The cancellariid fauna of South Africa was reviewed comprehensively by Barnard (1959) and Kensley (1973), and to a limited extent more recently in popular works by Richards (1981) and Steyn & Lussi (1998).

This paper describes four new species of cancellariids collected in South African waters by SCUBA and by the vessels R/V *Meiring Naudé* (1984–1988) and NMPD *Africana* (1995). These species are assigned to the genera *Admetula, Trigonostoma, Nipponaphera,* and *Zeadmete*. The new taxa are compared to related species from the Indian Ocean, New Zealand, and Australia.

All type specimens are housed in the collections of the Natal Museum (NM), Pietermaritzburg, Republic of South Africa.

Family Cancellariidae Forbes & Hanley, 1851

Genus *Admetula* Cossmann, 1889

Type species: Cancellaria evulsa (Solander, 1766) (=*Buccinum evulsum* Solander, 1766) by original designation.

Admetula epula Petit & Harasewych, 1991
Figs. 1–2, 18

Admetula epula Petit & Harasewych, 1991:181, figs. 1–3.

Diagnosis.—A small species with an ovately conical shell. Transition from protoconch to teleoconch gradual, indicated by appearance first of spiral, then axial sculpture. Teleoconch sculpture of strong spiral cords and less pronounced, rounded axial ribs. Outer lip thin, smooth within.

Gross anatomy.—Preserved animal yellowish tan, foot long, narrow, tapering posteriorly. Mantle cavity spanning 0.67 whorl. Osphradium slightly broader than ctenidium. Pericardium very small. Tentacles symmetrical, bluntly cylindrical, flanking central rostrum. Eyes small, black. Proboscis short, about 0.67 length of mantle cavity. Buccal mass large, nearly filling retracted proboscis. Salivary glands and accessory salivary glands in cephalic haemocoel, not contained within proboscis. Penis long, narrow, dorsoventrally compressed, distal end bluntly rounded.

Remarks.—This species was originally described based on seven specimens taken from the stomachs of fish. Its bathymetric range was inferred to overlap with that of *Congiopodus spinifer* (Smith) (55–146 m), one of the fish from which it was taken. Among the material collected by the NMPD *Africana* [sta. A17419D] was a live collected specimen of *A. epula* (Figs. 1–2, 18) trawled at a depth of 210 m off the mouth of the Tsitsikamma River.

We have examined a specimen of *Admetula* from deeper water (450–500 m) off the Mbashe River, Transkei (R/V *Meiring Naudé* sta. Q14), between the type localities of *A. epula* and the new species. This specimen (NM C9050) is too worn for the transition from protoconch to teleoconch to be clearly discerned, but there is no indication of a pronounced varix. Because it also has secondary spiral cords between all primary cords, this specimen is tentatively identified as *A. epula.* This record expands the geographic range of *A. epula* from Cape St. Blaize to Transkei, off of the mouth of the Mbashe River (32°22.8′S, 29°00.8′E). The bathymetric range is extended well into the bathyal zone (450 m).

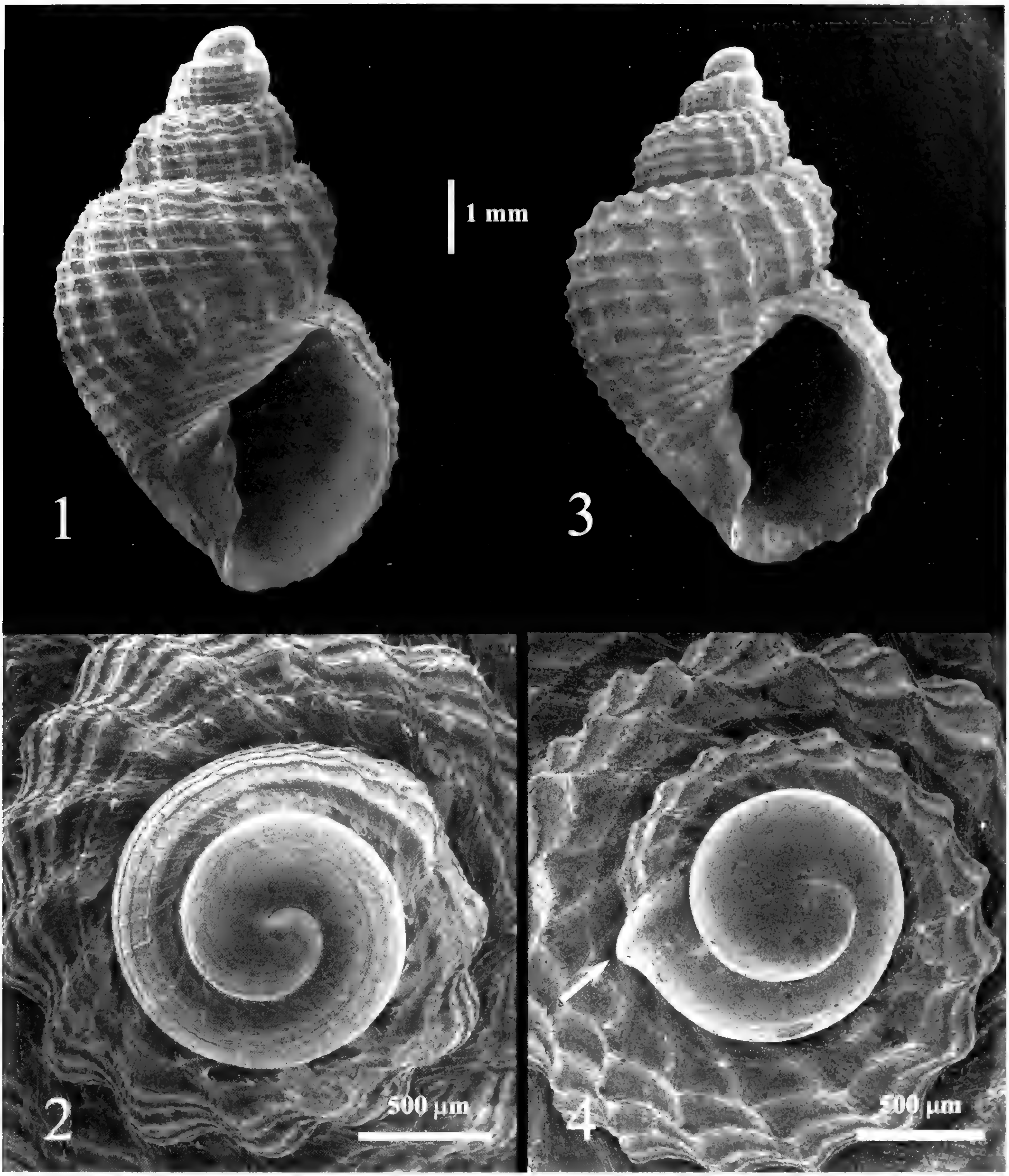
Admetula afra, new species
Figs. 3–4, 18

Diagnosis.—A small species with a broadly conical shell. Protoconch demarcated from teleoconch by broad, rounded varix. Teleoconch with sharply reticulated sculpture. Outer lip reflected posteriorly, with weak lirae beneath spiral cords.

Description.—Shell (Fig. 3) small, reaching 9.0 mm, ovately conical with rounded anterior. Protoconch (Fig. 4) of 1.67 smooth, inflated whorls deflected from coiling axis of teleoconch by about 7°. Transition to teleoconch (Fig. 4, arrow) demarcated by prominently rounded varix, followed immediately by onset of both spiral and axial sculpture. Teleoconch of 2.75–3 evenly rounded whorls. Suture weakly impressed. Shoulder rounded, weakly defined. Axial sculpture consists of narrow, regularly spaced, weakly prosocline ribs (14–16 on body whorl). Spiral sculpture of narrow, sharply defined primary cords (12–13 on body whorl, 6 on penultimate whorl). Single, weak, secondary cords may be present between primary cords on posterior half of body whorl. Spiral and axial sculpture intersect to form sharply reticulated pattern with small nodes at intersections of ribs and cords. Aperture broadly ovate, deflected from coiling axis by 16–19°. Outer lip thin, slightly flared posteriorly, weakly lirate beneath spiral cords. Parietal callus thin, translucent, overlying 5–6 spiral cords from previous whorl. Columella forming angle of 128–130° with parietal region, thick, straight, with two weak columellar folds and broad siphonal fold. Siphonal canal shallow but well-defined. Shell color white.

Type locality.—SE of Port Durnford, South Africa (29°01.5′S, 32°11.8′E), dredged in 310–320 m, glutinous sandy mud. R/V *Meiring Naudé* sta. ZQ9, 6 Jul 1985.

Type material.—Holotype, NM E3189/T1382, 8.0 mm; Paratype 1, 7.8 mm, and Paratype 2, 6.9 mm, NM V7006/T1383 from the type locality; Paratype 3, 9.0 mm, NM E3764, from off Cape Vidal (28°08.4′S,



Figs. 1–4. 1–2; *Admetula epula* Petit & Harasewych, 1991. Off Tsitsikamma River, South Africa (34°45′S, 24°47′E) in 210 m, sand, old shell grit and shell debris. NMPD *Africana* sta. A17419D. 1. Apertural view of shell. 2. Apical view of protoconch. 3–4. *Admetula afra* new species. Holotype, NM E3189/T1382, SE of Port Durnford, South Africa (29°01.5′S, 32°11.8′E), dredged in 310–320 m, glutinous sandy mud. R/V *Meiring Naudé* sta. ZQ9, 6 Jul 1985. 3. Apertural view of holotype. 4. Apical view of protoconch.

32°36.4′E), dredged in 165 m, moderately fine sand, R/V *Meiring Naudé* sta. ZM8, 11 June 1988.

Etymology.—Feminine form of the Latin *afer,* African.

Comparative remarks.—This new species appears most closely related to the more southern *Admetula epula* Petit & Harasewych, 1991, from which it differs in having uniformly rectangular sculpture formed by equally-sized axial ribs and spiral cords, and a posteriorly reflected outer lip with weak denticles beneath the spiral cords. The most striking difference between these two species is the presence of a strong varix at the termination of the protoconch in *A. afra.* In contrast, the transition from protoconch to teleoconch is indistinct and gradual in *Admetula epula.*

Genus *Trigonostoma* Blainville, 1827

Type species: Delphinula trigonostoma Lamarck, 1822 (?=*Buccinum scalare* Gmelin, 1791) by monotypy.

Trigonostoma kilburni, new species

Figs. 5–10, 18

Diagnosis.—A small species with a thin, angular, narrowly umbilicate shell. Shoulder rounded, not tabulate, lacking pronounced spines. Axial sculpture of numerous scabrous varices. Outer lip smooth, lacking lirae.

Description.—Shell (Fig. 5) small, reaching 14.3 mm, thin, angular, biconical, strongly shouldered, with deep, narrow umbilicus. Spire high (spire angle 55°), comprising over half of shell length. Protoconch (Figs. 6–7) of 2 smooth whorls, offset from coiling axis of shell by about 5°. Transition to teleoconch abrupt, marked by a slightly flared varix and the onset of spiral sculpture. Teleoconch of up to 5 sharply angular whorls. Suture deeply impressed behind the evenly rounded shoulder delineated by a sharp keel along the periphery of the shell. Axial sculpture consists of numerous, flared, weakly prosocline varices (Fig. 8), regularly spaced on early whorls (about 16–18 on first teleoconch whorl), increasing in number and becoming more irregularly spaced in subsequent whorls. Spiral sculpture of broad, crisply demarcated primary spiral cords (Fig. 8, p), with 1–3 slightly narrower secondary cords (Fig. 8, s) between adjacent primary cords, and much finer spiral threads (Fig. 8, t) between some cords. Aperture roundly triangular, deflected from coiling axis by 18–19°. Siphonal canal short, broad, barely discernible except externally as the siphonal fasciole. Outer lip thin, smooth within, slightly reflected with spiral cords visible through edge of lip. Posterior portion of inner lip adpressed against siphonal fasciole. Short parietal region forms angle of 150° with long, slightly concave columella that bears 2 weak, widely spaced columellar folds and 1 siphonal fold. Umbilicus deep, narrow. Shell white, sometimes with a yellowish cast.

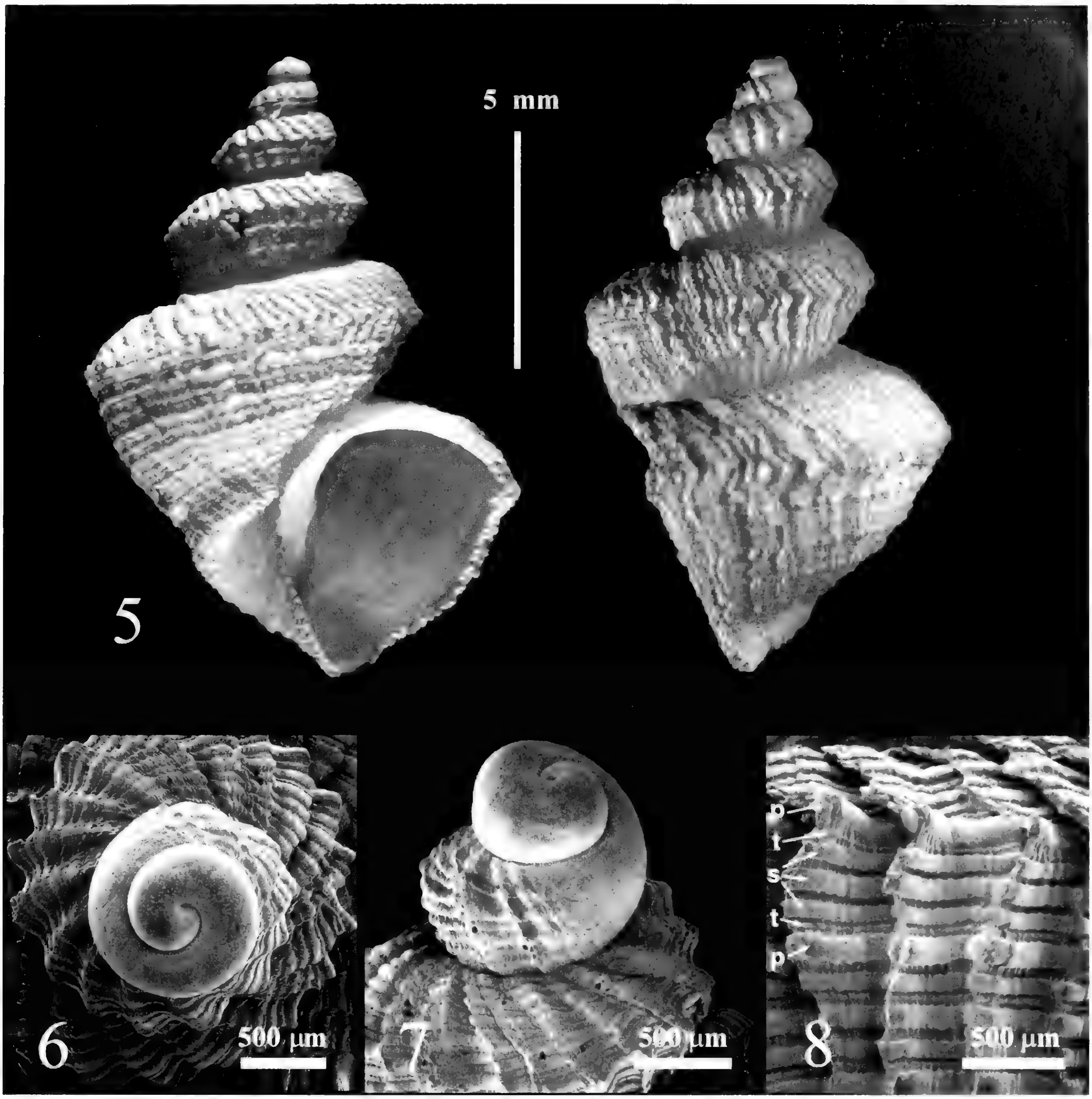
Radular teeth (Figs. 9–10) extremely long, ribbon-like, tricuspid. Central cusp smooth, with recurved rim. Lateral cusps long, folded toward central cusp, each with four, anteriorly directed secondary cusps. Second most proximal secondary cusp bifid.

Type locality.—Off East London, South Africa (33°04.7′S, 28°07.2′E) dredged in 90 m, associated with coarse sand, sponges, gorgonians. R/V *Meiring Naudé* sta. XX46, 17 Jul 1984.

Type material.—Holotype, NM D679, 12.9 mm, from type locality. Paratype, NM D680, 14.4 mm, off Kidd's Beach, South Africa (33°11.8′S, 28°03.2′E) dredged in 90 m, associated with coarse sand, sponges. R/V *Meiring Naudé* sta. XX50, 17 Jul 1984.

Etymology.—This species honors Dr. Richard N. Kilburn, Natal Museum, Pietermaritzburg, Republic of South Africa, for his many contributions to malacology.

Comparative remarks.—This new species differs from all other *Trigonostoma* in its distinctive shell outline. It may be distinguished from *Trigonostoma scalare* (Gmelin, 1791) and *T. thysthlon* (Petit & Harasewych, 1987) by its unornamented peripheral keel, its rounded rather than tabulate shoulder, and by its very narrow umbilicus. The only other South African *Trigonostoma* is the common shallow-water *T. semidisjuncta* (Sowerby, 1849), which has a heavier, more rounded shell with strong spiral cords.



Figs. 5–8. *Trigonostoma kilburni* new species. Holotype, NM D679, Off east London, South Africa (33°04.7′S, 28°07.2′E), dredged in 90 m, coarse sand, sponges, gorgonians. R/V *Meiring Naudé* sta. XX46, 17 Jul 1984. 5. Apertural and lateral views of holotype. 6. Apical and 7. Lateral views of protoconch. 8. Detail of surface sculpture on body whorl. p, primary spiral cords; s, secondary spiral cords; t, spiral threads.

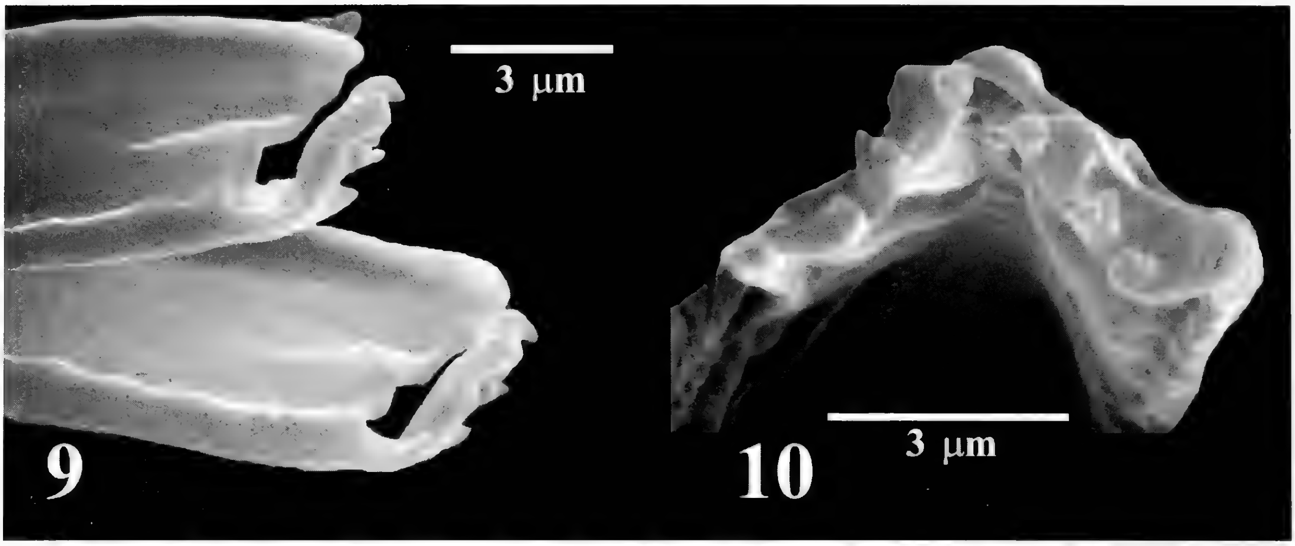
Genus *Nipponaphera* Habe, 1961

Type species: Nipponaphera habei Petit, 1972 by I.C.Z.N. Opinion 1052.

Nipponaphera wallacei new species
Figs. 11–13, 16

Diagnosis.—A small species with a heavy, strongly sculptured, narrowly umbilicate shell. Aperture sharply triangular, outer lip with strong teeth along inner edge of varix. Columella with two prominent, sharply keeled columellar folds and a strongly reflected siphonal fold.

Description.—Shell (Fig. 11) small for genus, to 12.4 mm, ovately conical, with rounded anterior. Spire relatively short (spire angle 70°), comprising less than half of shell length. Protoconch (Fig. 13) of 1.67 smooth, inflated whorls. Transition to teleoconch marked by onset of spiral cords followed immediately by strong axial ribs. Te-



Figs. 9–10. *Trigonostoma kilburni* new species. Distal ends of radular teeth of holotype. 9. Lateral view. 10. End-on view.

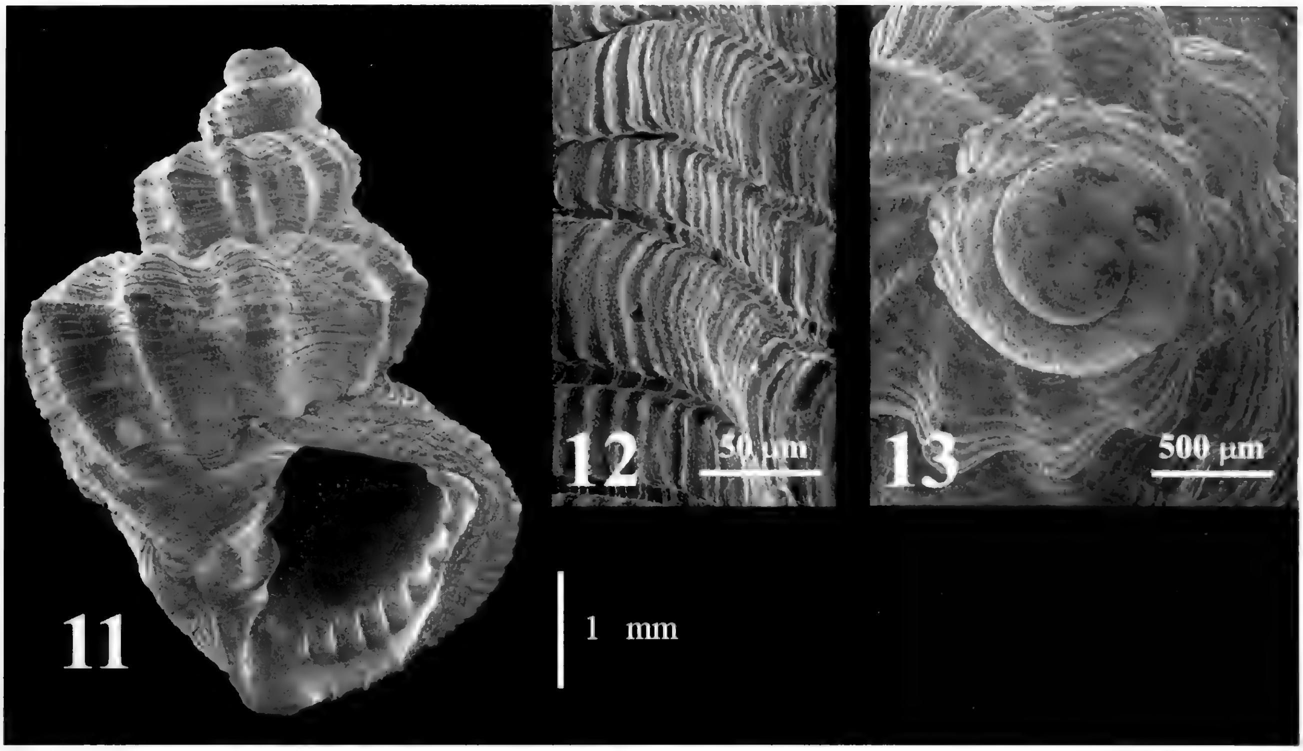
leoconch of up to 4 angular whorls. Suture impressed behind sloping shoulder that is delineated by peripheral keel. Axial sculpture of strong, broad, prosocline ribs (10 on penultimate whorl) that become more widely spaced on body whorl where they appear as varices with flared edges. Spiral sculpture of broad, flattish primary cords, 3 secondary cords between adjacent primary cords, with fine threads between some cords. Aperture sharply triangular, deflected from coiling axis by 20°. Siphonal canal short, well-defined. Outer lip reflected anteriorly, with spiral sculpture visible through thin edge, 9 strong teeth along inner edge of varix, small, angular indentation at shoulder. Parietal region short, columella straight, with small, thin callus, 2 sharply keeled columellar folds and strongly reflected siphonal fold. Umbilicus narrow, inconspicuous, bordered by well-developed, cord-like siphonal fasciole. Shell color chestnut brown, with lighter spiral bands along shoulder and middle of body whorl.

Type locality.—Off Phumula, Natal, South Africa, in 45 m, on reef. Jun 1997.

Type material.—Holotype, NM V4689, 6.6 mm, from type locality. Paratype 1, NM V3889, Off Phumula, Natal, South Africa, in 35 m, taken by SCUBA, living on shell of *Bolma andersoni* (E. A. Smith, 1902). 4 Sep 1996. Paratype 2, NM V303, 12.4 mm, Off Park Rynie, Natal, South Africa, in 53 m. Taken by SCUBA, living on the spire of the turbinid gastropod *Bolma andersoni.* 19 May 1990.

Etymology.—This species is named for Mr. Martin Wallace, who collected the type material and generously made it available for study.

Comparative remarks.—The genus *Nipponaphera* is distinguished from *Trigonostoma* primarily by the presence, in the latter, of an open umbilicus that extends back to the protoconch. Also, *Nipponaphera* has a wide and flat siphonal fold. Although the new species here described has an umbilicus, it is not profound. It differs from *N. paucicostata* (Sowerby, 1894) of the Arabian Sea area in being umbilicate, in having a more rounded shoulder, and more and finer spiral cords. Specimens of *N. paucicostata* figured by Verhecken (1986, Figs. 4–6) lack varix-like axial ribs on the body whorl, but the type specimen has very strong, unevenly spaced ribs on the body whorl. The Japanese *N. teramachii* (Habe, 1961) has a sharp keel, is umbilicate, with a cord-like siphonal fasciole, but lacks the squarish, finely imbricated spiral sculpture of this new species. Melvill and Standen (1901:451) reported *N. paucicostata* from the Gulf of Aden "adhering to the upper



Figs. 11–13. *Nipponaphera wallacei* new species. Holotype, NM V4689, Off Phumula, Natal, South Africa, SCUBA in 45 m, on reef. Jun 1997. 11. Apertural view of holotype. 12. Detail of sculpture on body whorl. 13. Apical view of protoconch.

part of *Rapana bulbosa,* 30–50 fathoms." The alimentary system of cancellariids is adapted to feed on body fluids of prey/host organisms (Petit & Harasewych, 1986; Harasewych & Petit, 1986). The association of species of *Nipponaphera* with other gastropods suggests that this group of cancellariids may be specialized ectoparasites of large gastropods.

Genus *Zeadmete* Finlay, 1926

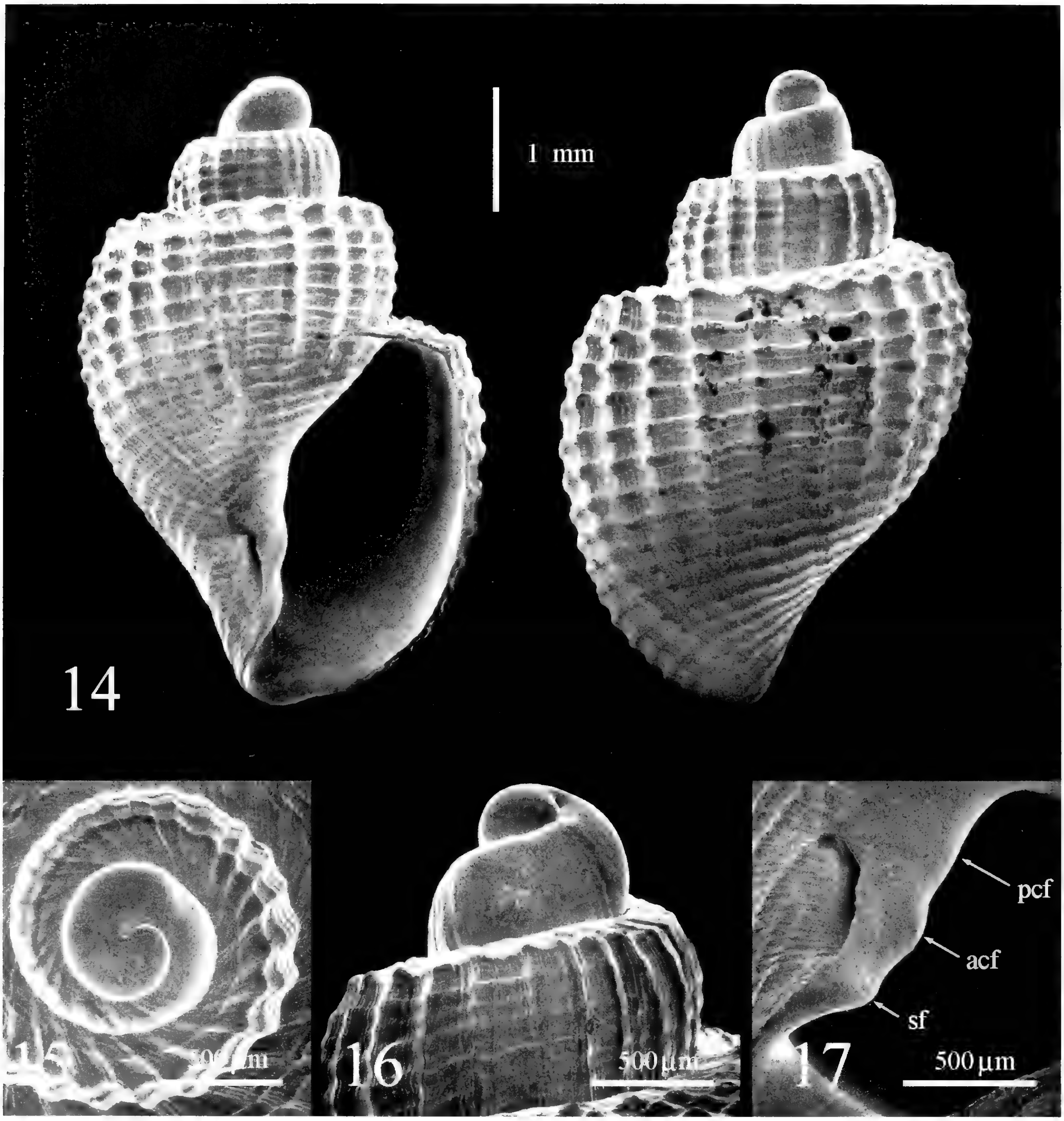
Type species: Cancellaria trailli Hutton, 1973 by original designation.

Zeadmete verheckeni, new species
Figs. 14–18

Diagnosis.—A small species with an ovate shell. Shoulder tabulate. Surface sculpture dominated by spiral cords. Pseudo-umbilicus narrow. Outer lip thin, smooth within. Buccal mass minute. Radula absent.

Description.—Shell (Fig. 14) small, reaching 7.9 mm, thin, with stepped spire, rounded anterior. Protoconch (Figs. 15–16) erect, smooth, of 1.5 whorls. Transition to teleoconch abrupt, marked by onset of weak, closely-spaced axial ribs that become stronger, more regularly spaced, when spiral cords first appear within 0.25 whorl. Teleoconch of 2 rounded, strongly tabulate whorls. Suture strongly impressed. Axial sculpture of evenly spaced, well-defined, axially aligned ribs (30 on body whorl) as broad as intervening spaces. Spiral sculpture of sharply demarcated evenly spaced cords (2 between suture and shoulder, 17 below shoulder) diminishing in strength abapically, forming small nodules as they cross axial ribs. Aperture elongated, narrowly elliptical. Outer lip faintly sinuate, smooth within. Columella with two broad, weak, columellar folds (Fig. 17, pcf, acf) and siphonal fold (Fig. 17, sf). Siphonal canal small but distinct, axially aligned, not forming siphonal fasciole. Anterior portion of inductura bordered by weak parietal wash, partially covering narrow pseudo-umbilicus. Shell color white. Periostracum thin, finely lamellate, straw-colored.

Preserved animal white, with short, narrow, posteriorly rounded foot. Tentacles tu-



Figs. 14–17. *Zeadmete verheckeni* new species. Holotype, NM C6800, Off Stony Point, Transkei, South Africa (32°37.5′S, 28°45.8′E), dredged in 390–400 m, muddy sand, small stones. R/V *Meiring Naudé* sta. V11, 12 Jul 1984. 14. Apertural and dorsal views of holotype. 15. Apical and 16. Lateral views of protoconch. 17. Columella. pcf, posterior columellar fold; acf, anterior columellar fold; sf, siphonal fold.

bular, symmetrical, with very large black eyes at their bases. Penis long, narrow, dorso-ventrally flattened, with small terminal papilla. Osphradium very broad, strongly asymmetrical, dorsal leaflets twice as broad as ventral leaflets. Ctenidium less than half as wide and twice as long as osphradium. Hypobranchial gland large, glandular. Retracted proboscis occupies anterior two-thirds of cephalic haemocoel, the rest occupied by long, convoluted mid-esophagus. Proboscis strongly coiled within proboscis sheath. Extended proboscis likely exceeds shell length. Proboscis thin, with minute buccal mass in anteriormost 0.125 of proboscis. Radula absent.

Type locality.—Off Stony Point, Transkei, South Africa (32°37.5′S, 28°45.8′E),

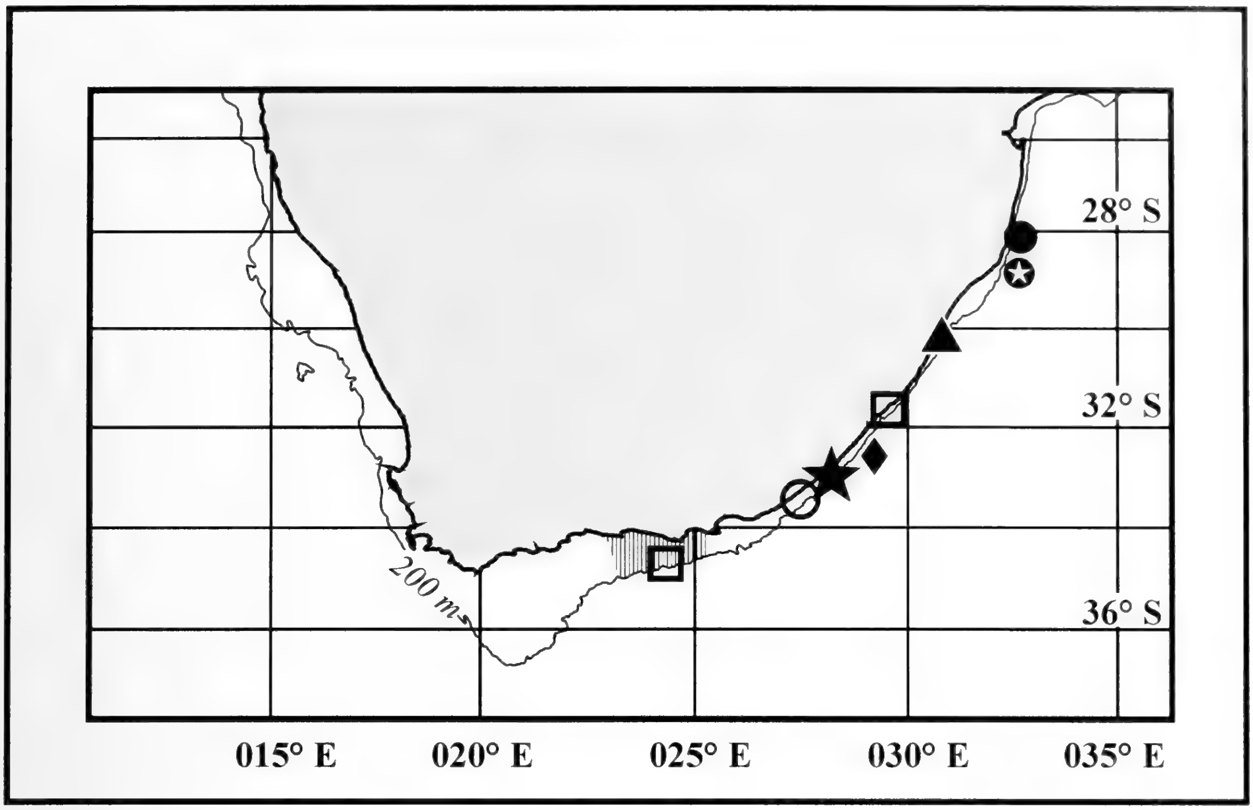


Fig. 18. Geographic distributions of South African Cancellariidae. *Admetula epula* Petit & Harasewych, 1991, vertically hatched area = type locality; open squares = new records. *Admetula afra* new species, star in circle = type locality; filled circle = additional record. *Trigonostoma kilburni* new species, black star = type locality; open circle = additional record. *Nipponaphera wallacei* new species, triangle = type locality. *Zeadmete verheckeni* new species, diamond = type locality.

dredged in 390–400 m, muddy sand, small stones. R/V *Meiring Naudé* sta. V11, 12 Jul 1984.

Type material.—Holotype, NM C6800, 5.1 mm, from type locality.

Etymology.—Named for Mr. André Verhecken, Mortsel, Belgium, in recognition of his contributions to the study of the Cancellariidae.

Comparative remarks.—Placement of this new species in the genus *Zeadmete* is tentative. *Zeadmete verheckeni* is conchologically most similar to a group of species from off the southern coasts of New Zealand and Australia that have been assigned to the genera *Oamaruia* Finlay, 1924 and *Zeadmete* Finlay, 1926. Powell (1979:224) treated *Zeadmete* as a subgenus of *Oamaruia.* Several New Zealand and Australian species presently assigned to *Zeadmete* agree with this South African species in shell form and sculpture (see Garrard 1975, Powell 1979). *Zeadmete subantarctica* Powell, 1933, from 50 fathoms off Snares Islands, New Zealand, has the same shell shape and columellar structure as *Z. verheckeni* but has deeply cancellated sculpture on the posterior half of the body whorl and only spiral cords on the anterior portion.

In the course of a study on Australian cancellariids, we found that the abyssal *Zeadmete kulanda* Garrard, 1975 has a radula similar to that of *Nothoadmete tumida* (Oliver, 1982:figs. 3, 5). The fact that no radula was found in *Z. verheckeni* argues against these species being congeneric. However, we are reluctant to introduce another genus-level taxon until more data on the species with this shell form are available. The problems of generic placement of small, deep-water cancellariids was briefly discussed by Verhecken (1997:296).

Among the South African taxa, this species most closely resembles "*Cancellaria*"*eutrios* Barnard, 1959, from which it is easily distinguished by its tabulate shoulder and lower spire.

Acknowledgments

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Erpobdella lahontana (Annelida: Hirudinea: Arhynchobdellida: Erpobdellidae), a new species of freshwater leech from North America

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Abstract.—new species of a leech, *Erpobdella lahontana,* is described from the Lahontan Basin in California and Nevada of the western United States. This species has four pairs of eyes, the preatrial loops of male paired ducts extend to ganglion XI, and the male and female gonopores are located in furrows of the annuli, separated by five annuli.

The zoological history of the Great Basin of the western United States has resulted in an area of high endemism of fishes (Hubbs & Miller 1948) and hydrobiid snails (Hershler 1998). However, amphibians have not morphologically evolved into endemics and may be the result of very recent immigration to the region (Hovingh 1997).

A general survey of the Great Basin and adjacent regions of the western United States was undertaken to determine if leeches had drainage specific distributions. Over 2300 aquatic sites were surveyed in the Great Basin including some 600 sites within the Lahontan Basin. Leeches show an entirely different pattern than fishes, hydrobiid snails, and amphibians with respect to basin specific distribution without morphological evolution, suggesting evolutionary stasis and an inhabitant of the Great Basin since its geological formation in the Miocene (Hovingh, unpublished data). Within this study, an erpobdellid leech was identified with the gonopores separated by five annuli. This leech was found in two separate drainages of the Honey Lake Subbasin (Eagle Lake and one other location out of the 2300 sites in the survey) in the Lahontan Basin of northeastern California. This paper describes this new leech species and is the first endemic species of leech to be found in the Great Basin.

Materials and Methods

Collection methods consisted of examining the underside of substrates such as rocks, logs, and anthropogenic debris in the periphery of aquatic systems (i.e., springs, streams, and lakes) up to 100 cm deep. Leeches were relaxed with dilute ethanol, wiped clean of mucous, fixed in 10% formalin overnight, and preserved in 70% ethanol. Histological examination of serial sections of the clitellum region, after staining with hematoxylin and eosin, was used for detailed morphological analysis of the genital atrium, cornua, and preatrial loops of the ejaculatory ducts. A model of the genital atrium, cornua, and preatrial loops was constructed from photographs taken of the serial sections.

Systematics

Family Erpobdellidae Blanchard, 1894
Genus *Erpobdella* Blainville, 1918
Erpobdella lahontana, new species

Type material.—Holotype, United States National Museum (USNM 186409) and 8 paratypes (USNM 186410), deposited in the National Museum of Natural History, Division of Worms, Smithsonian Institution, Washington, D.C., collected 15 Sep 1997, same locality.

Type locality.—Eagle Lake, Lassen County, California; latitude 40°33.5′N and longitude 120°48.8′W (selected by the abundance of leeches at this locality and public access to the lake).

Diagnosis.—Dorsal surface dark gray, heavily mottled with light gray spots; white or yellow irregular minute, transverse rows of papillae on the dorsal side of every annulus with some living specimens having prominent papillae on both dorsal and ventral sides; dorsum with a light black middorsal stripe or plain; five-annulate, each annulus of approximately equal size; four pairs of eyes: first pair of labial eyes large, second pair of smaller labial eyes behind first pair; buccal eyes two pairs, small; male and female gonopores separated by five annuli, located in furrows of segments XII and XIII and male gonopore large, raised, and especially glandular (Fig. 1); atrium with cornua (horns), with sperm ducts forming paired preatrial loops extending anteriorly to ganglion XI (Figs. 2, 3). Preatrial loops angle laterally and anteriorly from cornua. Cornua and preatrial loops dip ventrally to join each other. Ovisacs extend posteriorly to ganglion XV. Five annuli separate the segmental ganglia.

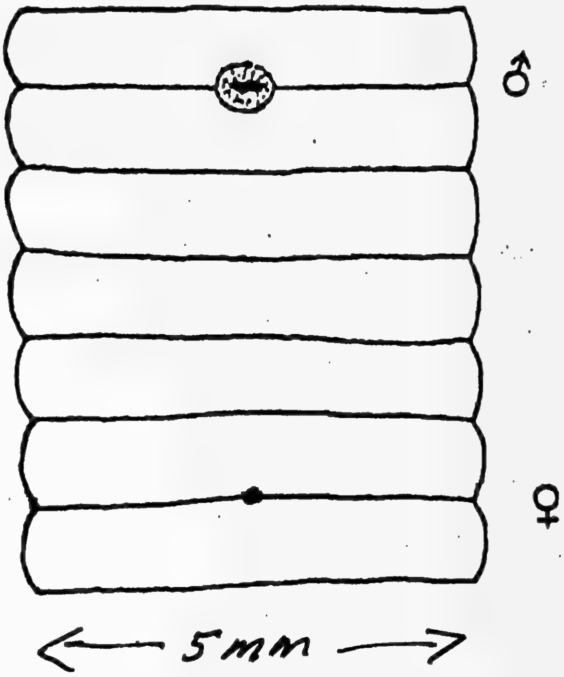

Fig. 1. *Erpobdella lahontana.* Ventral view, male and female gonopores (holotype).

Description of Holotype

External anatomy.—(based on holotype, USNM 186409): Body elongate, flattened, sides of body narrowing along most of length to pointed head (length 30 mm, maximum width 3 mm); body wall uniformly smoke-gray, dorsal surface darker gray than ventral surface, dorsal surface with a faint middorsal dark line, no black pigmentation; dorsal surface dark gray, heavily mottled with light gray spots; somites five-annulate; white irregular minute, transverse rows of papillae on every annulus; clitellum conspicuous, 15 annulate; nephridiopores on b_2 annulus of XI and XII (other nephridiophores not determined); mouth small (width of oral sucker 1 mm); eyes four pair, one large labial pair, second pair of small labial eyes behind first pair and two smaller buccal pairs on fourth annulus (further posterior); anus surrounded by papillae, located dorsally at the base of the caudal sucker; caudal sucker small (width 2 mm), less than one-half maximum body width; male gonopore large, raised, cylindrical and glandular, (Fig. 1) located in furrow of the clitellum region between annuli XIIb$_1$ and XIIb$_2$; distance from mouth to male gonopore, 14 mm; female gonopore inconspicuous, located in furrow between annuli XIIIb$_1$ and XIIIb$_2$.

Internal anatomy.—(based on dissection of paratypes): Atrium wider than long; atrial horns projecting anteriorly; preatrial loops of vas deferens extending to ganglion XI; ovisacs extend from segments XIII to XV.

Additional observations of paratypes (USNM 186410).—External anatomy. Paratypes resemble the holotype with the following additional observations: length

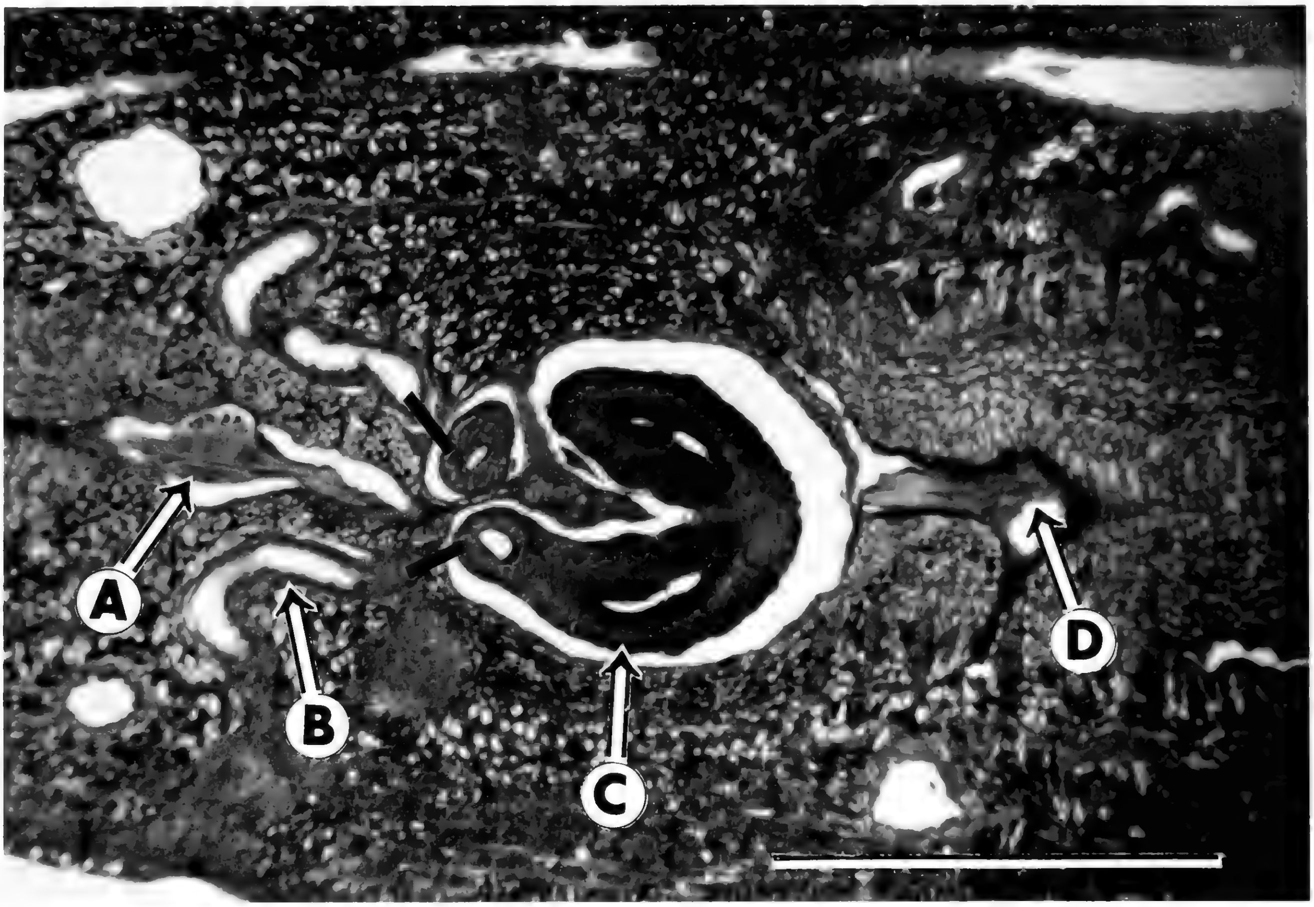

Fig. 2. Photograph of horizontal (parallel to dorsal and ventral surfaces) section of the region between Ganglion XI (denoted A) and Ganglion XII (denoted D) showing the preatrial loops (denoted B) and the genital atrium (denoted C) with cornua. The angle in which the preatrial loops join the cornua is indicated by short bars: 30° for the left side and 45° for the right side as viewed from the dorsum. Note that the right cornua displays an oval cross-section representing the section that has turned ventrally. Long bar = 1 mm.

(42–55 mm) and width (3.5–5 mm) of some individuals varies from the holotype; clitellum is inconspicuous in some individuals; female gonopore difficult to locate in some individuals; anus small to large in some paratypes.

Remarks.—The eyes in four pairs are arranged in two transverse rows; mouth with muscular ridges but no jaws; body segments (somites) five-annulate with all annuli of approximately equal in width. The structure of the reproductive system shows that this species belongs to the genus *Erpobdella* Blainville, 1918, with preatrial loops of the male paired ducts and testes in small, numerous bunched sacs.

Distribution, habitat, and ecology.—*Erpobdella lahontana* is found in two subbasins of the western Lahontan Basin (Fig. 4): Eagle Lake and Grasshopper Valley in Lassen County, California. The Pleistocene precursor of Eagle Lake and Grasshopper Valley (Madeline Plains) drained into Honey Lake Subbasin, the latter being an arm of Pleistocene Lake Lahontan. The new species was found in Buck Bay in the north part of Eagle Lake and along the south shore of Eagle Lake. In Eagle Lake, the leech was often found on vesicular basaltic rocks. When removing the leech, the posterior sucker would remain on the rocks. This occurred with five leeches after which sampling was from smoother artificial substrate. The leech was found in the outflow of springs in Grasshopper Valley. Elevations varied from 1555 to 1625 m above mean sea level (msl). Eagle Lake and, to a lesser extent, the Grasshopper Valley were associated with ponderosa pine (*Pinus ponderosa*) forest and both belong to the Mo-

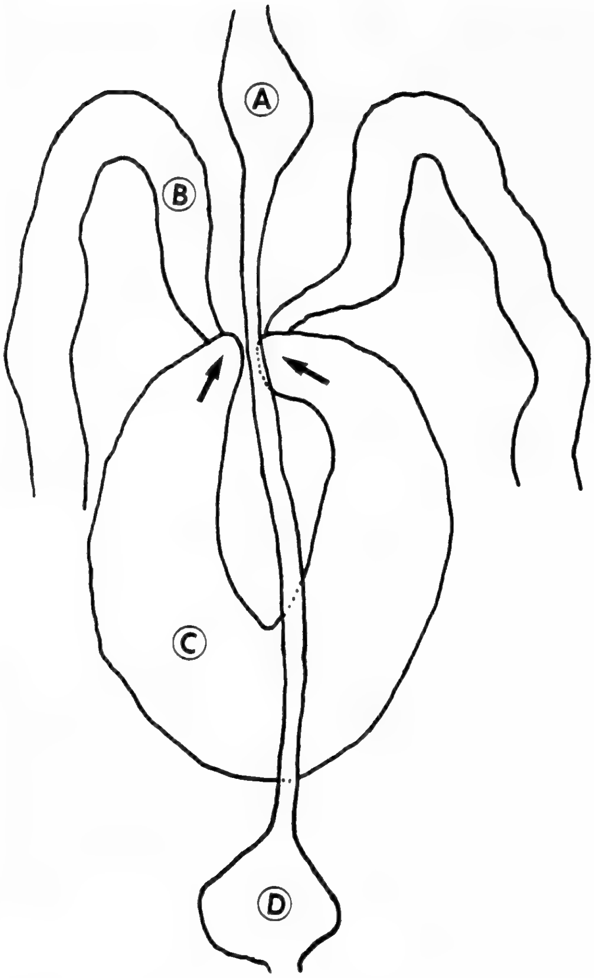

Fig. 3. Dorsal view of male genital atrium and ejaculatory ducts. Legend same as in Figure 2. Drawing made from a model constructed from photographs of serial sections of this region. The arrows denote where the cornua (paired horns) and the preatrial loops both turn ventrally before they are joined. The right cornua also makes a turn to the center.

doc Plateau geomorphic province, a region of numerous basalt-andesite flows which isolated these two basins from Honey Lake (Gester 1962). Eagle Lake (12,150 ha) has three subbasins of which two (north and central) basins do not stratify due to their shallow nature and strong winds. Conductivity of Eagle Lake is near 800 μMhos, probably as a result of the fact that 40% of Eagle Lake's inflow is derived from ground water (Huntsinger & Maslin 1976). Eagle Lake contains five species and Madeline Plains contains one species of native fish. The ecology of Eagle Lake is further described by Huntsinger & Maslin (1976). Two other locations in the Lahontan Basin (Winnemucca and Granite Springs Subbasins, east of Pyramid Lake, Nevada) contained leeches in which the gonopores were separated by five annuli, and these populations are still under investigation.

Associated leech species.—*Erpobdella lahontana* was associated with the leeches *Erpobdella punctata* (Leidy, 1870), *Helobdella stagnalis* (Linnaeus, 1758), and *Haemopis marmorata* (Say, 1824). In Grasshopper Valley, *H. marmorata* was associated with *E. lahontana.* Eagle Lake specimens at the National Museum of Natural History, Worm Division, include: *E. punctata* (USNM 42502, USNM 60061, USNM 60062), *Glossiphonia complanata* (USNM 2572), *Placobdella ornata* (USNM 60055), *Theromyzon trizonare* (USNM 42500), and *H. marmorata* (USNM 42570). The leech specimen (USNM 42571) was classified as *Dina fervida,* but this specimen is most likely *E. lahontana.* The gonopore separation was not unresolved, but the pigmentation and number of eyes suggested this species.

Variations.—All Eagle Lake specimens (22) were identical with respect to eyes and the number of annuli between gonopores. Some specimens contained dark annuli in which the papillae became conspicuous with an even darker dorsal strip, and this varied to uniform light color with invisible papillae and with no dorsal strip. Sizes of leech specimens were up to 55 mm long and 3.5 mm wide.

Similar species.—*Erpobdella lahontana* is distinguished from *E. dubia* (Moore & Meyer, 1951), *E. parva* (Moore, 1912), and *E. punctata* (Leidy, 1870) by the five annuli separating the gonopores. *Erpobdella dubia* (dorsum greenish, heavily mottled, usually with a variable dark mid-dorsal stripe; gonopores separated by 3.5–4 annuli) and *E. parva* (dorsum unpigmented or color uniformly smokey gray; gonopores separated by 2.5–3.5 annuli) have not been observed in the Great Basin collections with the gonopores separated by five annuli. If the gonopores are not distinguishable, the pigmentation patterns of *E. lahontana* could lead

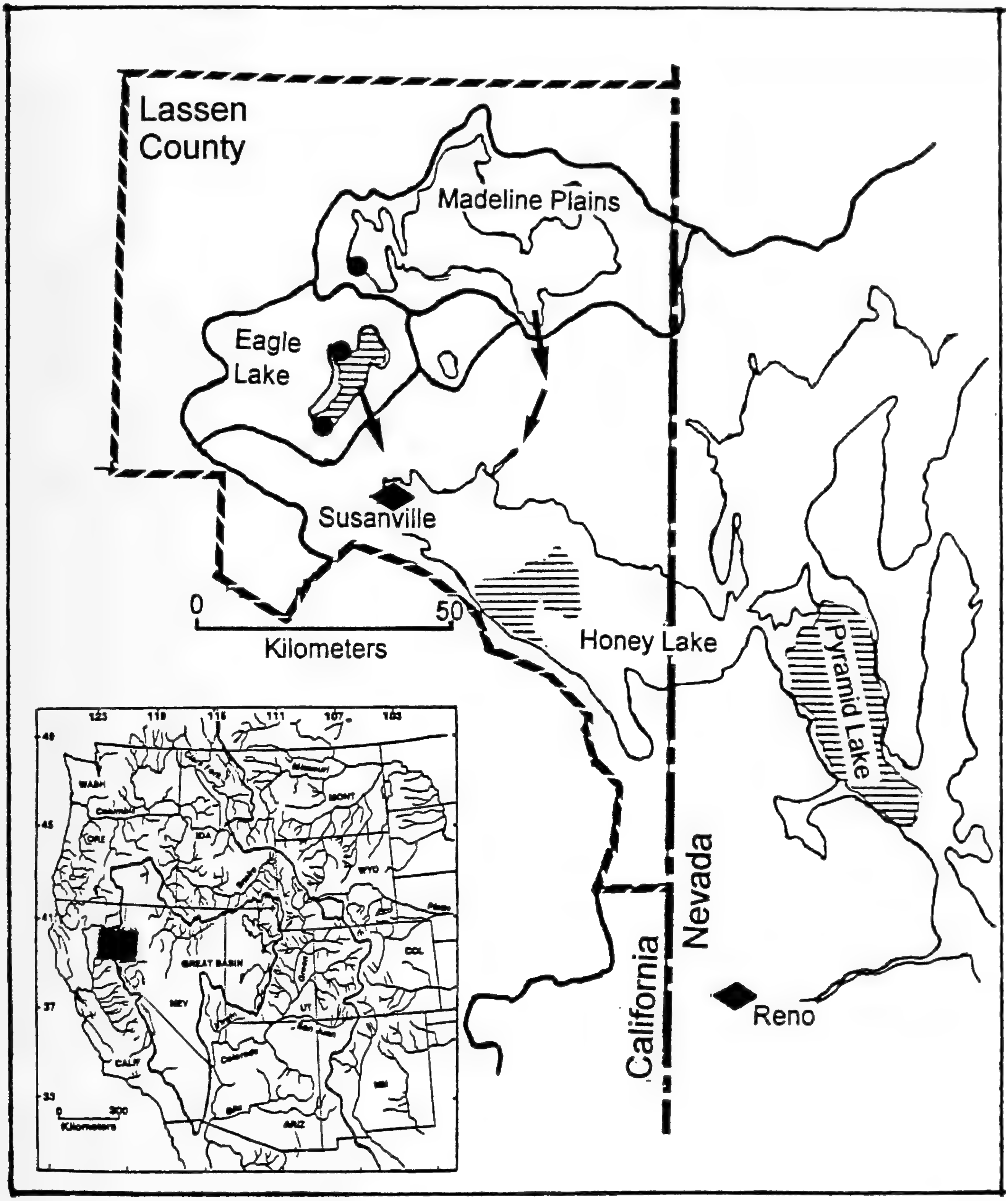

Fig. 4. Map of the western Lahontan Basin in California and Nevada. Lassen County is enclosed and the communities of Susanville, California and Reno, Nevada are designated by diamonds. The heavy solid line denotes the Lahontan Basin with arrows showing Pleistocene drainages from Eagle Lake and Madeline Plains Subbasins. The light solid line shows the extent of Pleistocene lakes with the patterned horizontal lines showing the present Eagle, Honey, and Pyramid Lakes. The three solid circles show location of *Erpobdella* lahontana in Eagle Lake and in Grasshopper Valley of the Madeline Plains Subbasin. Inset shows the locations in relation to the Great Basin and the western United States. Map derived from Snyder et al. (1964).

to some confusion with *E. dubia* and *E. parva,* neither of which has been found in the Lahontan Basin. *E. punctata* has been found in the Great Basin, but this species can be distinguished easily from *E. lahontana* by having only two annuli separating the male and female gonopores, and having three pairs of eyes. Taxonomic discussion and keys to the family Erpobdellidae and these North American species can be found in Sawyer (1972, 1986b), Klemm (1985, 1990, 1995) and Davies (1991).

Discussion

Similar species, *Erpobdella dubia* and *E. parva,* to the new species, *E. lahontana,* have been historically classified within the genus *Dina* (Soos 1963, 1966, 1968; Sawyer 1972, Klemm 1985, Davies 1991). The genus (or subgenus) *Dina* is identified by the fact that every fifth annulus (b_6) of a somite is distinctly wider or more broad than the other four annuli and is subdivided by a faint transverse furrow (Lukin 1976, Mann 1982, Sawyer 1986a, 1986b; Davies 1991, Nesemann 1995, Neubert & Nesemann 1995). Also, the genus *Dina* is reported from only the southern, western, and central areas of the Palaearctic region (Lukin 1976, Sawyer 1986b). Therefore, Sawyer (1986a, 1986b) revised the genus *Erpobdella* to include the two species of *Dina* from the Neartic region, including North America, based on the equal width of all the body annuli and distribution of *E. dubia* and *E. parva.* It was concluded that the genus *Dina* was not found in North America. This was later confirmed by Klemm (1990, 1995). The North America (Neartic region) genera *Nephelopsis, Mooreobdella,* and the Palearctic region genus *Dina* were grouped together by the feature that, of any five annuli of the body somites, there is one annulus that is distinctly wider than the other four annuli and usually subdivided by a faint transverse furrow (Mann 1962, Lukin 1976, Sawyer 1986b, Davies 1991). This anatomical feature was not seen in Great Basin species of Erpobdellidae. All the species of erpobdellids in North America have annuli of similar width.

Etymology.—Louis Armand de Lom d'Arce, Baron de Lahontan was a 17th century French explorer of the upper Mississippi River basin who suggested that the western continental flows drained into a saline lake and then into the ocean. Although Baron de Lahontan may never have entered the western drainages or the Great Basin, the large western basin, Lahontan Basin, within the Great Basin was named after the Baron (Cline 1963). The leech is, thus, named after the basin in which it is found.

The anatomical tradeoff in erpobdellid leeches having preatrial loops and having the gonopores separated by more annuli is that the preatrial loops and the cornua may become shorter. An evolutionary compensation would be for the cornua and the preatrial loop to form contortions. This may be what is happening in *Erpobdella lahontana* with the cornua and the preatrial loops both taking a ventral dip to their junction.

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A cladistic analysis of Sciomyzidae Fallén (Diptera)

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Abstract.—A preliminary cladistic analysis of adult characters is presented that illustrates the phylogenetic relationships among the genera of the family Sciomyzidae. The monophyly of Sciomyzidae is based primarily on larval characters: the habit of malacophagy and the presence of a serrate ventral arch that articulates with the lower margin of the mouth hooks. A reduction in the number of spermathecae, from three to two, is also likely to be a synapomorphy for Sciomyzidae. The analysis was done using Hennig86, and 37 morphological characters were arranged among 50 genera. After using successive weighting, six cladograms were produced, and from these a consensus cladogram was obtained. The subfamilies Salticellinae and Sciomyzinae are confirmed to be monophyletic, as are the tribes Sciomyzini and Tetanocerini. *Eutrichomelina* Steyskal, which has been placed in the tribe Sciomyzini, is transferred to the tribe Tetanocerini. The genus *Antichaeta* Haliday is confirmed to be in the tribe Tetanocerini. Illustrations of antenna and male terminalia are presented.

Among families of Acalyptrate Diptera, the Sciomyzidae Fallén (1820), more commonly known as marsh or snail-killing flies, are comparatively well studied, especially the biology of their immature stages (Berg & Knutson 1978, Ferrar 1987, Knutson 1987, Rozkošný 1997). Sciomyzid larvae are primarily parasitoids or predators on aquatic or terrestrial mollusks. This feeding proclivity may be of considerable importance to the biological control of certain parasitic, mostly tropical diseases, such as fascioliasis and schistosomiasis (Knutson 1976). The trematodes causing both diseases parasitize many of the same aquatic mollusks, as intermediate hosts, that are also fed upon by sciomyzid larvae.

Although the natural history and ecology and to a degree the descriptive taxonomy and cytology (Boyes et al. 1972) of the Sciomyzidae are relatively well known, no cladistic analysis at the generic level is available. As a step toward filling that void in our knowledge, this cladistic study was undertaken and is reported here. To provide perspective, we begin this report with a brief overview of the higher-level classification.

In the first comprehensive treatment of Palearctic Sciomyzidae, Hendel (1900) divided the family into two subfamilies: Sciomyzinae and Tetanocerinae. Hendel characterized these subfamilies by the proepisternal seta (present in Sciomyzinae, absent in Tetanocerinae) and the frontal vitta (well developed and shiny in most Tetanocerinae, absent or reduced in most Sciomyzinae).

Cresson (1920), in a study limited to the Nearctic fauna of Sciomyzidae, recognized Sciomyzinae, as characterized by Hendel, and described two additional subfamilies: Dryomyzinae and Euthycerinae. Cresson also proposed five tribes that were divided among two of the subfamilies as follows: (1) Sciomyzinae with Oidematopsini and Sciomyzini; and (2) Euthycerinae with

Chaetomacerini, Euthycerini, and Sepedontini.

Hendel (1924) published a key to the Palearctic genera and distinguished the genus *Tetanura* Fallén as a separate subfamily, Tetanurinae, based on the following combination of characters: arista subapical, forefemur bare, and ovipositor telescoped. In the same paper and within the subfamily Tetanocerinae, Hendel also proposed the tribe Salticellini for the genus *Salticella* Robineau-Desvoidy.

Over 30 years ago, Steyskal (1965) proposed a classification for the Sciomyzidae that has been the most extensive treatment for the family from the standpoint of higher categories. Steyskal's classification, which has been adopted by most subsequent workers (Knutson et al. 1976, Barnes 1979, Rozkošný & Elberg 1984, Knutson 1987, Barnes & Knutson 1989, McAlpine 1989), recognized five subfamilies: Huttonininae, Salticellinae, Helosciomyzinae, Phaeomyiinae, and Sciomyzinae. The subfamily Sciomyzinae included two tribes, Sciomyzini and Tetanocerini. Although Steyskal's characterization of Sciomyzidae did not identify apomorphic characters, he distinguished the family from related families by the following set of morphological characters: costal vein (C) without breaks; subcostal vein (Sc) complete, free from vein R_1; vein A_1 complete; oral vibrissae absent; postvertical setae divergent to parallel; midfemur bearing a seta on the anterior surface; and at least one tibia with a preapical seta (Knutson 1987, McAlpine 1989). The tribes Tetanocerini and Sciomyzini are distinguished by the presence (Sciomyzini) or absence (Tetanocerini) of a proepisternal seta.

Griffiths (1972), who incorporated many characters of the male genitalia in his higher level phylogenetic study, introduced the prefamily as a category between the superfamily and the family categories. Using this classificatory structure, the prefamily Sciomyzoinea comprises the families Coelopidae, Phaeomyiidae, Dryomyzidae, Sciomyzidae, Helosciomyzidae, Ropalomeridae, Sepsidae, Megamerinidae, and Cremifanidae. Griffiths' studies of Sciomyzidae were based on the following species: *Pherbellia guadrata* Steyskal, *Pherbellia griseola* (Fallén), *Sciomyza simplex* Fallén, *Pteromicra apicata* (Loew), *Elgiva sundewalli* Kloet & Hincks, and *Tetanocera robusta* (Loew). The family Sciomyzidae, as characterized by Griffiths (1972), includes Salticellinae + Sciomyzinae, and the family's monophyly is based primarily on the malacophagous habits of the larvae and the presence of a ventral arch in the cephalopharyngeal skeleton (Knutson et al. 1970, Barnes 1981, McAlpine 1989). The reduced number of spermathecae, from three to two, is likely to be another synapomorphy for the Sciomyzidae, although in Salticellinae, the number of spermathecae is four. We interpret the latter condition to be secondarily derived from two and to be an autapomorphy for the subfamily Salticellinae.

The subfamily Salticellinae has three species in two genera, the extant *Salticella* Robineau-Desvoidy and the fossil *Prosalticella* Hennig. The Sciomyzinae, which include 505 recent species, have 57, mostly widespread genera.

The purpose of this paper is to present a classification for the genera of Sciomyzidae sensu Griffiths that is based on a cladistic analysis of primarily morphological characters. Our analysis is intended more specifically to test the hypotheses that the subfamilies Salticellinae and Sciomyzinae and, within the latter subfamily, the tribes Sciomyzini and Tetanocerini are monophyletic.

Material and Methods

Fifty of the 57 genera belonging to the Salticellinae and Sciomyzinae were examined and analyzed (Appendix 1). The seven genera not examined are: *Ditaeniella* Sack, *Eulimnia* Tonnoir & Malloch, *Neodictya* Elberg, *Oligolimnia* Mayer, *Pseudomelina* Malloch, *Tetanoptera* Verbeke, and *Verbekaria* Knutson. We also studied a new genus and species from India, *Steyskalina picta*

Ghorpadé & Marinoni, that was recently described (Ghorpadé et al. 1999). Since it was virtually impossible to examine all species of each genus and suspecting that some genera may be polyphyletic (e.g., *Pherbellia* Robineau-Desvoidy with 81 species; *Sepedon* Latreille with 75 species; and *Tetanocera* Duméril with 49 species) the analysis was done with the type species serving as exemplars of each genus. The type species are always linked to the appropriate generic name.

Pelidnoptera, represented by *P. fuscipennis* (Meigen 1830), was used as the outgroup. This genus, which is in the family Phaeomyiidae (Griffiths 1972), was selected because it is morphologically similar and closely related, perhaps the sister group (Steyskal 1965, included it as a subfamily) of the Sciomyzidae. Its characters are directly comparable to those of Sciomyzidae. The family Helosciomyzidae (Griffiths 1972), represented by *Helosciomyza aliena* Malloch (1928); *Huttonina abrupta* Tonnoir & Malloch (1928); *Huttonina furcata* Tonnoir & Malloch (1928), and *Huttonina scutellaris* Tonnoir & Malloch (1928), was studied to further confirm the polarization of characters.

A matrix with 37 morphological characters of adults and one of the larval morphology was produced (Table 1). Autapomorphies for particular genera were not included in the analysis.

Multistate characters in the analysis were first treated as unordered (Carvalho 1989, Pape 1992, Marinoni & Carvalho 1993). The ordination of the characters was done in accordance with standard procedures for cladistic analysis (Wiley 1981). The polarization was done using the outgroup comparison (Watrous & Wheeler 1981, Wiley 1981, Brooks 1989).

The analysis was facilitated with the computer program Hennig86, version 1.5 (Farris 1988). To find cladograms supported by the most consistent characters, the following command sequence was used: "mhennig" (mh), "branch and swapping" (*) and "successive weighting" (xs w) (Carpenter 1988, Dietrich & McKamey 1995). The option "nelsen" (ne) was used to construct a strict, consensus cladogram (Pape 1992, Marinoni & Carvalho 1993).

Characters and Character States Used in the Analysis

The characters used in the analysis are listed and discussed in the same sequence as they appear in the cladogram (Figs. 323–324). The letters A and P represent the relative apomorphic (derived) and plesiomorphic (primitive) conditions respectively.

1a. Larval feeding behavior: P (0) feeding on Diplopoda; A (1) feeding as a parasitoid or predator on terrestrial or aquatic Mollusca.

This is one of just a few characters in the matrix that establishes the monophyly of Salticellinae + Sciomyzinae. The genus *Pelidnoptera* is a parasitoid on Diplopoda, and numerous larval characters distinguish it from the larvae of Sciomyzidae (Vala et al. 1990). Although malacophagy characterizes nearly all Sciomyzidae and is a synapomorphy for the family, there is at least one species, *Sepedonella nana* Verbeke, that feeds on oligochaetes (Vala et al 2000) as a secondary departure from the groundplan of the more basal clades of the family.

1b. Ventral arch in the larval cephalopharyngeal skeleton: P (0) absent; A (1) present.

The serrated ventral arch articulates with the ventral margin of the larval mouth hooks. This is the only larval structural character that is an autapomorphy for Salticellinae + Sciomyzinae and may be related with the malaphagous feeding behavior.

2. Number of spermathecae: P (0) three; A (1) two; A (2) four.

According to McAlpine (1989) the immediate ancestor of Muscomorpha had three sclerotized spermathecae. This is the basic number in the main sections of Muscomorpha: Aschiza, Schizophora, Acalyptratae, and Calyptratae. In *Pelidnoptera,* the

Table 1.—Matrix of taxa and character states.

	000 123	000 456	000 789	111 012	111 345	111 678	122 901	222 234	222 567	223 890	333 123	333 456	3 7
Pelidnoptera	001	010	001	000	000	000	000	000	000	000	000	000	0
Salticella	120	010	000	020	000	000	000	000	000	000	000	000	0
Sciomyza	110	120	110	101	000	000	000	000	000	000	000	000	0
Oidematops	110	020	110	101	000	000	000	000	000	000	000	000	0
Atrichomelina	110	120	110	100	000	000	000	000	000	000	000	000	0
Tetanura	110	102	110	110	000	000	000	000	010	000	100	000	0
Colobaea	111	110	110	110	000	000	000	000	000	000	000	000	0
Calliscia	110	110	110	000	100	010	000	000	000	000	000	000	0
Parectinocera	110	010	110	000	100	000	000	000	000	000	000	000	0
Pteromicra	110	010	110	000	000	000	000	000	000	000	000	000	0
Pherbellia	110	010	110	000	000	000	000	000	000	000	000	000	0
Eutrichomelina	111	101	001	000	001	000	000	000	000	000	000	000	0
Ectinocera	111	101	001	000	011	000	001	000	000	010	000	000	0
Renocera	111	101	001	000	011	000	000	000	000	000	000	000	0
Antichaeta	111	101	100	020	010	100	000	100	000	000	000	000	0
Chasmacryptum	111	101	001	000	011	110	000	000	000	000	000	000	0
Shannonia	111	101	001	000	000	112	001	000	000	000	000	000	0
Perilimnia	111	101	001	000	000	112	001	000	000	000	000	000	0
Hoplodictya	111	101	001	000	012	112	101	000	000	000	000	000	0
Dictya	111	101	001	000	012	112	100	000	000	000	000	000	0
Hydromya	111	101	001	000	011	112	110	000	000	000	000	000	0
Neolimnia	111	101	000	000	011	112	110	000	000	000	000	000	0
Tetanoceroides	111	101	011	010	011	112	110	000	000	000	000	000	0
Euthycerina	111	102	001	000	011	112	110	000	000	000	000	000	0
Tetanocera	111	102	001	000	011	112	110	000	000	000	000	000	0
Trypetolimnia	111	102	001	010	011	111	110	000	000	000	000	000	0
Psacadina	111	102	000	000	011	112	110	000	000	000	000	000	0
Steyskalina	111	102	000	000	011	112	110	000	000	000	000	000	0
Dictyodes	111	101	001	010	012	112	110	110	000	000	000	000	0
Ilione	111	101	001	010	011	112	110	100	000	000	000	000	0
Pherbina	111	101	001	010	011	112	110	100	000	000	000	000	0
Trypetoptera	111	101	001	010	011	112	110	100	000	000	000	000	0
Limnia	111	101	001	000	011	111	120	100	000	000	000	000	0
Poecilographa	111	101	001	010	011	112	130	100	000	000	000	000	0
Pherbecta	111	101	001	010	011	112	130	111	000	000	000	000	0
Protodictya	111	101	001	010	011	112	130	111	000	000	000	000	0
Guatemalia	111	101	001	010	011	112	110	000	100	000	000	000	0
Elgiva	111	102	001	000	011	112	110	000	111	000	000	000	0
Hedria	111	101	001	010	011	111	110	000	110	001	000	000	0
Dichetophora	111	101	001	010	011	111	110	000	111	000	110	000	0
Coremacera	111	101	001	000	011	111	120	000	101	000	000	000	0
Dictyacium	111	101	001	000	011	101	120	000	101	000	000	000	0
Euthycera	111	101	001	000	011	111	120	000	101	000	000	000	0
Ethiolimnia	111	101	000	000	011	003	120	000	010	110	000	000	0
Teutoniomya	111	101	001	0?0	011	11?	220	000	210	010	000	100	0
Thecomyia	111	102	001	000	011	113	220	000	110	111	111	010	0
Sepedoninus	111	102	101	000	012	113	230	000	110	111	111	110	0
Sepedonella	111	102	102	020	012	113	200	000	111	111	111	111	0
Sepedon	111	102	101	020	012	113	230	000	210	111	110	111	0
Sepedomerus	111	102	101	020	012	113	230	000	210	111	110	111	1
Sepedonea	111	102	102	020	012	113	230	000	210	111	110	111	1

number of spermathecae is also three, this number being considered the plesiomorphic condition for the Sciomyzidae. Only in *Salticella* is the number of spermathecae four, which we interpret to be a secondary condition, probably being derived from two. Thus, four spermathecae are an autapomorphy for the Salticellinae, and two spermathecae remain a synapomorphy for Sciomyzinae.

3. Position of sixth left abdominal spiracle of the male (Figs. 115–159): P (0) in membrane; A (1) in sclerotized tergite.

Within the Sciomyzidae the abdominal spiracles of males may occur in the membrane or the sclerotized tergite. Primitively in Muscomorpha, the spiracles are in the membrane, which is considered the plesiomorphic condition for the Sciomyzidae. The position of the sixth spiracle in the sclerotized portion of the tergite is a synapomorphy for the Tetanocerini. Males of *Colobaea* Zetterstedt have the spiracle in the sclerotized tergite, a condition that probably represents a secondary reversal.

4. Sixth abdominal tergite of the male (Figs. 69, 74–76): P (0) present; A (1) absent.

Having all abdominal sclerites present is undoubtedly the plesiomorphic condition. According to McAlpine (1989) the reduction of the sixth abdominal tergite in males is an apomorphy for the superfamily Sciomyzoidea. Griffiths (1972) considered this reduction to be a synapomorphy, confirming the monophyly of Sciomyzidae. In Sciomyzidae, however, there is a complete absence of this tergite in most genera. Only in *Salticella* and in four genera of Sciomyzini, *Oidematops* Cresson, *Parectinocera* Becker, *Pherbellia,* and *Pteromicra* Lioy, is there a sixth tergite, which, however, is reduced.

5. Subepandrial plate (Figs. 161–169, 197): A (0) absent; P (1) vestigial; A (2) well developed.

The common, plesiomorphic condition, is the presence of a vestigial subepandrial plate found in *Pelidnoptera, Salticella, Colobaea, Calliscia Steyskal, Parectinocera, Pteromicra,* and *Pherbellia.* It is lacking in all genera of the Tetanocerini. In *Sciomyza* Fallén, *Oidematops,* and *Atrichomelina* Cresson, the subepandrial plate is well developed and is a synapomorphic condition that characterizes these three genera. In *Tetanura* (tribe Sciomyzini), the plate is also absent, a condition we consider to be homoplastic.

6. Anterior surstylus (Figs. 161–203): P (0) well developed; A (1) vestigial; A (2) absent.

The transformation series for this character is linear: 0 → 1 → 2. *Pelidnoptera* has two pairs of well-developed, paired surstyli, and thus the presence of an anterior well-developed surstylus is the plesiomorphic condition for this character. Within the Sciomyzidae, the tribe Sciomyzini also has an anterior, well-developed surstylus. The genera *Tetanura* (tribe Sciomyzini) and *Elgiva* Meigen; the assemblage formed by the genera *Euthycerina* Malloch, *Tetanocera, Trypetolimnia* Mayer, *Psacadina* Enderlein, and *Steyskalina* Knutson; and the group of *Thecomyia* Perty, *Sepedoninus* Verbeke, *Sepedonella* Verbeke, *Sepedon, Sepedomerus* Steyskal + *Sepedonea* Steyskal; lack an anterior surstylus, having only the posterior one. The remaining genera of Tetanocerini have a vestigial, anterior surstylus.

7. Shape of aedeagus (Figs. 61–63, 66–67, 204–322): P (0) asymmetrical; A (1) symmetrical.

Asymmetry in the postabdomen of male Acalyptratae may involve internal structures, including the aedeagus. Within genera of Sciomyzidae, the aedeagus demonstrates great variation in shape and symmetry. *Pelidnoptera* has an asymmetrical aedeagus, a condition that is considered to be plesiomorphic. In most Tetanocerini, except for *Antichaeta,* the aedeagus is a complex structure with several completely asymmetrical sclerites. In the Sciomyzini and in the group of *Sepedoninus, Sepedo-*

nella, Sepedon, Sepedomerus + *Sepedonea,* the aedeagus is completely symmetrical.

8. Attachment of gonopod (Figs. 204–322): P (0) fused to the hypandrium; A (1) free.

McAlpine (1989) postulated the fusion of the gonopod to the hypandrium as a plesiomorphic condition for the Acalyptratae. All groups examined that are closely related to the Sciomyzidae have the gonopod fused to the hypandrium. The presence of a gonopod that is well developed and free is a condition that supports the monophyly of the tribe Sciomyzini. In *Tetanoceroides* Malloch, a free gonopod is apparently homoplastic.

9. Paramere (Figs. 204–322): A (0) not digitiform, elongate and well developed; P (1) digitiform and well developed; A (2) absent.

Pelidnoptera has a digitiform, well-developed paramere that is considered to be plesiomorphic. In *Salticella,* the paramere is elongate and well developed, as in the Sciomyzini and in the genera *Antichaeta, Psacadina, Neolimnia, Ethiolimnia,* and *Steyskalina.* Two genera, *Sepedonea* and *Sepedonella,* lack a paramere, a condition that is considered homoplastic.

10. Shape of aedeagal apex (Figs. 204–213): P (0) variously shaped, but not flattened; A (1) flattened.

The presence of an aedeagus with a flattened apex is a synapomorphy for the group of *Sciomyza, Oidematops, Atrichomelina, Tetanura,* and *Colobaea* within the Sciomyzini.

11. Basiphallus (Figs. 203–322): P (0) well developed; A (1) present but poorly developed; A (2) absent.

This character has the greatest number of steps in the matrix and analysis, indicating a large number of homoplasies and reversals. The taxa that have the intermediate apomorphic condition, the basiphallus poorly developed, are *Colobaea, Tetanura, Trypetolimnia, Tetanoceroides, Dictyodes* Malloch, *Ilione* Verbeke, *Pherbina* Robineau-Desvoidy, *Trypetoptera* Hendel, *Guatemalia* Steyskal, *Hedria* Steyskal, *Dichetophora* Rondani, *Poecilographa* Melander, *Protodictya* Malloch + *Pherbecta* Steyskal (the later two genera are sister groups, as indicated by the "+" connection). The genera *Salticella, Antichaeta, Sepedonella, Sepedon, Sepedomerus,* and *Sepedonea* lack a basiphallus. The remaining genera have a well-developed basiphallus.

12. Setal investment of foretibia: P (0) without preapical setae; A (1) bearing a pair of preapical setae.

The presence of a pair of preapical setae on the foretibia is a synapomorphy for *Oidematops* and *Sciomyza.*

13. Vestiture of the aedeagus (Figs. 214–217): P (0) without scalelike structures; A (1) with scalelike structures.

In *Calliscia* and *Parectinocera,* the aedeagus is covered with small scalelike structures, a synapomorphy for these genera.

14. Proepisternal seta: P (0) present; A (1) absent.

Steyskal (1965) used the presence of the proepisternal seta to distinguish the tribe Sciomyzini from the Tetanocerini. Most genera of Tetanocerini lack this seta, although *Shannonia* Malloch and *Perilimnia* Becker possess one. For the latter genera this condition is considered to be homoplastic.

15. Male terminalia (Figs. 57–59, 64–65, 68–160): P (0) with the 6th, 7th, and 8th sternites separated, the 6th and 7th asymmetrical; A (1) with the synsternite 7+8 and 6th sternite separated and asymmetrical; A (2) with the synsternite 6+7+8 symmetrical.

According to Steyskal (1957) the asymmetry of the male Acalyptratae postabdomen, including segments beyond the fifth, is due to three basic movements within the pupa: circumversion, reflection, and "strophe." The symmetry may occur as a result of the obliteration of these movements. Asymmetry in Sciomyzidae is restricted to the sixth, seventh, and eighth segments. There is a modification gradient of these segments, changing from completely asymmetrical to completely symmetrical, associated to the fusion of the segments mentioned above.

16. Placement of sixth right abdominal spiracle of the male (Figs. 68–114): P (0) in membrane; A (1) in sclerotized tergite.

Sciomyzini and *Eutrichomelina, Renocera* Hendel, and *Ectinocera* Zetterstedt have the plesiomorphic condition of this character, the spiracle is in the membrane. From *Antichaeta* to *Sepedonea,* the spiracle is in the tergite. In *Ethiolimnia,* there is a reversal to the plesiomorphic condition.

17. Placement of seventh right abdominal spiracle of the male (Figs. 68–114): P (0) in membrane; A (1) in sclerotized tergite.

The plesiomorphic condition occurs in most Sciomyzini except for *Calliscia.* From *Chasmacryptum* Becker to *Sepedonea* most genera have the spiracle in the tergite, except for *Dictyacium* Steyskal and *Ethiolimnia.*

18. Shape of head: P (0) as in Fig. 52a; A (1) as in Fig. 52b; A (2) as in Fig. 52c; A (3) as in Fig. 52d.

The head, from the ancestor to *Chasmacryptum,* has the shape shown in Fig. 52a. Beyond the group of *Shannonia* + *Perilimnia* the intermediate apomorphic condition, represented by Fig. 52c, is present. From this state the other two apomorphic states evolved. The pattern of head shape, as in Fig. 52b, is present in *Trypetolimnia* and *Limnia* Robineau-Desvoidy as homoplasies and in *Hedria, Dichetophora, Coremacera* Rondani, *Dictyacium,* and *Euthycera* Latreille. The shape, as in Fig. 52d, defines the group of *Ethiolimnia, Thecomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus,* and *Sepedonea.* Because *Teutoniomyia* Hennig has a very different head, compared to other genera, this character was coded as missing in the matrix (Table 1).

19. Proportion between the length of the pedicel and first flagellomere (Figs. 1–51): P (0) pedicel approximately half of first flagellomere; A (1) pedicel subequal to the length of the first flagellomere; A (2) pedicel approximately twice the length of the first flagellomere.

The plesiomorphic condition is present from Sciomyzini until *Shannonia* + *Perilimnia.* From this group to *Ethiolimnia* the intermediate apomorphic condition (1) is present. The apomorphic condition (2) is present in the following genera: *Teutoniomyia, Thecomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus,* and *Sepedonea.*

20. Condition of sternites of female terminalia (Figs. 53–56): P (0) with sternites 6th, 7th, and 8th separate; A (1) with 6th separate and 7th and 8th fused; A (2) 6th, 7th, and 8th incompletely fused; A (3) 6th, 7th, and 8th completely fused.

The transformation series was linear. Two lineages arose from state 1. One of these goes through the third state and the second goes through the fourth state. The evolution occurred from separated sternites passing through steps of fusion to the complete fusion of 6th, 7th, and 8th. All Sciomyzini and the Tetanocerine genera until *Hoplodictya* Cresson + *Dictya* Meigen have sternites 6th, 7th, and 8th separate. From the polytomy of *Hydromya* Robineau-Desvoidy to the ancestor of *Ethiolimnia* the 7th and 8th sternites are fused. *Protodictya* + *Pherbecta* and *Poecilographa* have the three sternites completely fused as *Sepedoninus, Sepedon, Sepedomerus,* and *Sepedonea.* In *Sepedonella,* a genus belonging to this group, the three sternites are separate. The monophyletic group formed by *Coremacera, Dictyacium,* and *Euthycera,* and the genera *Limnia, Teutoniomyia,* and *Thecomyia* have the sternites 6, 7, and 8 almost fused. Lines separating these sternites are perceptible.

21. Aedeagus with lobed apex (Figs. 222–224, 230–238): P (0) absent; A (1) present.

Ectinocera, Hoplodictya, and *Perilimnia* + *Shannonia* have the aedeagus with the distal end lobed. This character apparently appeared independently in these genera. In the other genera, the distal end of the aedeagus has several different shapes.

22. Subalar setae: P (0) absent; A (1) present.

The subalar setae are present in *Dictyodes, Ilione, Pherbina, Trypetoptera, Limnia, Poecilographa, Pherbecta* + *Protodictya.* The apomorphic state apparently evolved independently in *Antichaeta.*

23. Aedeagus convoluted as in Figs. 263–265, 281–286: P (0) absent; A (1) present.

A convoluted aedeagus occurs in *Protodictya, Pherbecta, and Dictyodes.* For *Protodictya* and *Pherbecta* this character defines the common ancestor.

24. Fourth abdominal sternite of the male fused to fifth, forming a medioapical process: P (0) absent; A (1) present.

The presence of a well-developed, medioapical process in the fifth abdominal sternite of the male as a complex structure is a synapomorphy for the species of *Protodictya* (Marinoni & Knutson 1992, Marinoni & Carvalho 1993). In *Pherbecta,* however, there is, at the same position, a process that is less well developed and which may be homologous to that of *Protodictya.*

25. Lunula: P (0) not exposed; A (1) exposed; A (2) greatly exposed.

In the outgroup, *Pelidnoptera,* genera of Sciomyzini, and genera of Tetanocerini from *Eutrichomelina* to *Protodictya,* the lunula is not exposed. From *Guatemalia* to *Sepedonella,* the intermediate state (1) is present. In *Ethiolimnia,* there is a reversal to the plesiomorphic state. In the apical genera, *Sepedon, Sepedomerus,* and *Sepedonea,* the lunula is greatly exposed, which is interpreted as an even more derived condition from the intermediate state. In *Teutoniomyia,* which also has a greatly exposed lunula, this character state is homoplastic.

26. Presutural supra-alar setae: P (0) present; A (1) absent.

The plesiomorphic condition of this character is the presence of presutural supra-alar setae. The absence of these setae is a synapomorphy for the group *Elgiva, Hedria, Dichetophora, Ethiolimnia, Teutoniomyia, Thecomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus,* and *Sepedonea.* In *Coremacera, Dictyacium,* and *Euthycera,* there is a reversal to the plesiomorphic state. *Tetanura* has this seta, a condition that is considered homoplastic.

27. Seventh and 8th abdominal tergites of the female: P (0) separate; A (1) fused.

The fusion of the 7th and the 8th abdominal tergites of the female is a character state that links the genera *Dichetophora, Coremacera, Dictyacium,* and *Euthycera.* In *Elgiva* and *Sepedonella,* the fusion is homoplastic.

28. Prominent eyes: (0) absent; (1) present.

Ethiolimnia, Thecomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus, and *Sepedonea* have prominent eyes, a synapomorphy for these genera. As *Ethiolimnia* is in a polytomy with *Teutoniomyia,* prominent eyes are a confirmed synapomorphy for *Thecomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus,* and *Sepedonea* and only perhaps for *Ethiolimnia.*

29. Number of postalar setae: P (0) 2; A (1) 0–1.

The presence of two postalar setae is the plesiomorphic condition. In *Ectinocera* and in the genera beyond *Ethiolimnia,* the number of postalar setae is reduced to one or none.

30. Ocellar setae: P (0) present; A (1) absent.

The presence of a pair of strong ocellar setae has been considered a plesiomorphic condition for the Muscomorpha (McAlpine 1989). In *Pelidnoptera,* these setae are present, as they are in most Sciomyzidae, including *Salticella.* These setae are absent in *Hedria* and in the group of *Thecomyia, Sepedoninus, Sepedonella, Sepedomerus* + *Sepedonea.*

31. Postpronotal setae: P (0) present; A (1) absent.

Most Sciomyzidae have postpronotal setae. The absence of these setae characterizes the group of genera beyond *Thecomyia.* In *Dichetophora* and *Tetanura,* the absence of postpronotal setae is considered to be homoplastic.

32. Number of scutellar setae: P (0) 2 pairs; A (1) 1 pair.

Primitively the family Sciomyzidae has two pairs of scutellar setae. One pair of scutellar setae occurs in *Dichetophora* and the group of genera beyond *Thecomyia.*

33. Number of notopleural setae: P (0) 2; A (1) 1.

Two notopleural setae are present in most Sciomyzidae and in *Pelidnoptera.* Only the genera *Thecomyia, Sepedoninus,* and *Sepedonella* have a single notopleural seta. A reversal of this characters to the plesiomorphic state of two notopleural setae occurs in the genera *Sepedon, Sepedomerus,* and *Sepedonea.*

34. Hindtibia arch-shaped: P (0) absent; A (1) present.

The genera *Teutoniomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus,* and *Sepedonea* have an arch-shaped hindtibia. Only *Thecomyia* does not have the hindtibia arch-shaped.

35. Head with sutures: P (0) distinct; A (1) indistinct.

The head sutures of *Thecomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus,* and *Sepedonea* are indistinct. This condition is considered a synapomorphy for this group.

36. Epandrium (Figs. 68–160): P (0) free; A (1) fused to the 8th sternite.

The fusion of the epandrium to the 8th sternite is a synapomorphy for the genera *Sepedonella, Sepedon, Sepedomerus,* and *Sepedonea.*

37. Hindtibia with a spinelike projection: P (0) absent; A (1) present.

In most Sciomyzidae, there is no projection from the hindtibia. *Sepedonea* and *Sepedomerus* have a hindtibia that bears a spinelike projection, which is a synapomorphy that links these two genera.

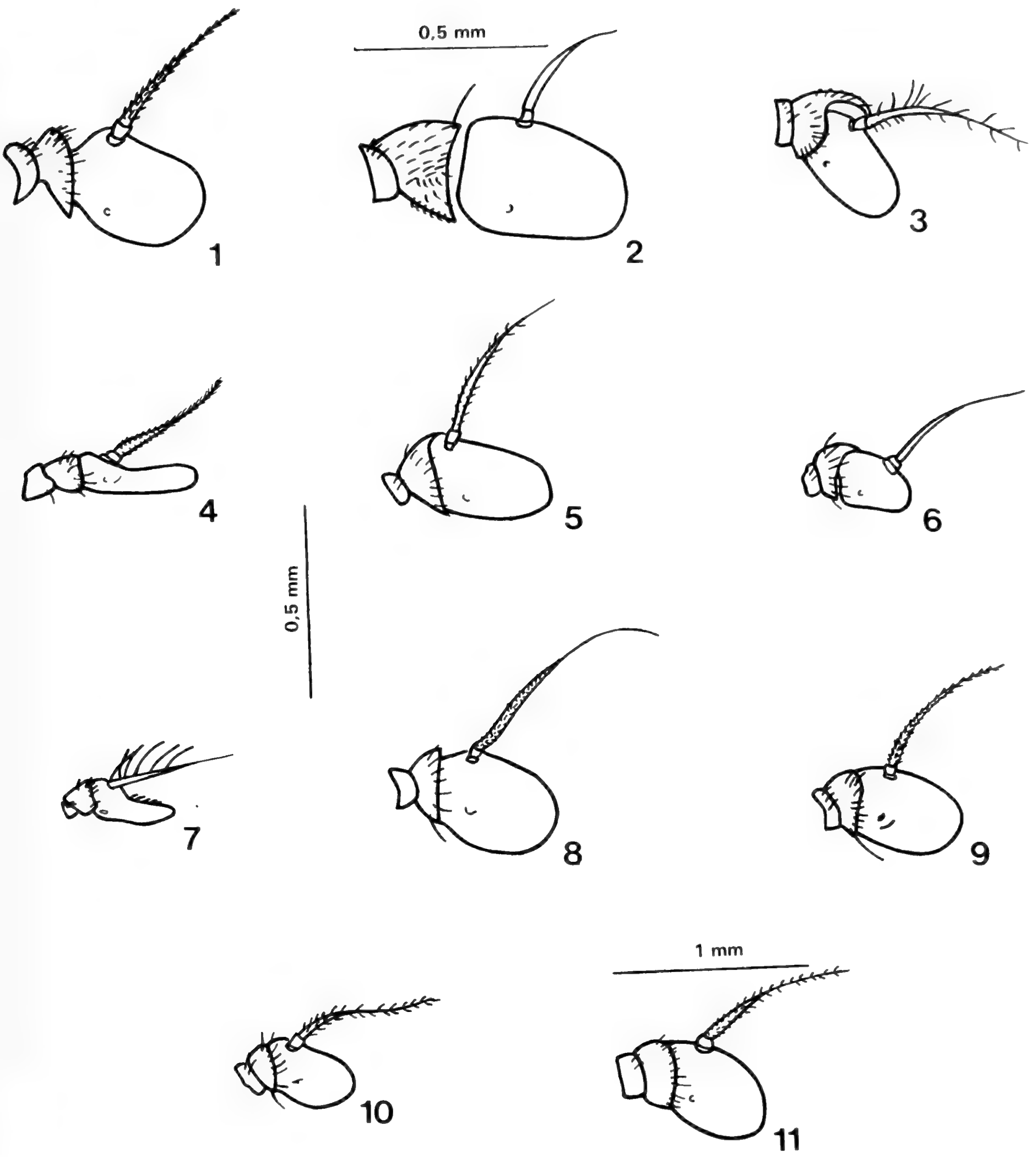
Discussion

Relationships.—The monophyly of the Sciomyzidae is defined by a behavioral character, the larvae are predators or parasitoids on aquatic or terrestrial Mollusca (Berg 1953, Knutson et al. 1970, Griffiths 1972, Barnes 1979) and the presence of a serrate ventral arch below the mouth hooks in the larvae (Griffiths 1972). The serrate ventral arch could be closely correlated with the malacophagous feeding behavior.

The genus *Salticella,* representing the Salticellinae, remains at the base of the cladogram, being distinguished from the subfamily Sciomyzinae and its monophyly confirmed by the following three autapomorphies: four spermathecae; cell M narrowed apically (this character was not used in the analysis because of its variability among genera of Sciomyzidae); and three pairs of surstyli. Knutson et al. (1970), working on the biosystematics of *Salticella fasciata* (Meigen), concluded that this genus is more closely related to Sciomyzini than to the Tetanocerini in morphological and biological aspects. This relationship is corroborated in the present analysis.

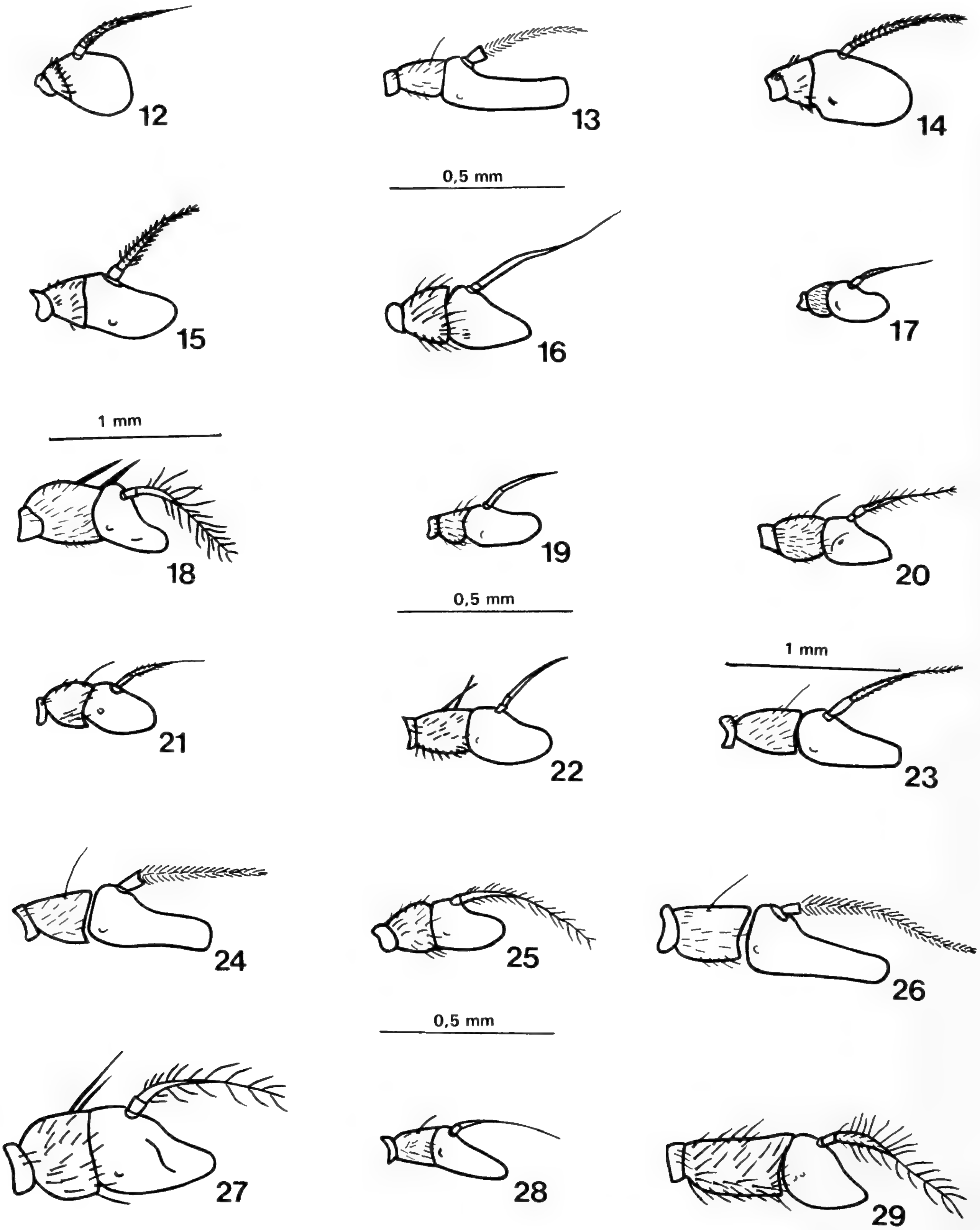
Among genera of the subfamily Sciomyzinae, two main monophyletic clades were formed, the first including *Pherbellia, Pteromicra, Calliscia, Parectinocera, Tetanura, Colobaea, Atrichomelina, Oidematops,* and *Sciomyza*; and the second including the 40 remaining genera. The two clades are concordant with the tribes Sciomyzini and Tetanocerini of Steyskal (1965). The genus *Eutrichomelina,* which traditionally has been placed in the Sciomyzini, is shown to be allied to the Tetanocerini in this analysis.

Behavioral aspects of the larvae have been discussed as possible synapomorphies for the tribes (Knutson & Lyneborg 1965, Abercrombie 1970). Toward one end of the scale, where the Sciomyzini are placed, the species that have been reared are parasitoids on stranded aquatic or terrestrial mollusks (*Colobaea* (Knutson

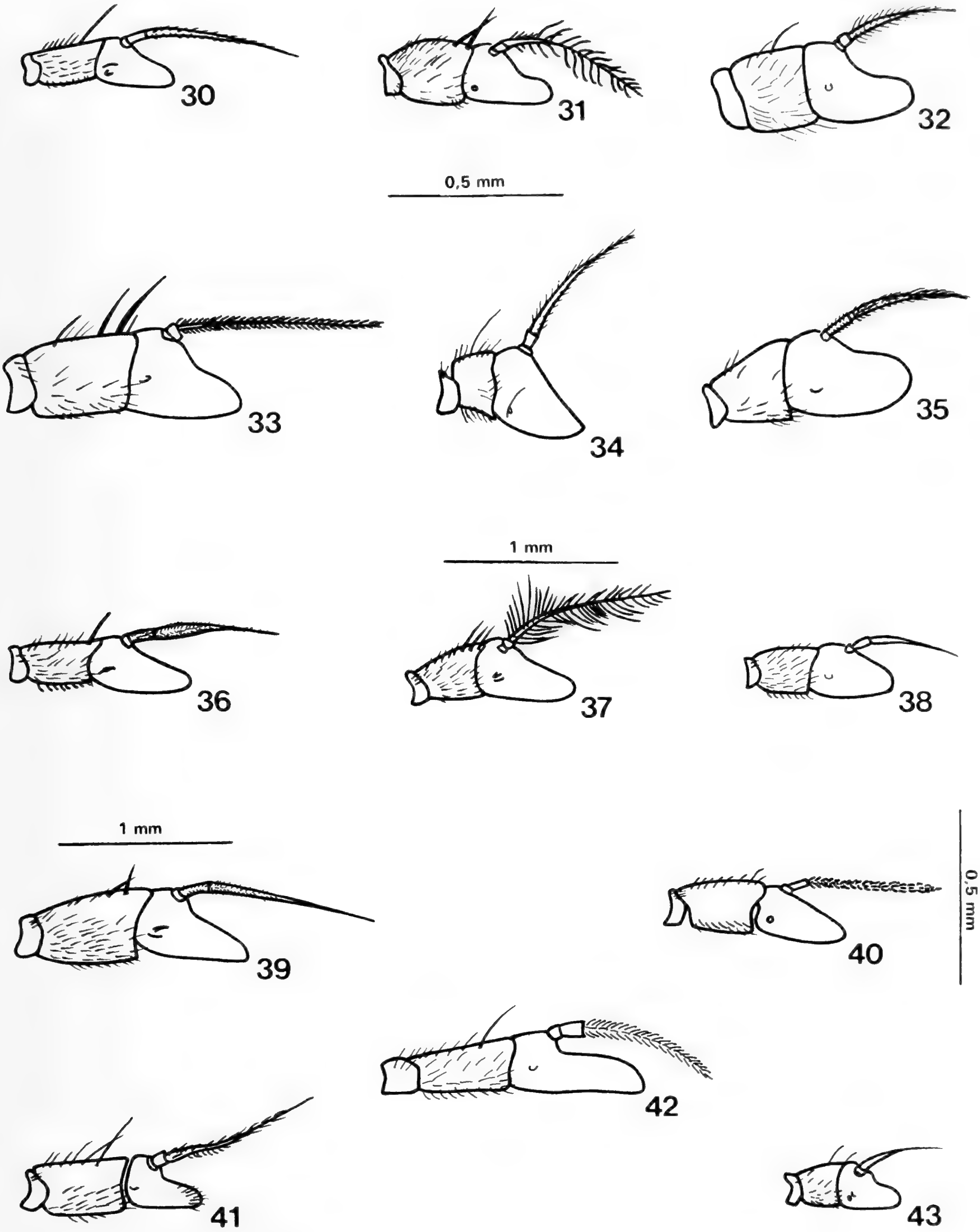


Figs. 1–11. Right antenna, right lateral view: 1, *Pelidnoptera*; 2, *Salticella*; 3, *Sciomyza*; 4, *Oidematops*; 5, *Atrichomelina*; 6, *Tetanura*; 7, *Colobaea*; 8, *Calliscia*; 9, *Parectinocera*; 10, *Pteromicra*; 11, *Pherbellia*. Fig. 11, scale = 1.0 mm; remaining Figs. scale = 0.5 mm.

1973); *Pherbellia* (Bratt et al. 1969); *Pteromicra* (Rozkošný & Knutson 1970); *Sciomyza* (Foote 1959); *Tetanura* (Knutson 1970)). Toward the other end, most Tetanocerini are predaceous on aquatic or terrestrial mollusks (*Coremacera* (Knutson 1973); *Dichetophora* (Vala et al. 1987); *Dictya* (Valley & Berg 1977); *Dictyodes* (Abercrombie 1970, Abercrombie & Berg 1978); *Elgiva* (Knutson & Berg 1964a, Orth & Knutson 1987); *Euthycera* (Vala et al. 1983, Vala & Caillet 1985); *Hoplodictya* (Neff & Berg 1962); *Hydromya* (Knutson & Berg 1963); *Ilione* (Knutson & Berg 1964b); *Limnia* (Vala & Knutson 1990); *Perilimnia* (Kaczynski et al. 1969); *Pherbecta* (Knutson 1972); *Pherbina* (Knutson et al. 1975, Vala & Gasc 1990); *Protodictya* (Abercrombie 1970, Neff & Berg 1961); *Psacadina* (Knutson et al. 1975); *Renocera* (Foote & Knutson 1970); *Sepedon* (Neff & Berg 1966, Knutson et al.



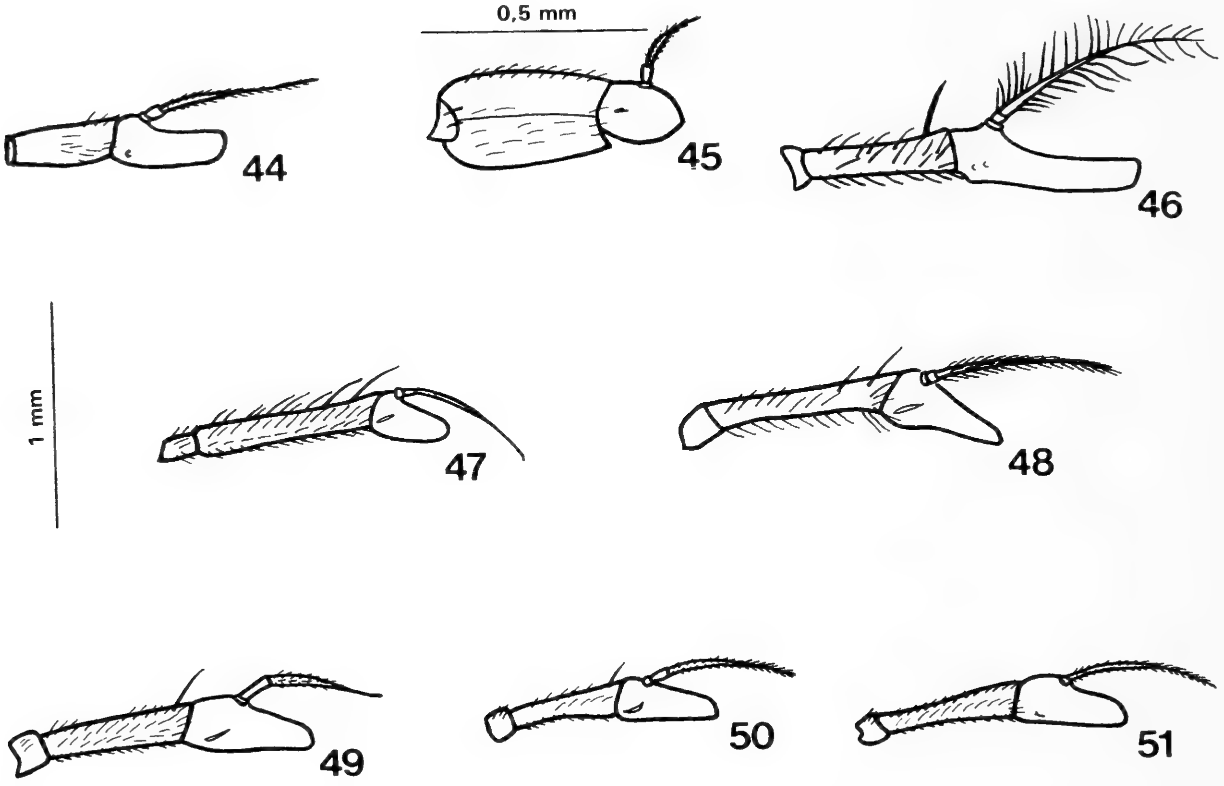
Figs. 12–29. Right antenna, right lateral view: 12, *Eutrichomelina*; 13, *Ectinocera*; 14, *Renocera*; 15, *Antichaeta*; 16, *Chasmacryptum*; 17, *Shannonia*; 18, *Perilimnia*; 19, *Hoplodictya*; 20, *Dictya*; 21, *Hydromya*; 22, *Neolimnia*; 23, *Tetanoceroides*; 24, *Euthycerina*; 25, *Tetanocera*; 26, *Trypetolimnia*; 27, *Psacadina*; 28, *Steyskalina*; 29, *Dictyodes*. Figs. 18 and 23 with scale 1.0 mm; the remaining Figs. 0.5 mm.



Figs. 30–43. Right antenna, right lateral view: 30, *Ilione*; 31, *Pherbina*; 32, *Trypetoptera*; 33, *Limnia*; 34, *Poecilographa*; 35, *Pherbecta*; 36, *Protodictya*; 37, *Guatemalia*; 38, *Elgiva*; 39, *Hedria*; 40, *Dichetophora*; 41, *Coremacera*; 42, *Dictyacium*; 43, *Euthycera*. Figs. 30–35 and 40 with scale 0.5 mm; Figs. 37–39 and 41–43 with scale 1.0 mm.

1967); *Sepedonea* (Abercrombie 1970, Knutson & Valley 1978); *Shannonia* (Kaczynski et al. 1969); *Tetanocera* (Knutson et al. 1965); *Tetanoceroides* (Abercrombie 1970); *Thecomyia* (Abercrombie & Berg 1975); *Trypetoptera* (Vala 1986)).

A few species of Sciomyzini and Tetanocerini, however, have an intermediate be-



Figs. 44–51. Right antenna, right lateral view: 44, *Ethiolimnia*; 45, *Teutoniomyia*; 46, *Thecomyia*; 47, *Sepedoninus*; 48, *Sepedonella*; 49, *Sepedon*; 50, *Sepedomerus*; 51, *Sepedonea*. Fig. 45 with scale 0.5 mm; the remaining Figs. with scale 1.0 mm.

havior between these two behaviors, i.e., sometimes they have parasitoid trends, sometimes predaceous. Examples of these kinds of behavior are evident in the species *Atrichomelina pubera* Loew and *Antichaeta analis* Zetterstedt. *Atrichomelina pubera* belongs to the Sciomyzini. Depending on circumstances this species has a predatory, parasitoid or even saprophagous behavior (Berg et al. 1959, Foote et al. 1960). Saprophagy may be the primitive condition, similar to that found in *Salticella* (Knutson et al. 1970) and the ancestor of Sciomyzidae (Abercrombie 1970). *Antichaeta analis* has some parasitoid characteristics, such as host specificity and oviposition on the host, but its behavior is predatory with the larvae feeding on snail eggs (Fisher & Orth 1964, Knutson 1966, Knutson & Abercrombie 1977).

More studies related to the evolution of the larval behavior are necessary to confirm that the larval habit is responsible for relationships among the genera within the family.

Most genera in the analysis remained in unresolved polytomies due to the great number of homoplasies and low number of synapomorphies.

Within the Sciomyzini, the relationships of *Pteromicra* and *Pherbellia* are not well resolved. Rozkošný & Knutson (1970), studying the biology and immature stages of *Pteromicra,* discovered that this genus is closely related to *Pherbellia.* However, even in our analysis, where these two genera are in close proximity on the cladogram, there is no adult character to corroborate this relationship.

Knutson et al. (1990) considered *Colobaea, Pherbellia,* and *Pteromicra* to be related but did not elaborate any synapomorphies to support their grouping. In the same paper they also suggest that *Pherbellia* is paraphyletic.

Parectinocera and *Calliscia* appear in the analysis as having the same ancestor. These two genera are the only two within the Sciomyzini with Neotropical distributions.

The genera *Tetanura, Colobaea, Atricho-*

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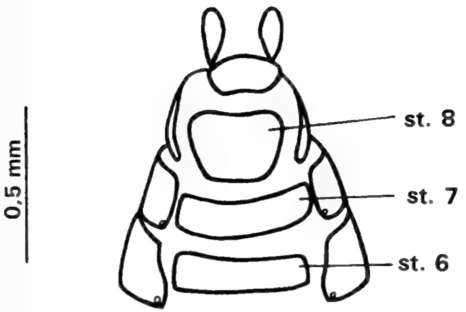

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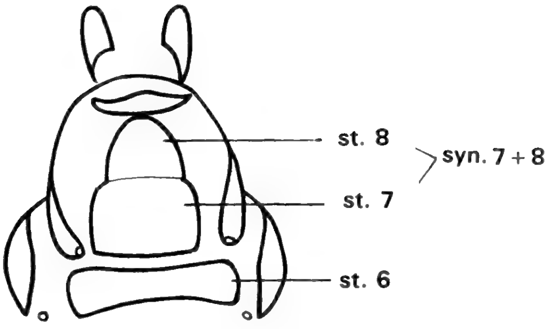

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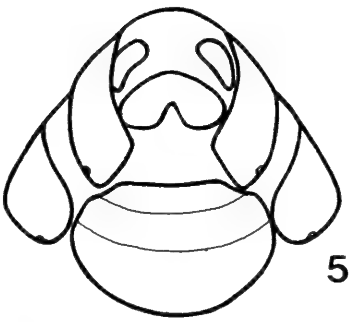

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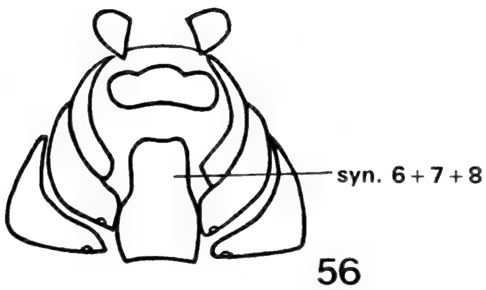

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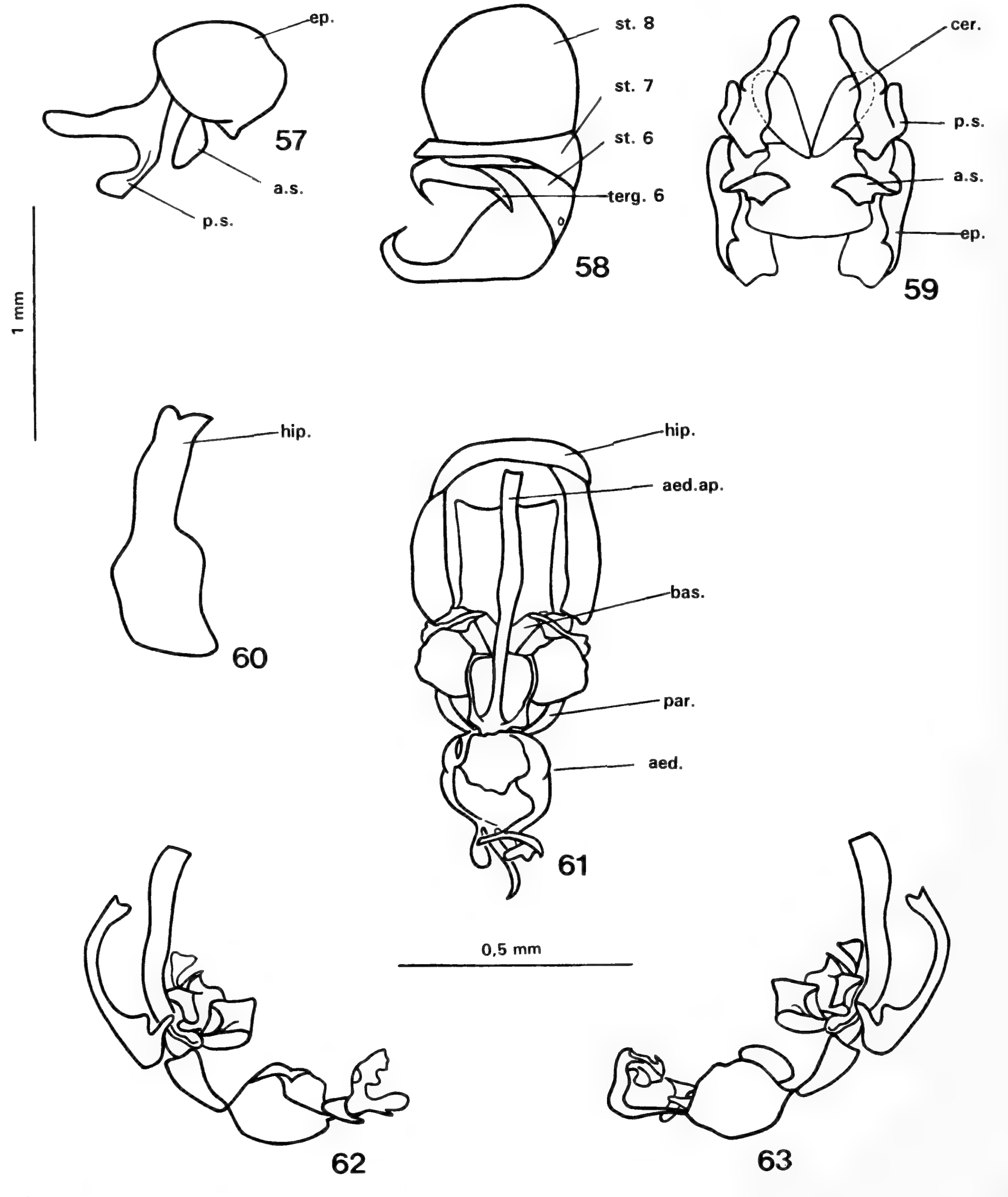
Figs. 52–56. 52. Shape of head: (a), State 0; (b), state 1; (c) state 2; (d) state 3. 53–56. Female terminalia, ventral view: 53, *Perilimnia*; 54, *Elgiva*; 55, *Coremacera*; 56, *Protodictya*. Sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); synsternite 6+7+8 (syn. 6+7+8).

melina, Sciomyza, and *Oidematops* form a clade established by characters 4 and 10 (Figs. 323–324). In this group *Atrichomelina, Sciomyza + Oidematops* have their relationships well defined. The synapomorphic character that links the three genera is the presence of a well-developed male subepandrial plate (Character 5). The other two genera remain in polytomy.

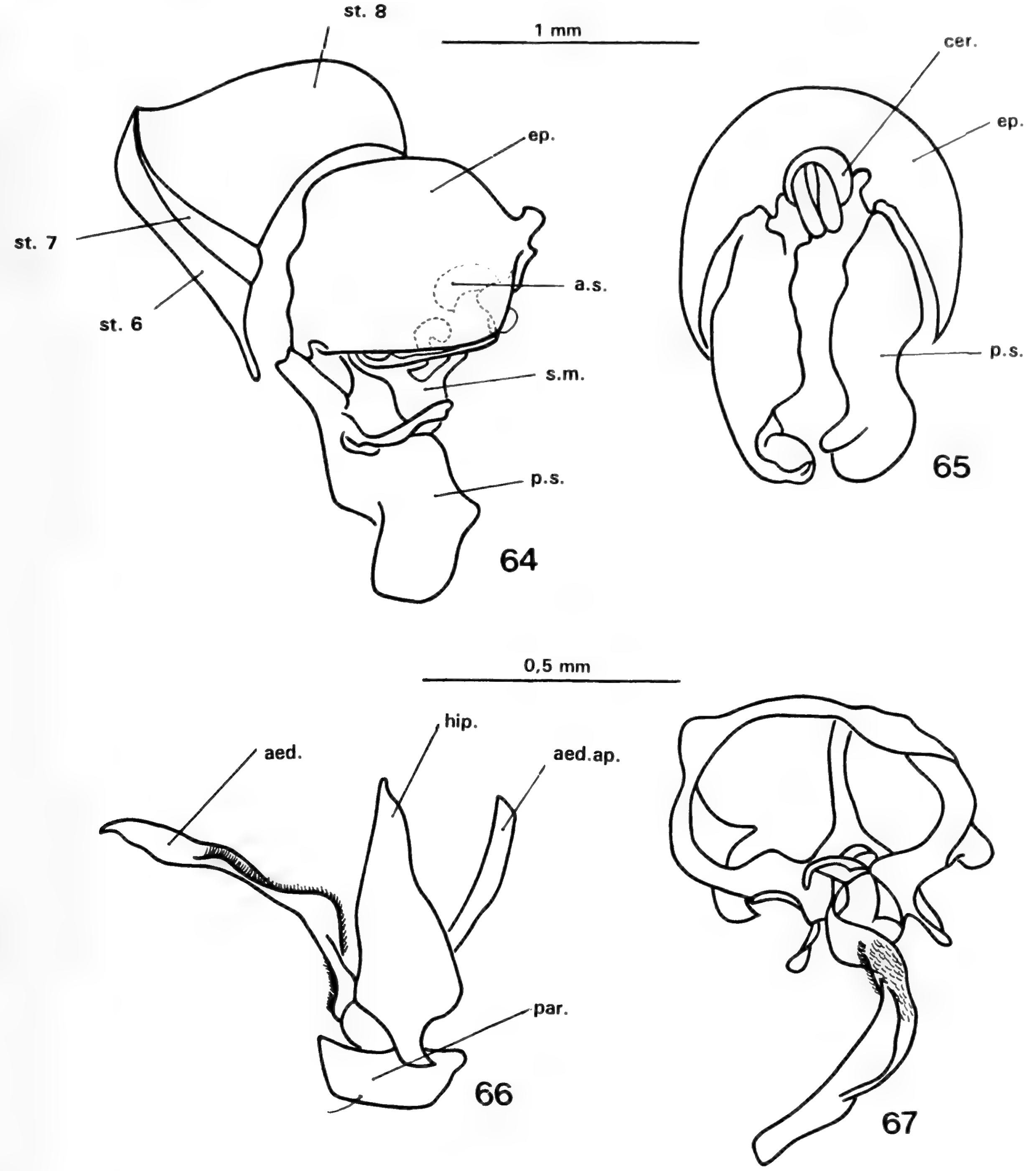
In the Tetanocerini, *Eutrichomelina, Ectinocera, Renocera, Antichaeta,* and *Chasmacryptum* are at the base of the clade. *Ec-*



Figs. 57–63. Male terminalia. *Pelidnoptera.* Aedeagal apodeme (aed. ap.); basiphallus (bas.); cerci (cer.); aedeagal complex (aed. c.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); hypandrium (hip.); paramere (par.); subepandrial plate (sub. pl.); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 57–60 with scale 1.0 mm; Figs. 61–63 with scale 0.5 mm.

tinocera and *Renocera* remain in polytomy. Steyskal (1959), using intuitive analysis, considered *Renocera, Chasmacryptum,* and *Tetanocera* to be morphologically related.

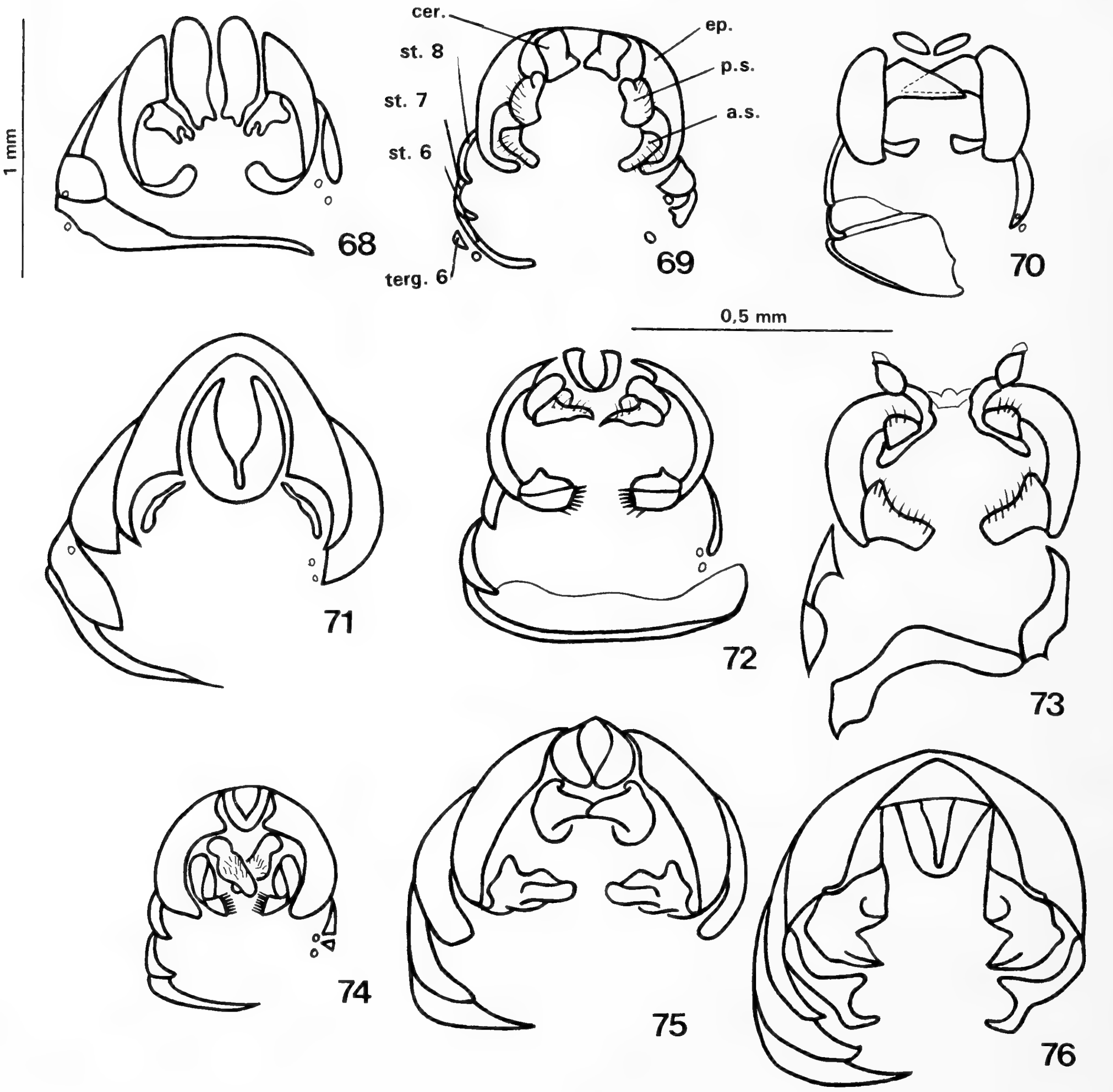
The uncertain position of *Antichaeta* was already discussed by Fisher & Orth (1964) & Knutson (1966). Adult characters suggest that this genus belongs to the Tetanocerini, while larval characters indicate its position to be within the Sciomyzini. Boyes et al.



Figs. 64–67. Male terminalia. *Salticella.* Aedeagal apodeme (aed. ap.); cerci (cer.); aedeagal complex (aed. c.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); hypandrium (hip.); paramere (par.); anterior surstylus (a. s.); medial surstylus (s. m.); posterior surstylus (p. s.). Figs. 64–65 with scale 1.0 mm; Figs. 66–67 with scale 0.5 mm.

(1969), studying the karyotype of *Antichaeta melanosoma* Melander, observed its similarity with those of the Tetanocerini genera. In the present analysis, *Antichaeta* is placed in the Tetanocerini group of genera near *Chasmacryptum.*

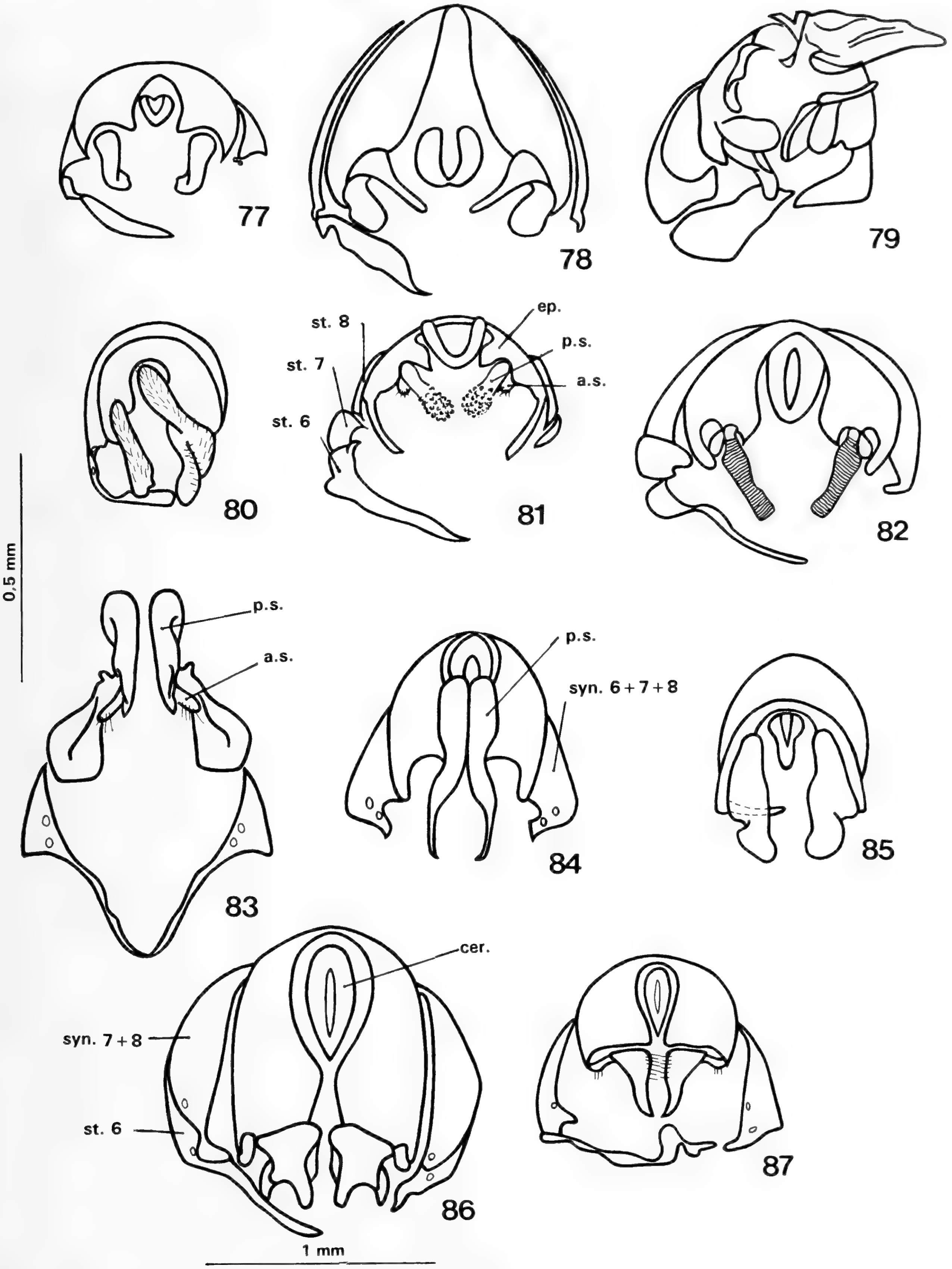
After *Chasmacryptum,* the clade of *Shannonia* + *Perilimnia* appears as the sister group of the other genera. Kaczynski et al. (1969) studied the biosystematics of the immature stages of these two genera and observed morphological and behavioral affinities between them. As observed by these authors, the main similarities between the larvae of *Shannonia* and *Perilimnia* are in the cephalopharyngeal skeleton. They also suggested the position of both genera within the Tetanocerini.



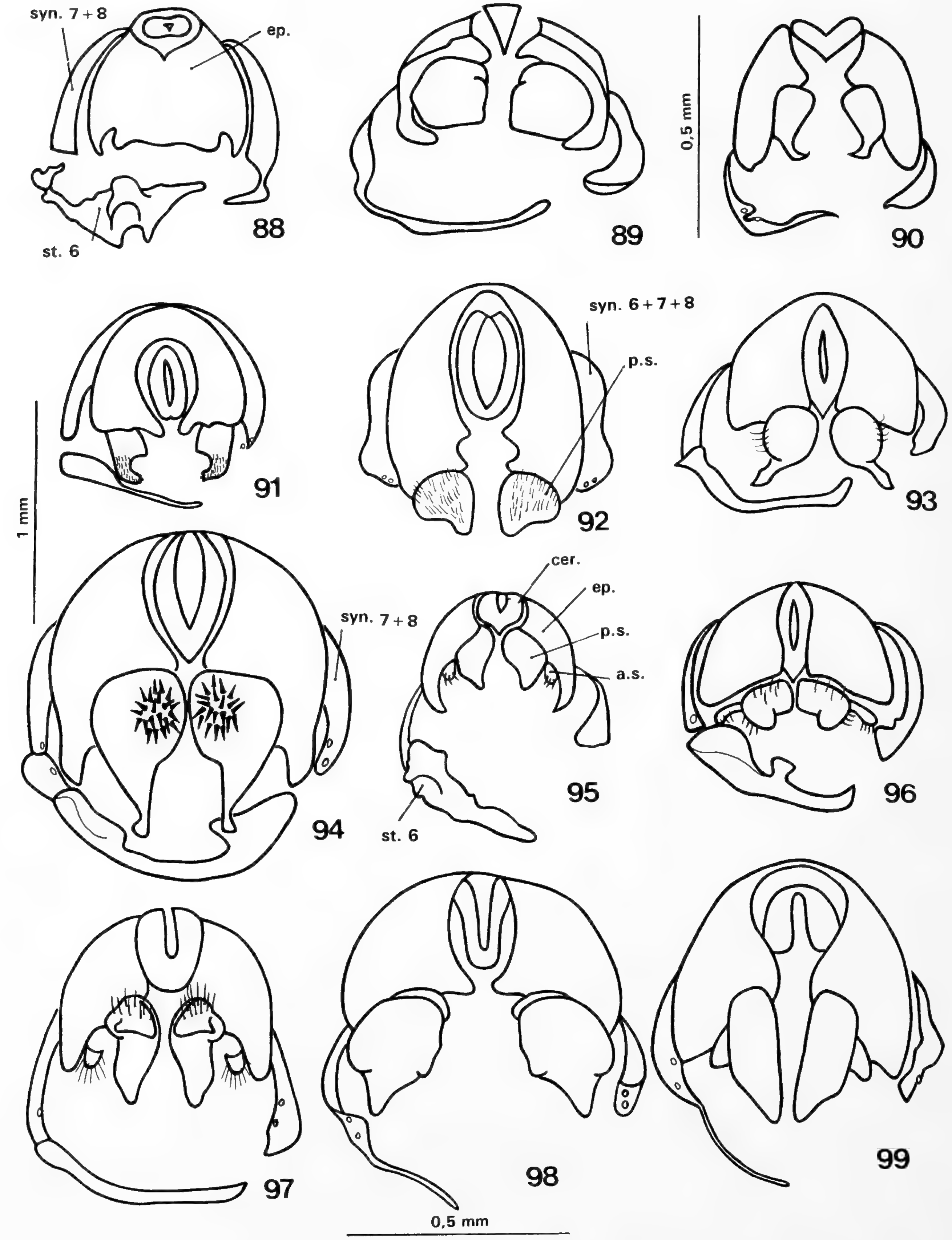
Figs. 68–76. Male terminalia, ventral view: 68, *Sciomyza*; 69, *Oidematops*; 70, *Atrichomelina*; 71, *Tetanura*; 72, *Colobaea*; 73, *Calliscia*; 74, *Parectinocera*; 75, *Pteromicra*; 76, *Pherbellia*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); anterior surstylus (a. s.); posterior surstylus (p. s.); tergite 6 (terg. 6). Fig. 68 with scale 1.0 mm; the remaining Figs. with scale 0.5 mm.

Hoplodictya + *Dictya* form the next clade. Boyes et al. (1969) compared its karyotypes and recognized the proximity of these two genera.

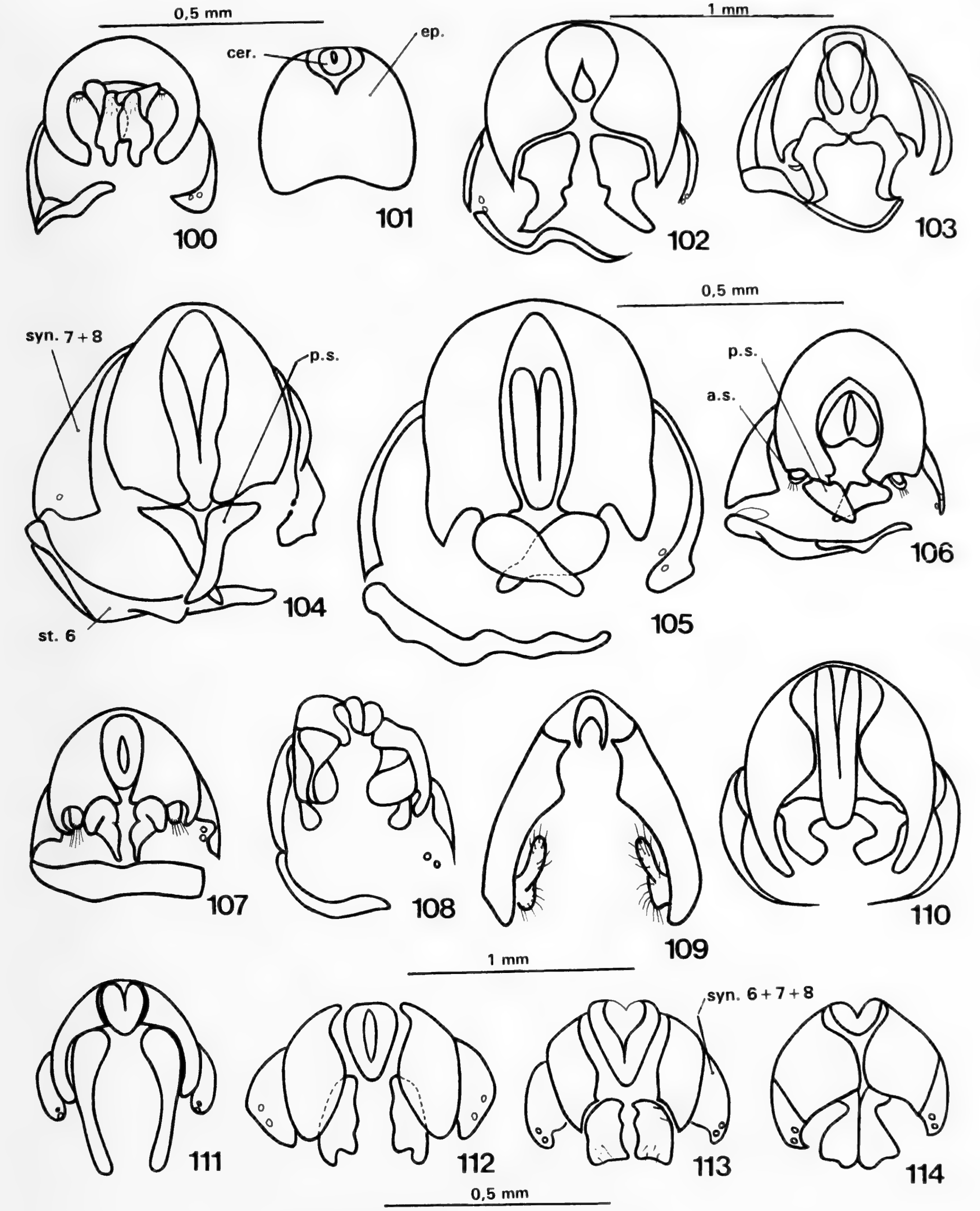
Hydromya, Neolimnia, and *Tetanocerowides* remain as a polytomy with three other groups formed. The components of one of these groups are: *Euthycerina, Tetanocera, Trypetolimnia, Psacadina,* and *Steyskalina.* The other group is formed by *Dictyodes, Ilione, Pherbina, Trypetoptera, Limnia, Poecilographa, Pherbecta* + *Protodictya.* Within the latter group the genera *Limnia, Poecilographa, Pherbecta* + *Protodictya* are monophyletic. In the third group, which comprises the last fifteen genera, we recognize two subgroups. One is formed by *Hedria, Dichetophora, Coremacera, Dictyacium,* and *Euthycera,* and the other by *Ethiolimnia, Teutoniomyia, Thecomyia, Sepedoninus, Sepedonella,* and *Sepedomerus* + *Sepedonea.* The monophyly of the first



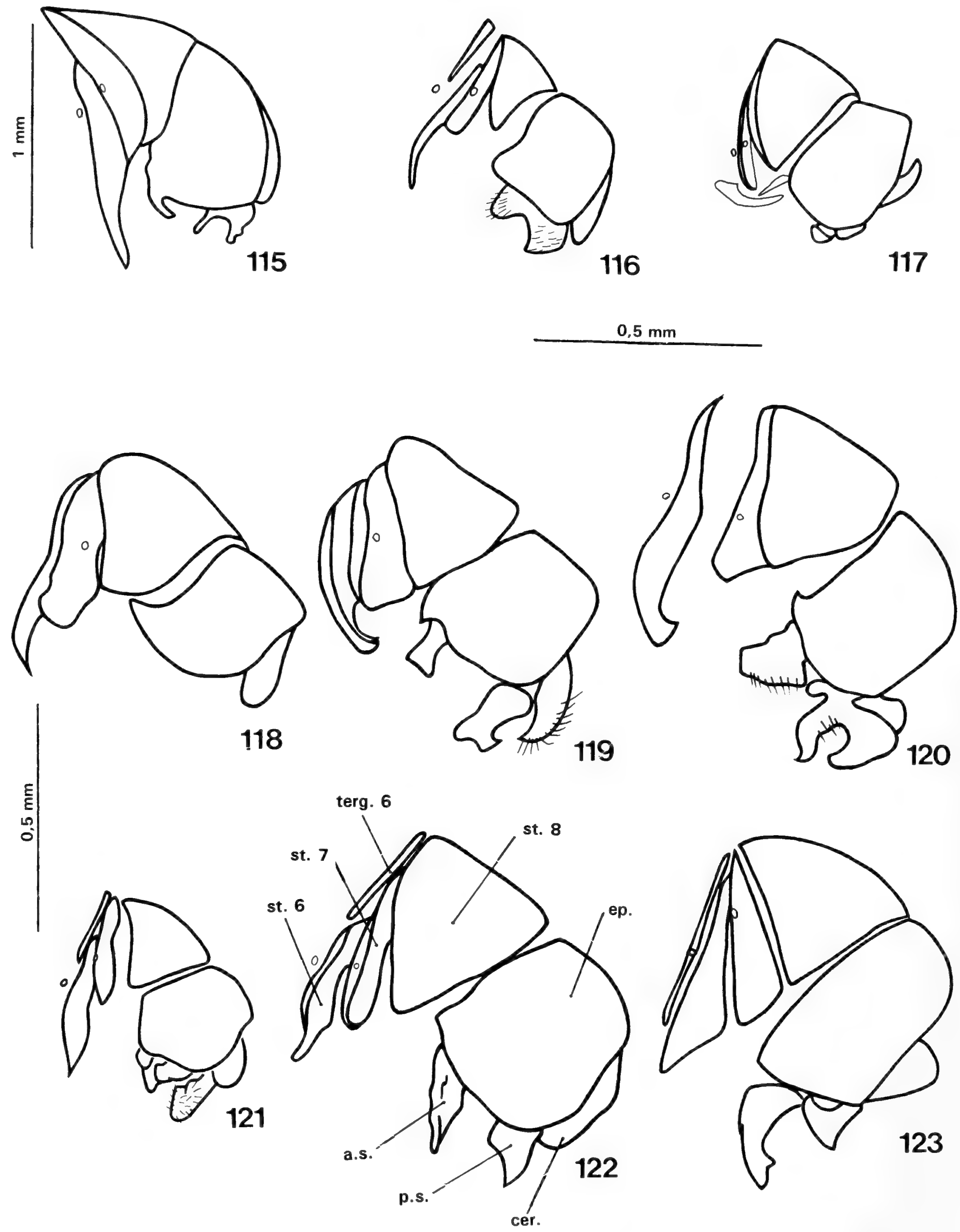
Figs. 77–87. Male terminalia, ventral view: 77, *Ectinocera*; 78, *Renocera*; 79, *Antichaeta*; 80, *Chasmacryptum*; 81, *Shannonia*; 82, *Perilimnia*; 83, *Hoplodictya*; 84, *Dictya*; 85, *Hydromya*; 86, *Neolimnia*; 87, *Euthycerina*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Fig. 86 with scale 1.0 mm; the remaining Figs. with scale 0.5 mm.



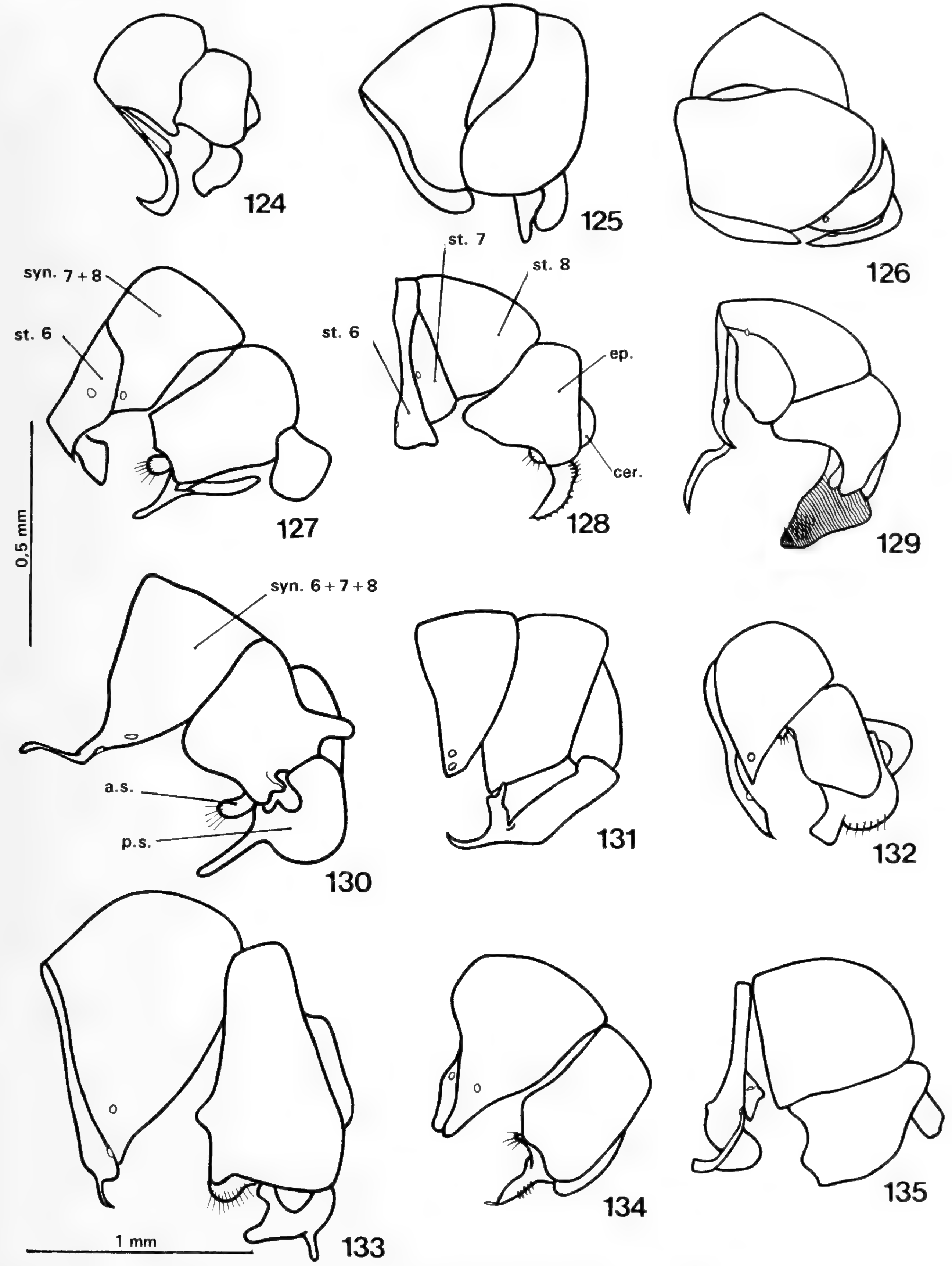
Figs. 88–99. Male terminalia, ventral view: 88, *Tetanocera*; 89, *Trypetolimnia*; 90, *Psacadina*; 91, *Steyskalina*; 92, *Dictyodes*; 93, *Ilione*; 94, *Pherbina*; 95, *Trypetoptera*; 96, *Limnia*; 97, *Poecilographa*; 98, *Pherbecta*; 99, *Protodictya*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 90 and 98 with scale 0.5 mm; the remaining Figs. with scale 1.0 mm.



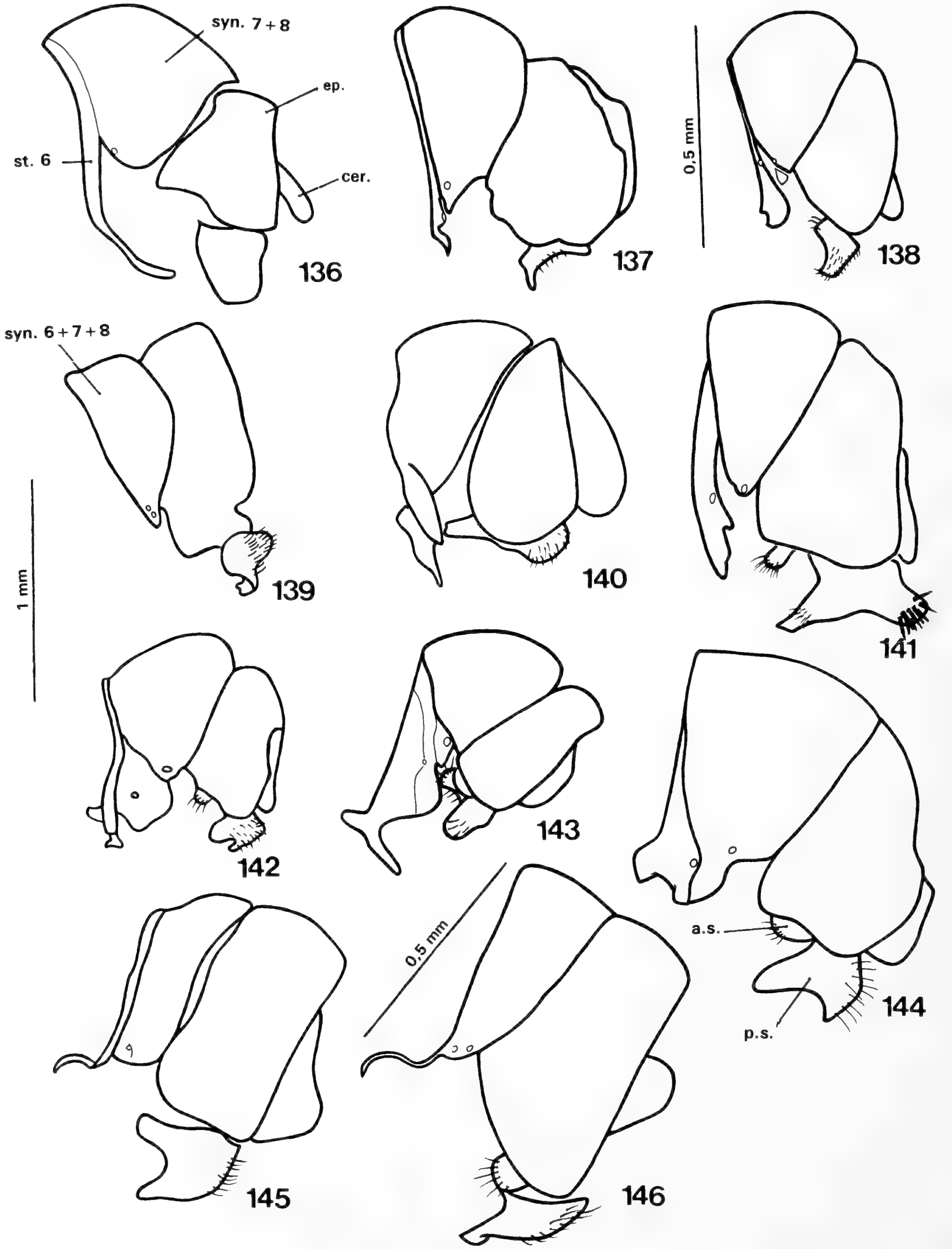
Figs. 100–114. Male terminalia, ventral view: 100–101, *Guatemalia*; 102, *Elgiva*; 103, *Hedria*; 104, *Dichetophora*; 105, *Coremacera*; 106, *Dictyacium*; 107, *Euthycera*; 108, *Ethiolimnia*; 109, *Thecomyia*; 110, *Sepedoninus*; 111, *Sepedonella*; 112, *Sepedon*; 113, *Sepedomerus*; 114, *Sepedonea.* Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 100, 101, 104–106, 111–114 with scale 0.5 mm; the remaining Figs. with scale 1.0 mm.



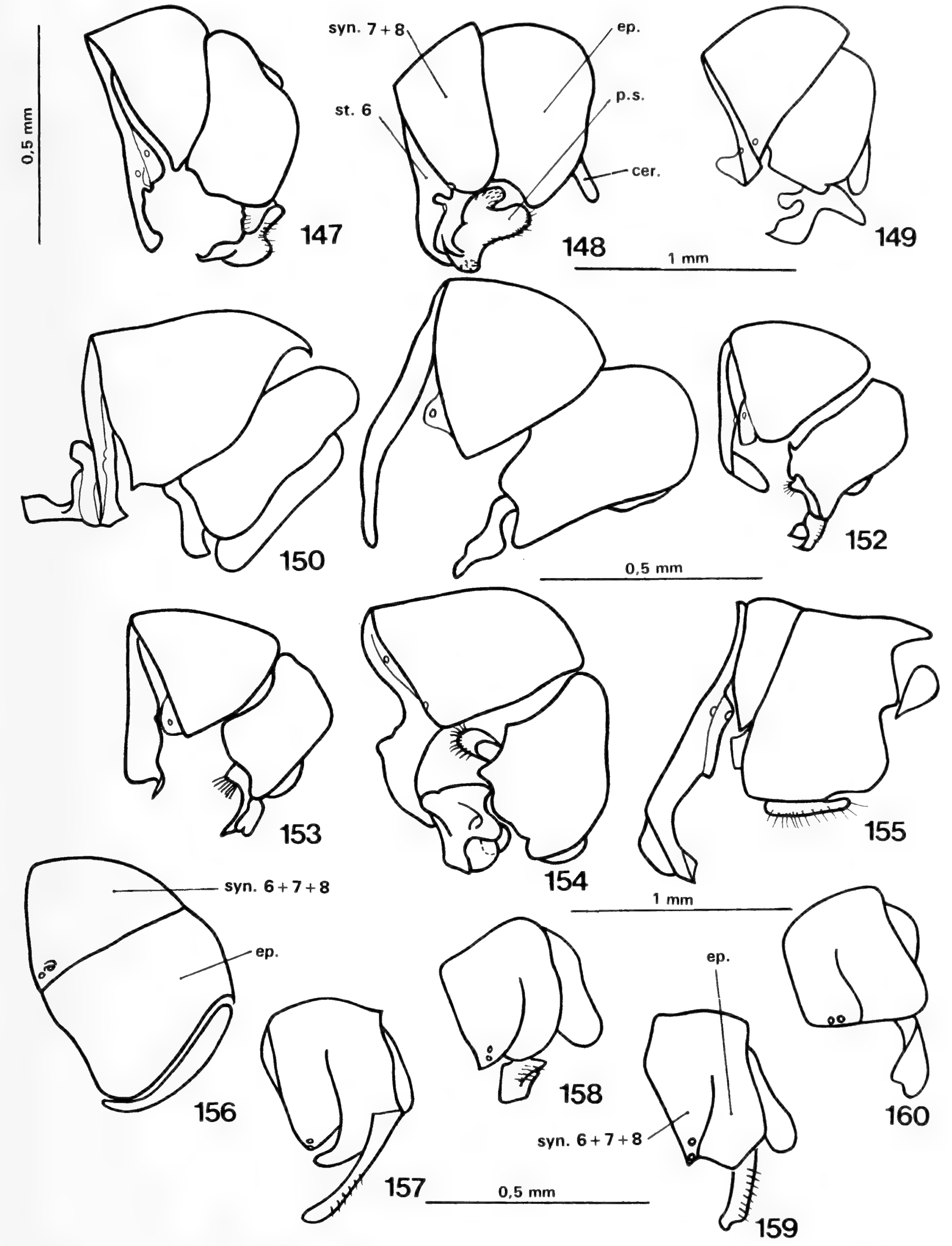
Figs. 115–123. Male terminalia, left lateral view: 115, *Sciomyza*; 116, *Oidematops*; 117, *Atrichomelina*; 118, *Tetanura*; 119, *Colobaea*; 120, *Calliscia*; 121, *Parectinocera*; 122, *Pteromicra*; 123, *Pherbellia*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); sternite 7 (st. 7); sternite 8 (st. 8); anterior surstylus (a. s.); posterior surstylus (p. s.); tergite 6 (terg. 6). Fig. 115 with scale 1.0 mm; the remaining Figs. with scale 0.5 mm.



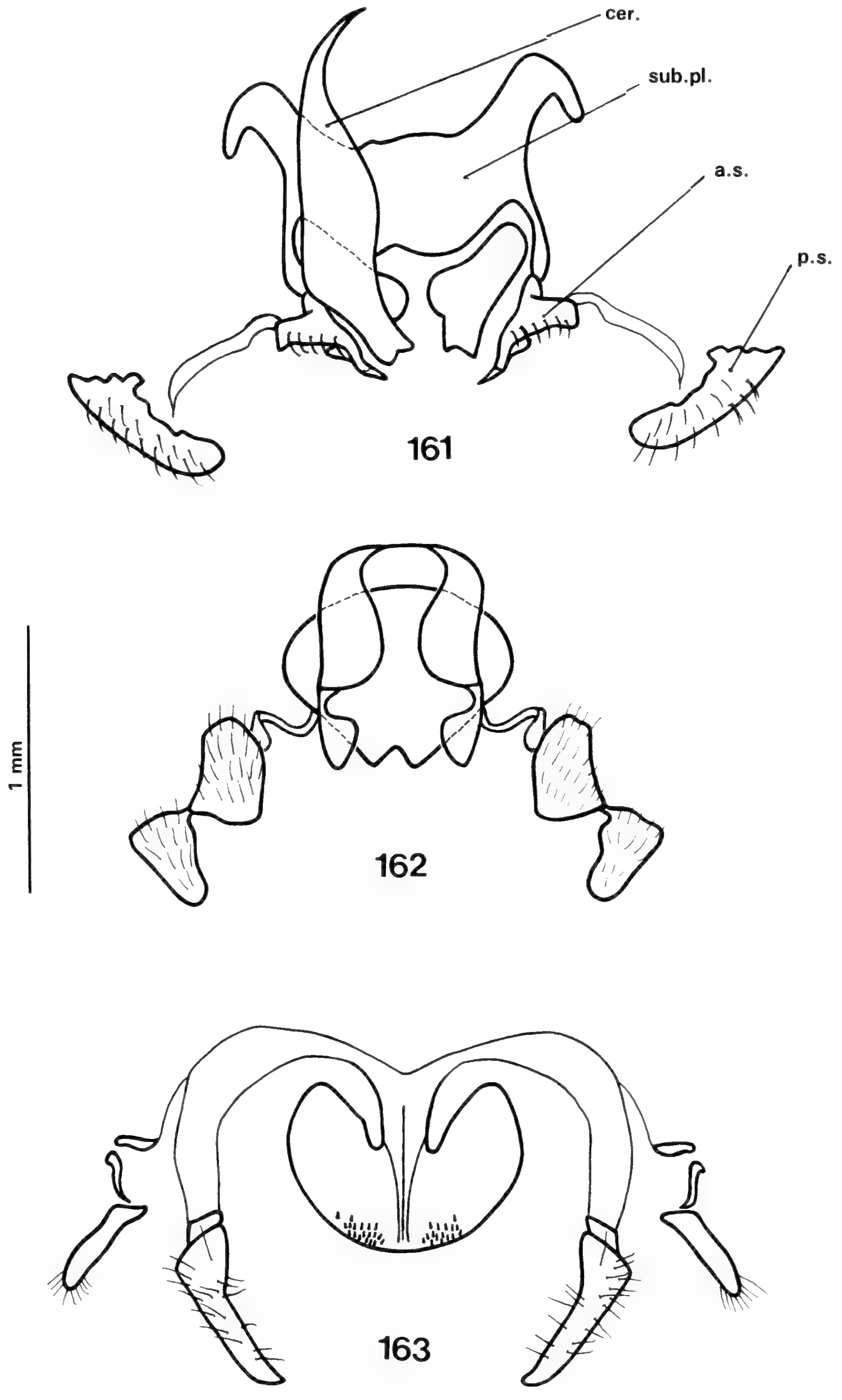
Figs. 124–135. Male terminalia, left lateral view: 124, *Ectinocera*; 125, *Renocera*; 126, *Antichaeta*; 127, *Chasmacryptum*; 128, *Shannonia*; 129, *Perilimnia*; 130, *Hoplodictya*; 131, *Dictya*; 132, *Hydromya*; 133, *Neolimnia*; 134, *Euthycerina*; 135, *Tetanocera*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 133 with scale 1.0 mm; the remaining Figs. with scale 0.5 mm.



Figs. 136–146. Male terminalia, left lateral view: 136, *Trypetolimnia*; 137, *Psacadina*; 138, *Steyskalina*; 139, *Dictyodes*; 140, *Ilione*; 141, *Pherbina*; 142, *Trypetoptera*; 143, *Limnia*; 144, *Poecilographa*; 145, *Pherbecta*; 146, *Protodictya*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); anterior surstylus (a. s.); posterior surstylus (p. s.). Figs. 138 and 146 with scale 0.5 mm; the remaining Figs. with scale 1.0 mm.



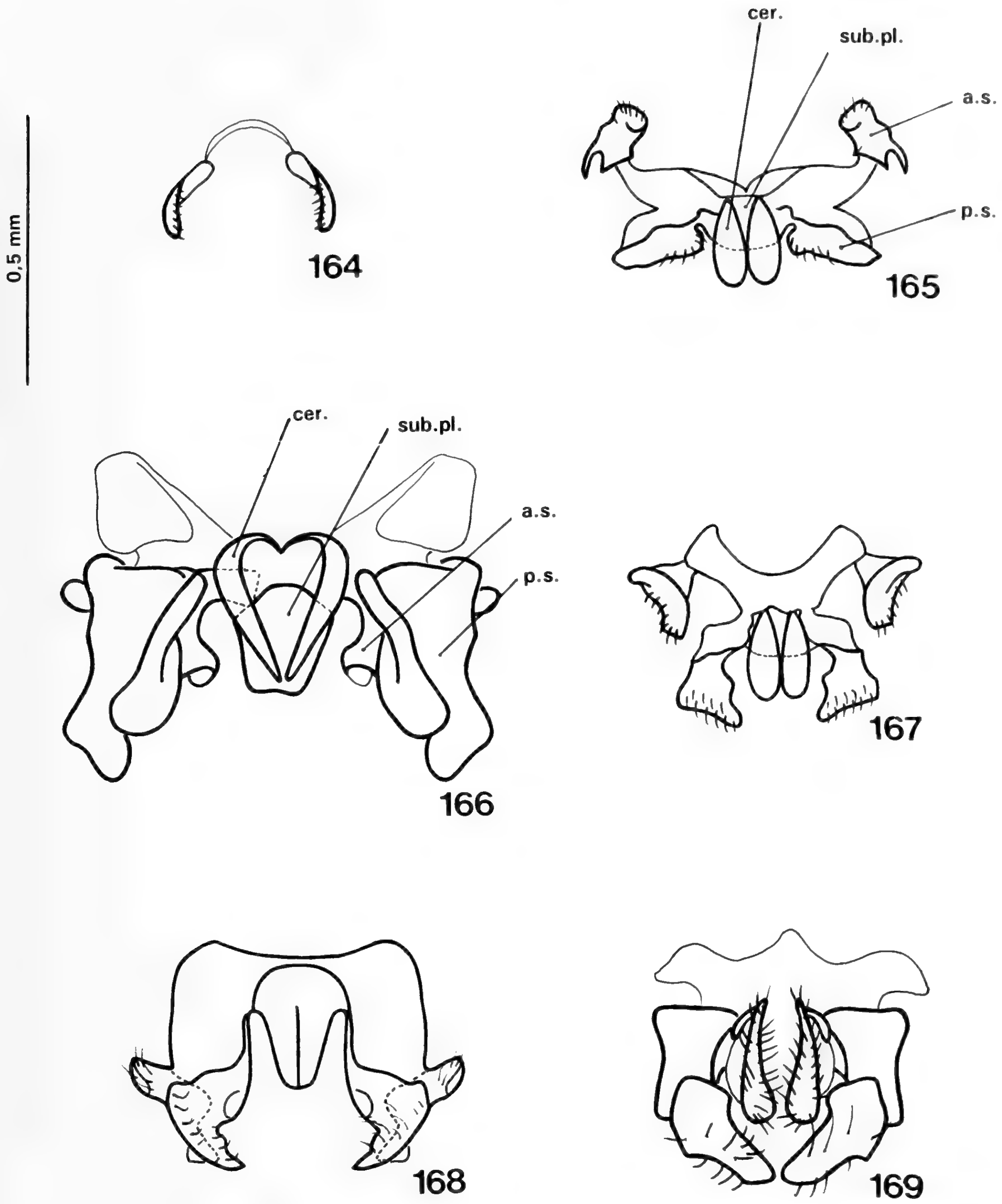
Figs. 147–160. Male terminalia, left lateral view: 147, *Guatemalia*; 148, *Elgiva*; 149, *Hedria*; 150, *Dichetophora*; 151, *Coremacera*; 152, *Dictyacium*; 153, *Euthycera*; 154, *Ethiolimnia*; 155, *Thecomyia*; 156, *Sepedoninus*; 157, *Sepedonella*; 158, *Sepedon*; 159, *Sepedomerus*; 160, *Sepedonea*. Cerci (cer.); epandrium (ep.); sternite 6 (st. 6); synsternite 7+8 (syn. 7+8); synsternite 6+7+8 (syn. 6+7+8); posterior surstylus (p. s.). Figs. 148–150, 154, 155 with scale 1.0 mm; the remaining Figs. 0.5 mm.



Figs. 161–163. Male terminalia, posterior view: 161, *Sciomyza*; 162, *Oidematops*; 163, *Atrichomelina*. Cerci (cer.); subepandrial plate (sub. pl.); anterior surstylus (a. s.); posterior surstylus (p. s.).

subgroup, from *Thecomyia* to *Sepedonea*, is established by eight characters: 6, 19, 28, 30, 31, 32, 33 and 35. It is the most corroborated lineage within this analysis.

Steyskal (1973) placed *Sepedon* in a group comprising the genera *Thecomyia, Sepedon, Sepedonella, Sepedoninus, Sepedomerus,* and *Sepedonea.* Steyskal (1973: 143) stated that "I do not believe that this group is sufficiently distinct from more typ-

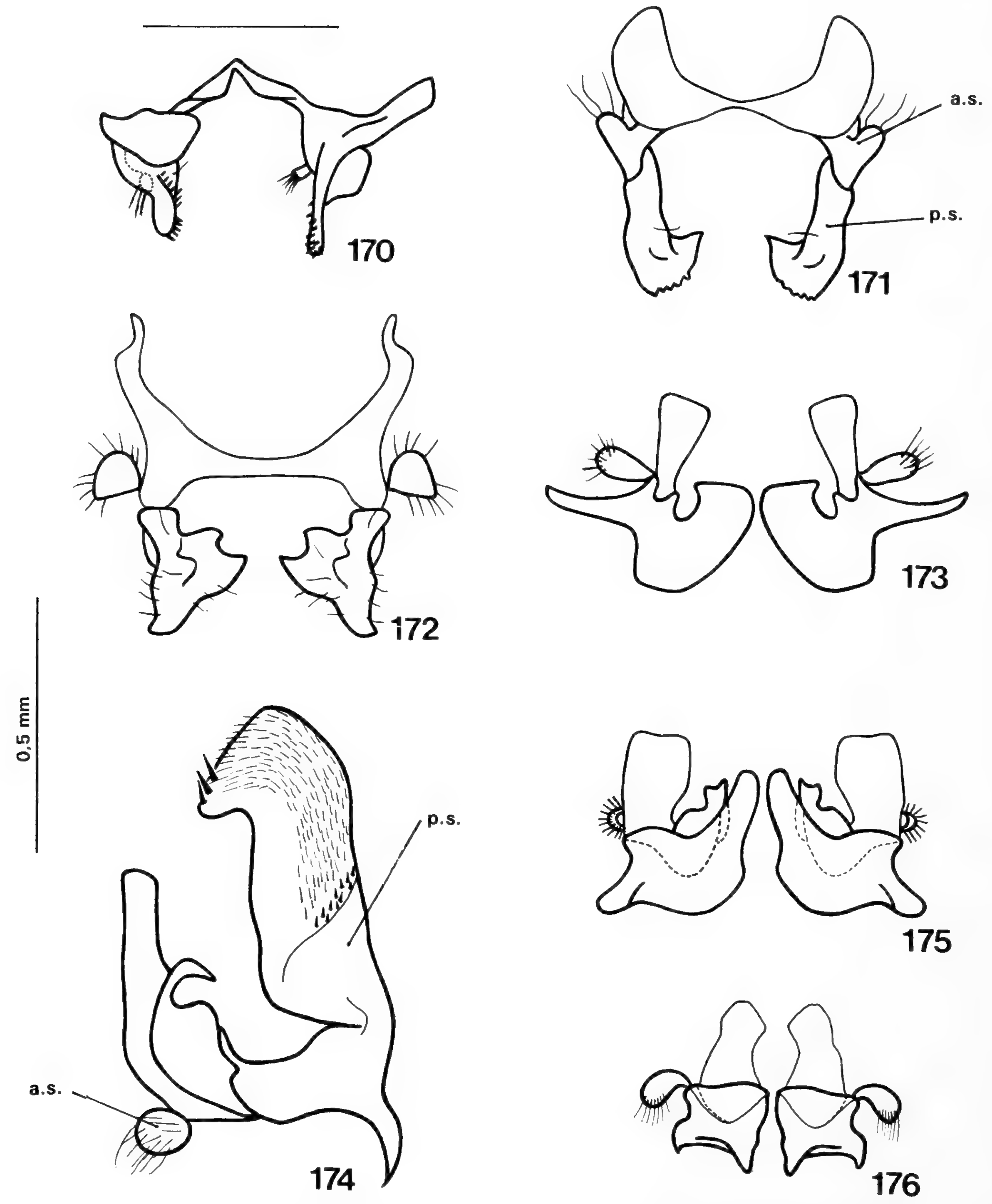


Figs. 164–169. Male terminalia, posterior view: 164, *Tetanura*; 165, *Colobaea*; 166, *Calliscia*; 167, *Parectinocera*; 168, *Pteromicra*; 169, *Pherbellia*. Cerci (cer.); subepandrial plate (sub. pl.); anterior surstylus (a. s.); posterior surstylus (p. s.).

ical Tetanocerini, especially from such genera as *Hedria* and *Dichetophora,* to be given the rank of tribe or even subtribe. We would prefer to call it merely "the *Sepedon* group." " This statement agrees with the result of the present analysis, but with the addition the genera *Ethiolimnia* and *Teutoniomyia* to the *Sepedon* group.

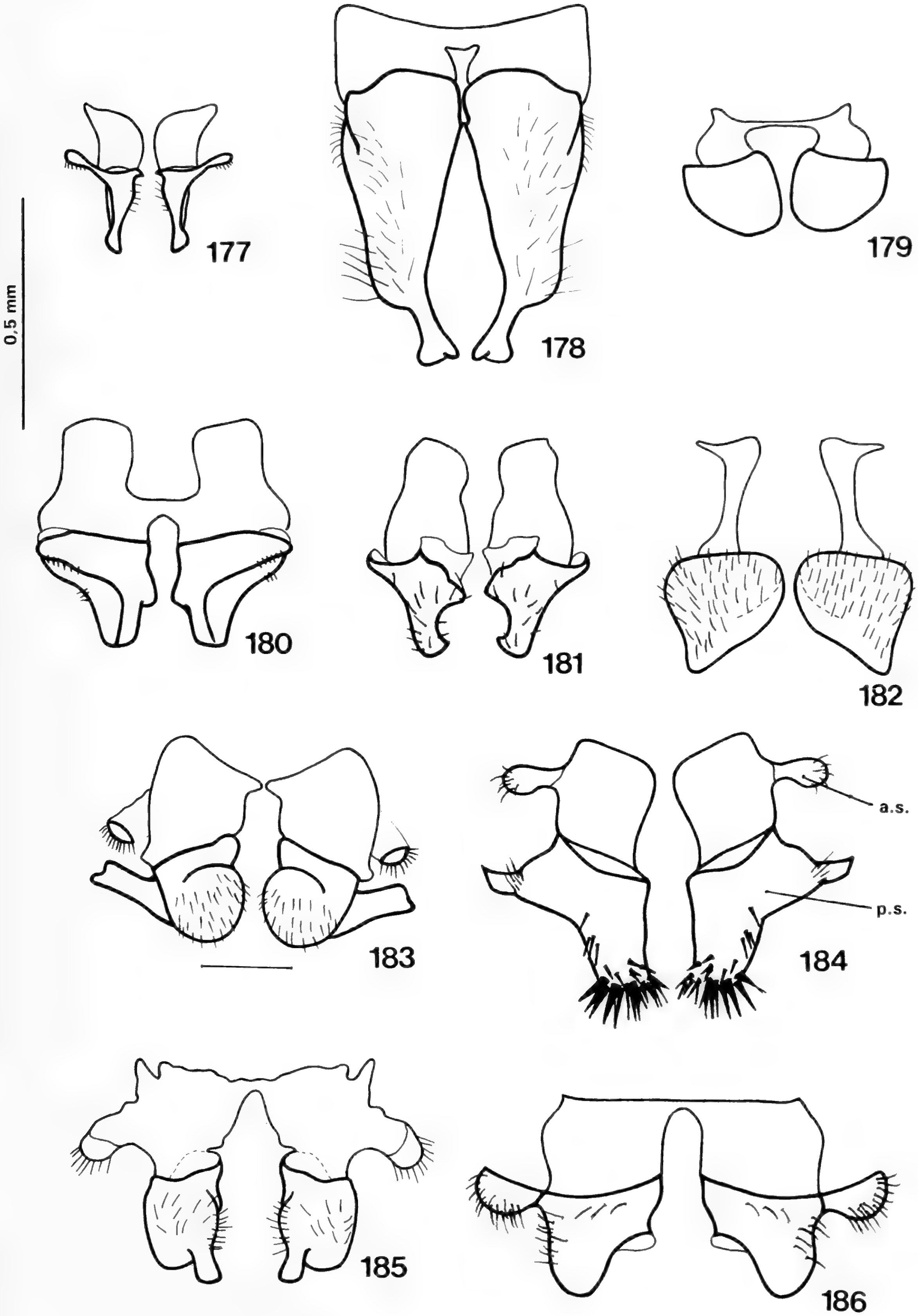
Proposal of classification.—The following natural classification was done using the sequencing convention (Wiley 1981). The subfamilies Salticellinae and Sciomyzinae and the tribes Sciomyzini and Tetanocerini are confirmed.

Sciomyzidae Fallén, 1820
Salticellinae Hendel, 1924
Salticella Robineau-Desvoidy, 1830
Sciomyzinae Fallén, 1820
Sciomyzini Fallén, 1820
Pherbellia Robineau-Desvoidy, 1830

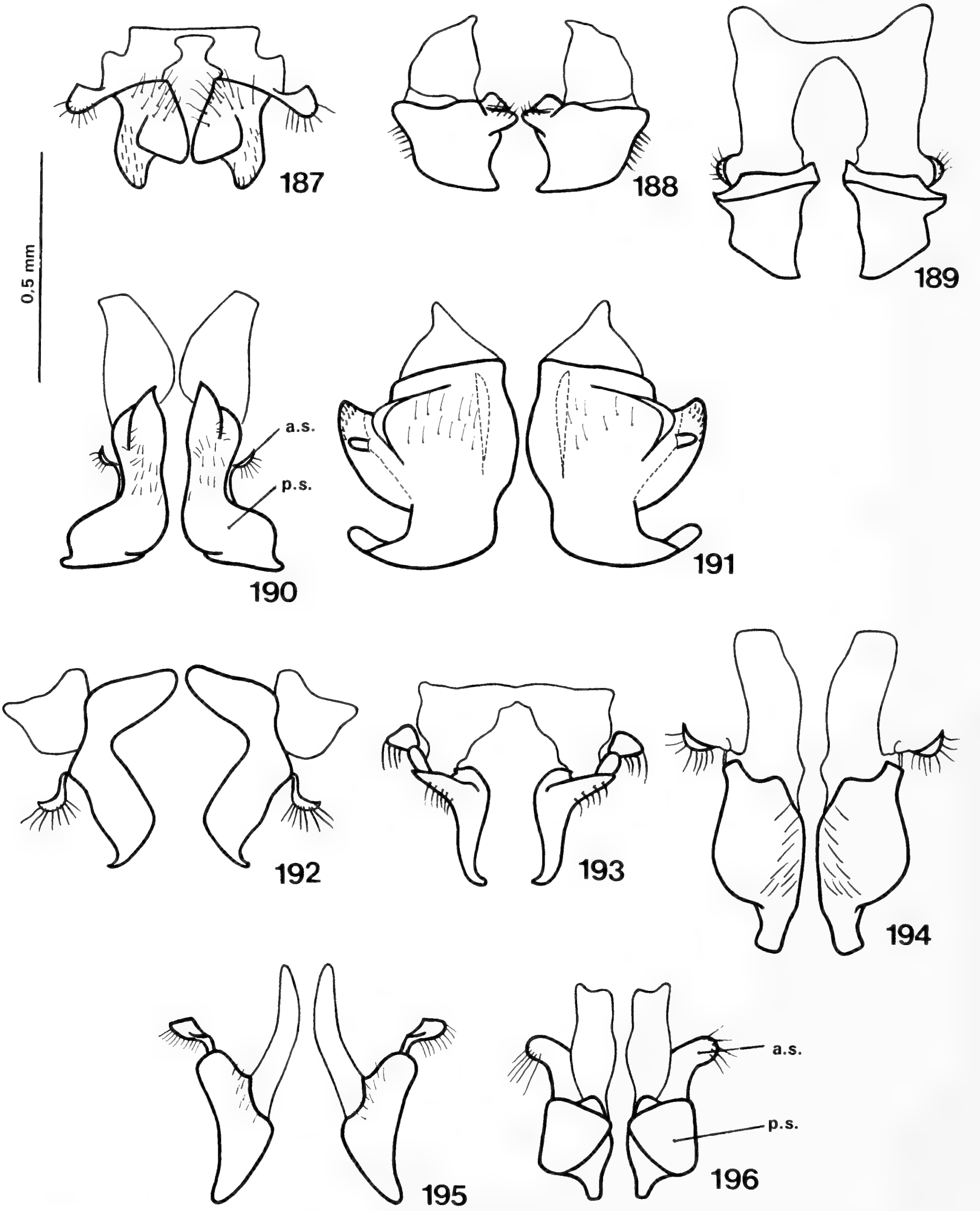


Figs. 170–176. Male terminalia, posterior view: 170, *Antichaeta*; 171, *Shannonia*; 172, *Perilimnia*; 173, *Hoplodictya*; 174, *Dictya* (lateral view), 175, *Hydromya*; 176, *Neolimnia*. Anterior surstylus (a. s.); posterior surstylus (p. s.).

Pteromicra Lioy, 1864
Calliscia Steyskal, 1975
Parectinocera Becker, 1919
Colobaea Zetterstedt, 1837
Tetanura Fallén, 1820
Atrichomelina Cresson, 1920
Oidematops Cresson, 1920
Sciomyza Fallén, 1820
Tetanocerini Hendel, 1900
Eutrichomelina Steyskal, 1975
Ectinocera Zetterstedt, 1838
Renocera Hendel, 1900
Antichaeta Haliday, 1838
Chasmacryptum Becker, 1907
Shannonia Malloch, 1933
Perilimnia Becker, 1919
Hoplodictya Cresson, 1920
Dictya Meigen, 1803

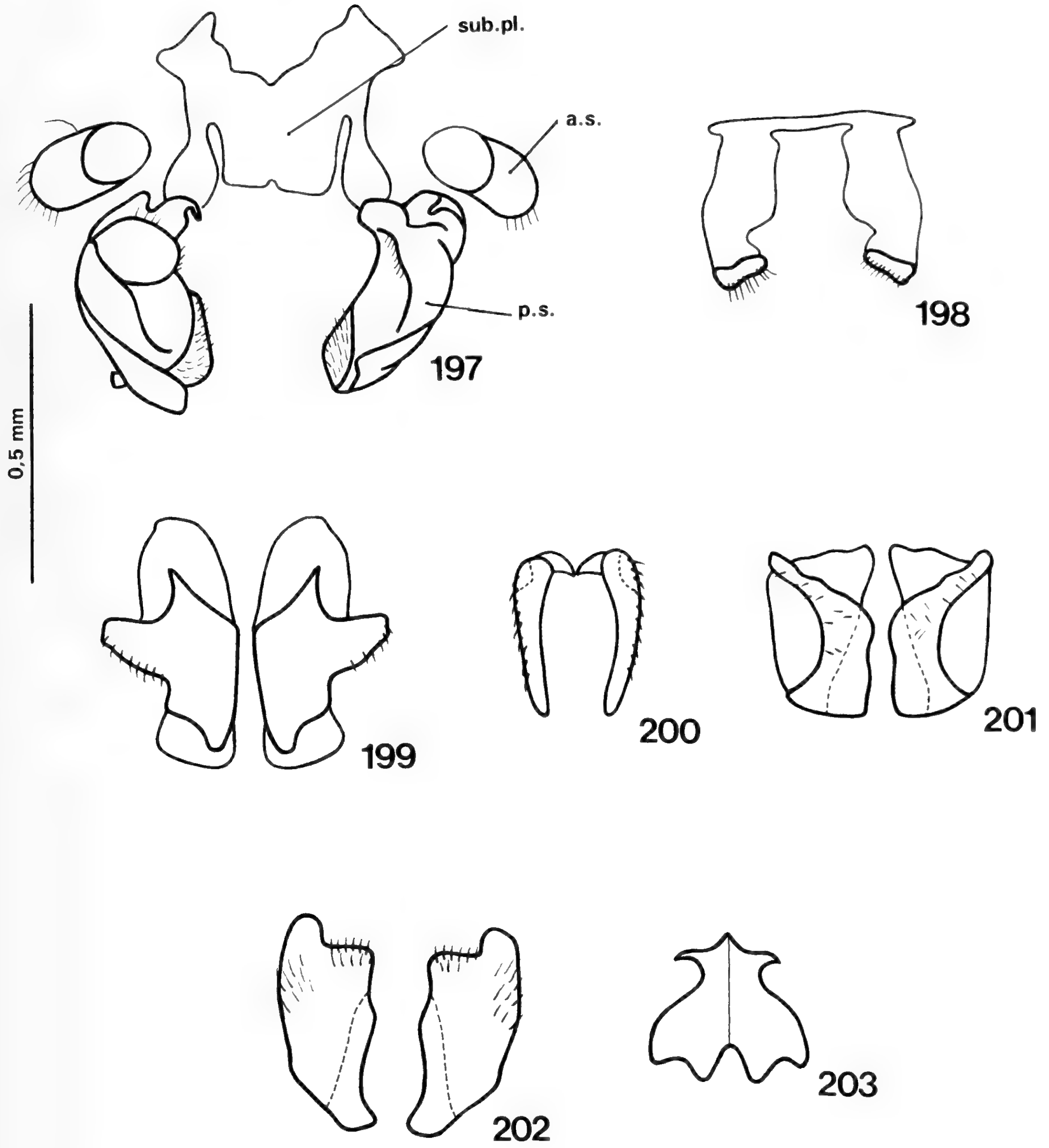


Figs. 177–186. Male terminalia, posterior view: 177, *Euthycerina*; 178, *Tetanocera*; 179, *Trypetolimnia*; 180, *Psacadina*; 181, *Steyskalina*; 182, *Dictyodes*; 183, *Ilione*; 184, *Pherbina*; 185, *Trypetoptera*; 186, *Limnia*. Anterior surstylus (a. s.); posterior surstylus (p. s.).



Figs. 187–196. Male terminalia, posterior view: 187, *Poecilographa*; 188, *Pherbecta*; 189, *Protodictya*; 190, *Guatemalia*; 191, *Elgiva*; 192, *Hedria*; 193, *Dichetophora*; 194, *Coremacera*; 195, *Dictyacium*; 196, *Euthycera*. Anterior surstylus (a. s.); posterior surstylus (p. s.).

Hydromya Robineau-Desvoidy, 1830
Neolimnia Barnes, 1976
Tetanoceroides Malloch, 1933
Euthycerina Malloch, 1933
Tetanocera Duméril, 1800
Trypetolimnia Mayer, 1953
Psacadina Enderlein, 1939
Dictyodes Malloch, 1933

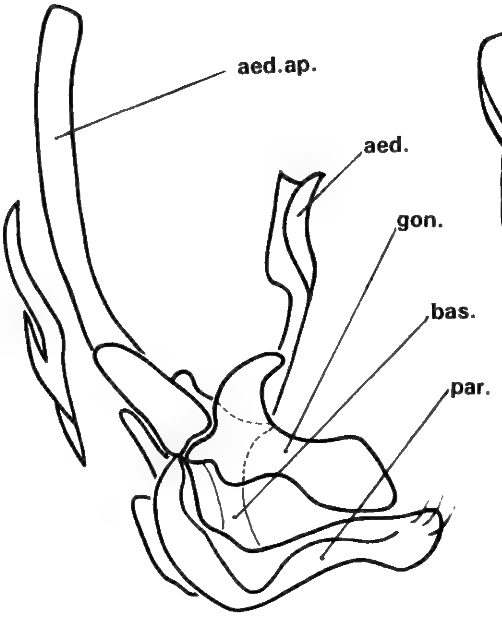


Figs. 197–203. Male terminalia, posterior view: 197, *Ethiolimnia*; 198, *Thecomyia*; 199, *Sepedoninus*; 200, *Sepedonella*; 201, *Sepedon*; 202, *Sepedomerus*; 203, *Sepedonea*. Anterior surstylus (a. s.); posterior surstylus (p. s.).

Ilione Verbeke, 1964
Pherbina Robineau-Desvoidy, 1830
Trypetoptera Hendel, 1900
Limnia Robineau-Desvoidy, 1830
Poecilographa Melander, 1913
Pherbecta Steyskal, 1956
Protodictya Malloch, 1933
Guatemalia Steyskal, 1960
Elgiva Meigen, 1838
Hedria Steyskal, 1954
Dichetophora Rondani, 1868
Coremacera Rondani, 1856
Dictyacium Steyskal, 1920
Euthycera Latreille, 1829
Ethiolimnia Verbeke, 1950
Teutoniomyia Hennig, 1952
Thecomyia Perty, 1833
Sepedoninus Verbeke, 1950
Sepedonella Verbeke, 1950
Sepedon Latreille, 1804
Sepedomerus Steyskal, 1973
Sepedonea Steyskal, 1973
Steyskalina Knutson, 1999

Conclusions

The subfamilies Salticellinae and Sciomyzinae are monophyletic. In the Sciomy-



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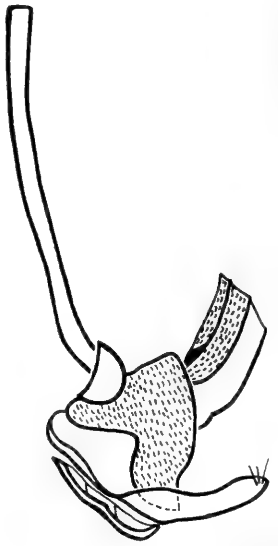

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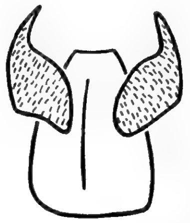

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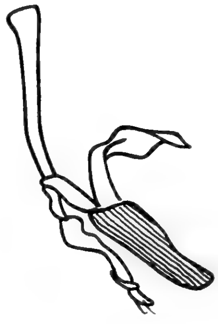

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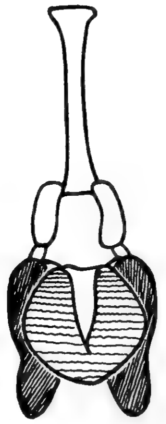

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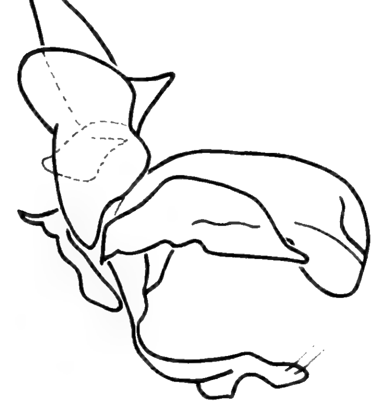

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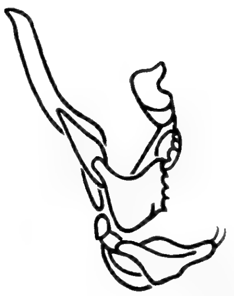

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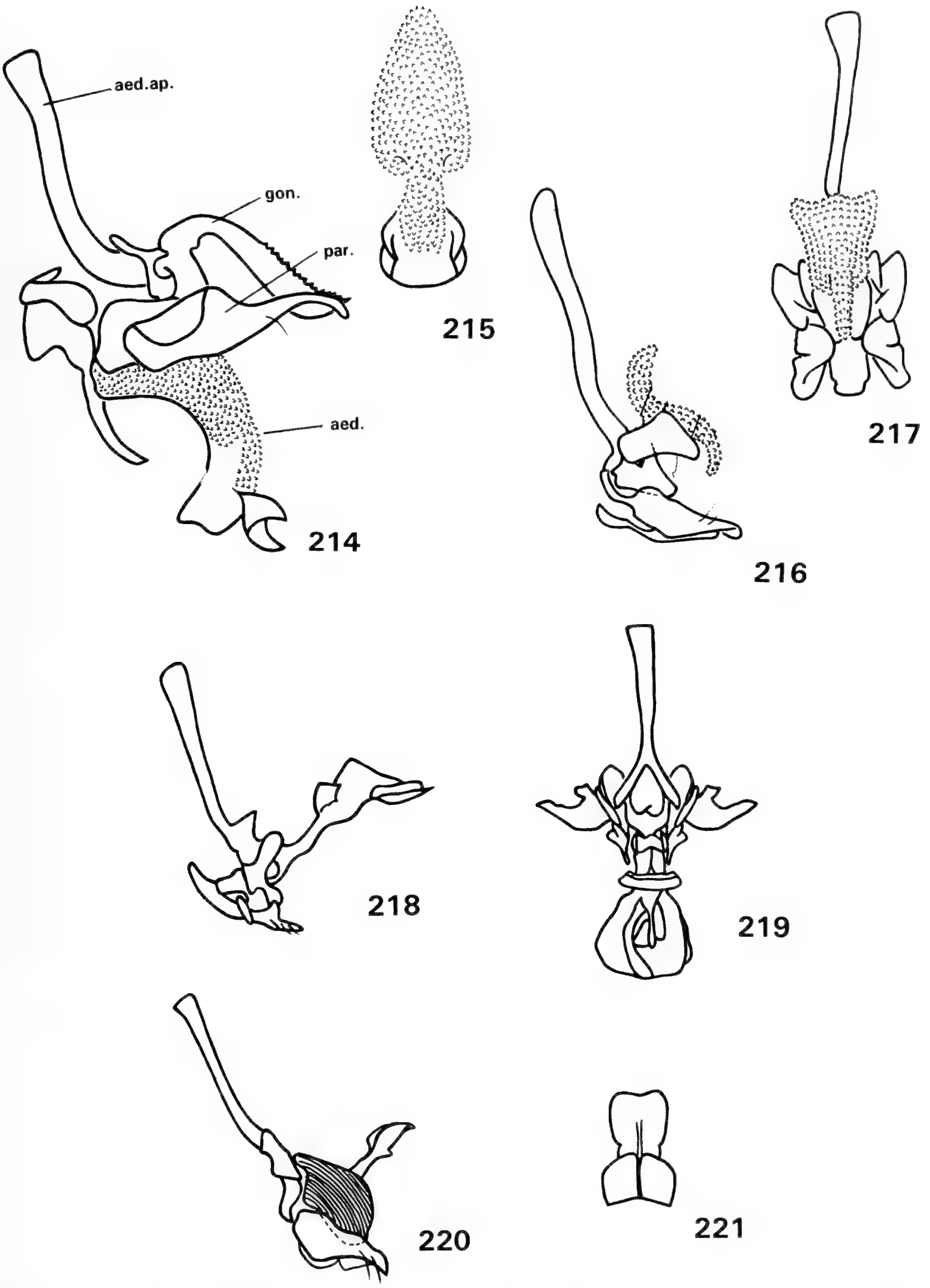
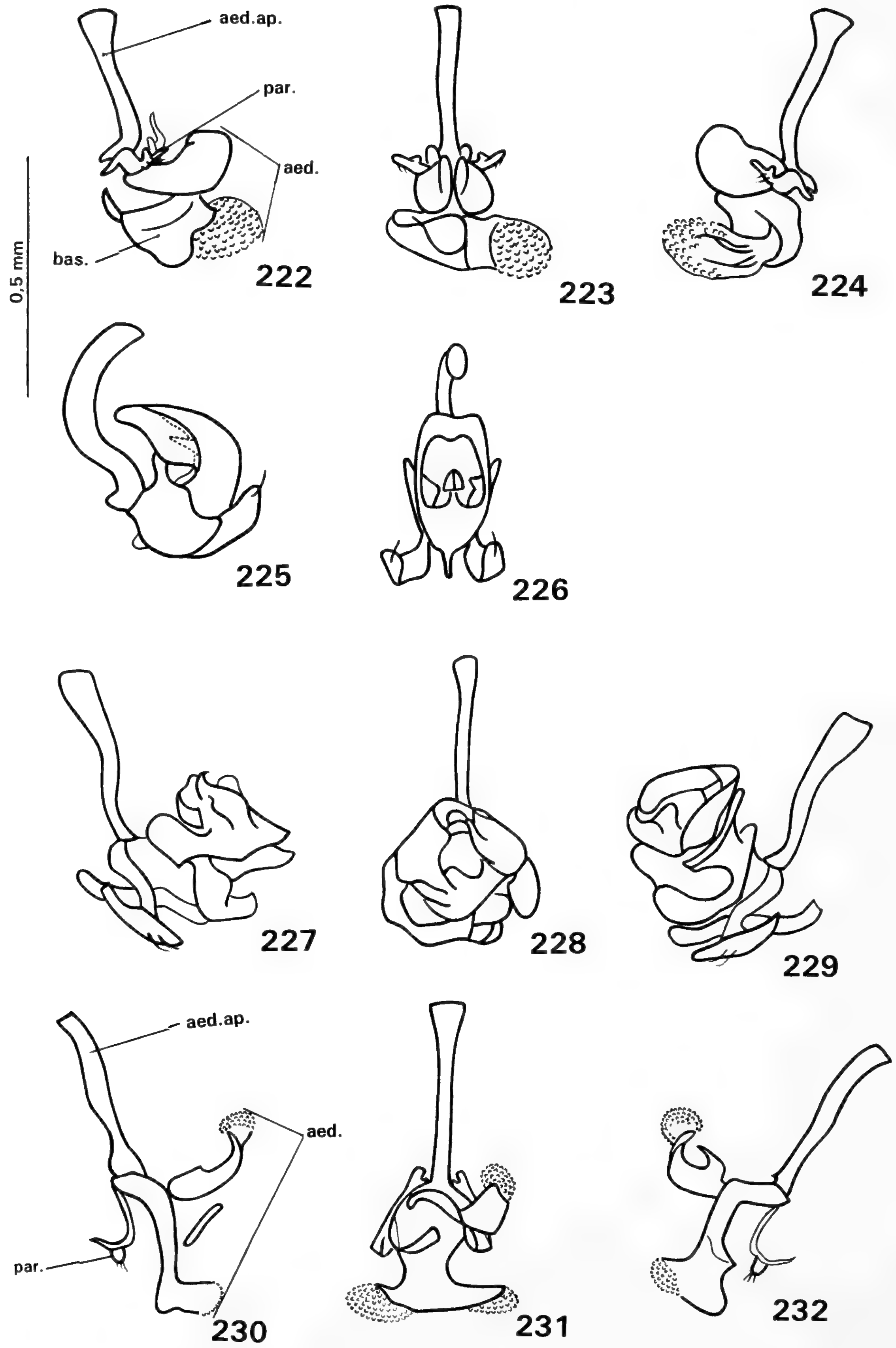
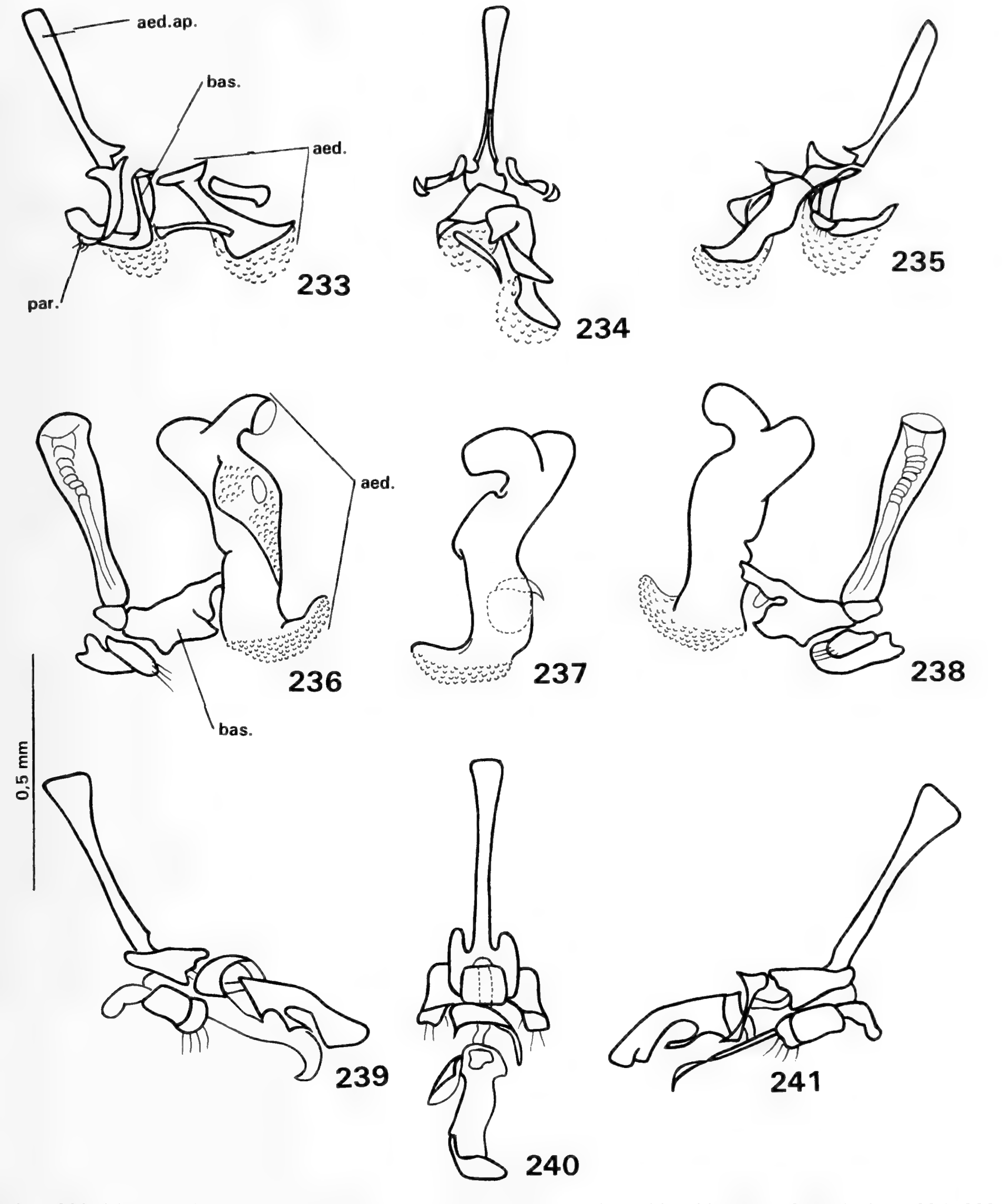
Figs. 204–213. Male terminalia. 204, 208, 206, 210, 212, Right lateral view; 205, 207, 209, 211, 213, frontal view. 204, 205, *Sciomyza*; 206, 207, *Oidematops*; 208–209, *Atrichomelina*; 210–211, *Tetanura*; 212–213, *Colobaea.* Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); gonopod (gon.); hypandrium (hip.); paramere (par.).



Figs. 214–221. Male terminalia. 214, 216, 218, 220, Right lateral view; 215, 217, 219, 221, frontal view. 214, 215, *Calliscia*; 216, 217, *Parectinocera*; 218, 219, *Pteromicra*; 220, 221, *Pherbellia*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); gonopod (gon.); hypandrium (hip.); paramere (par.).



Figs. 222–232. Male terminalia. 222, 225, 227, 230, Right lateral view; 223, 226, 228, 231, frontal view; 224, 229, 232, left lateral view. 222–224, *Ectinocera*; 225–226, *Antichaeta*; 227–229, *Chasmacryptum*; 230–232, *Shannonia*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

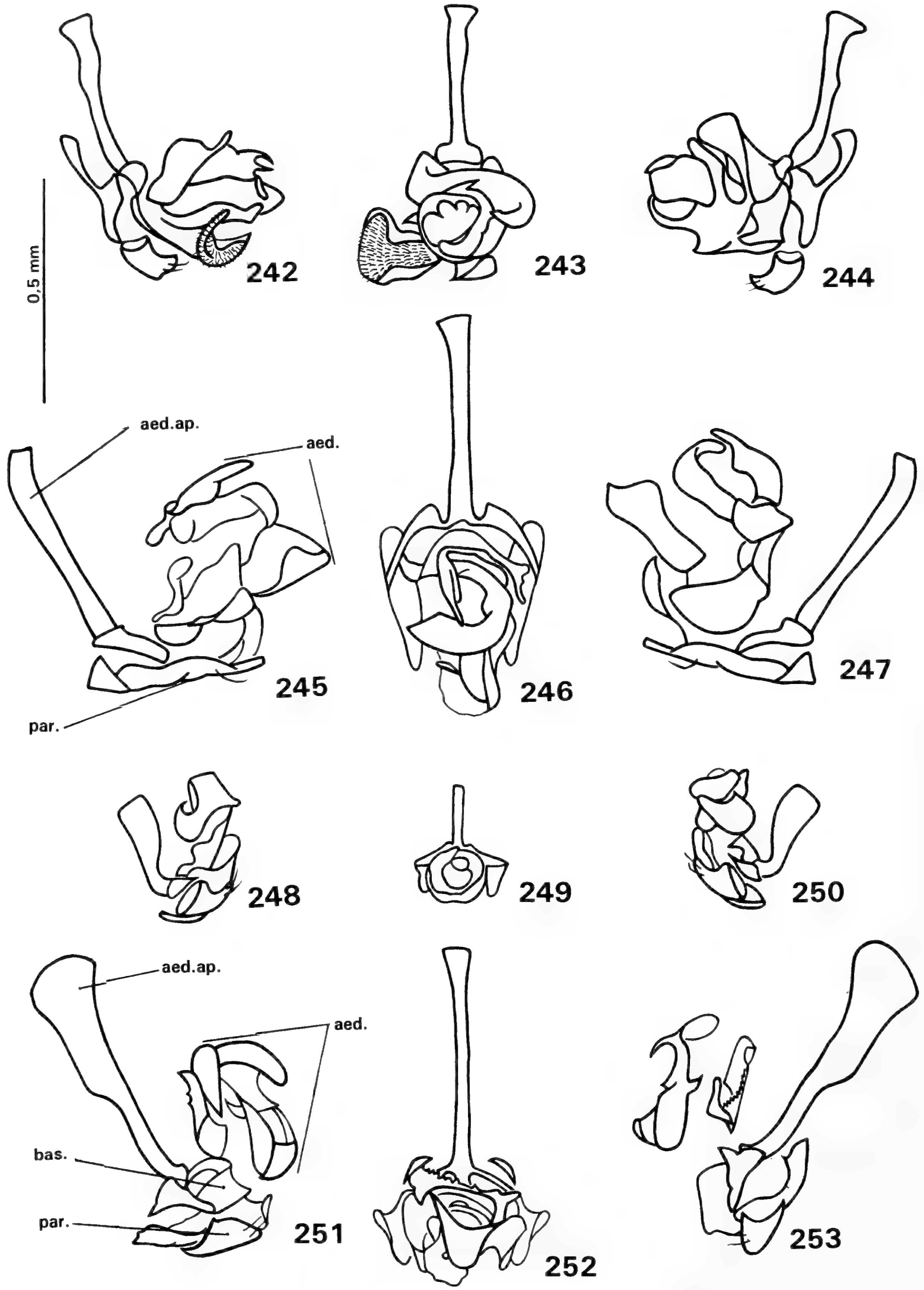


Figs. 233–241. Male terminalia. 233, 236, 239, Right lateral view; 234, 237, 240, frontal view; 235, 238, 241, left lateral view. 233–235, *Perilimnia*; 236–238, *Hoplodictya*; 239–241, *Dictya*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

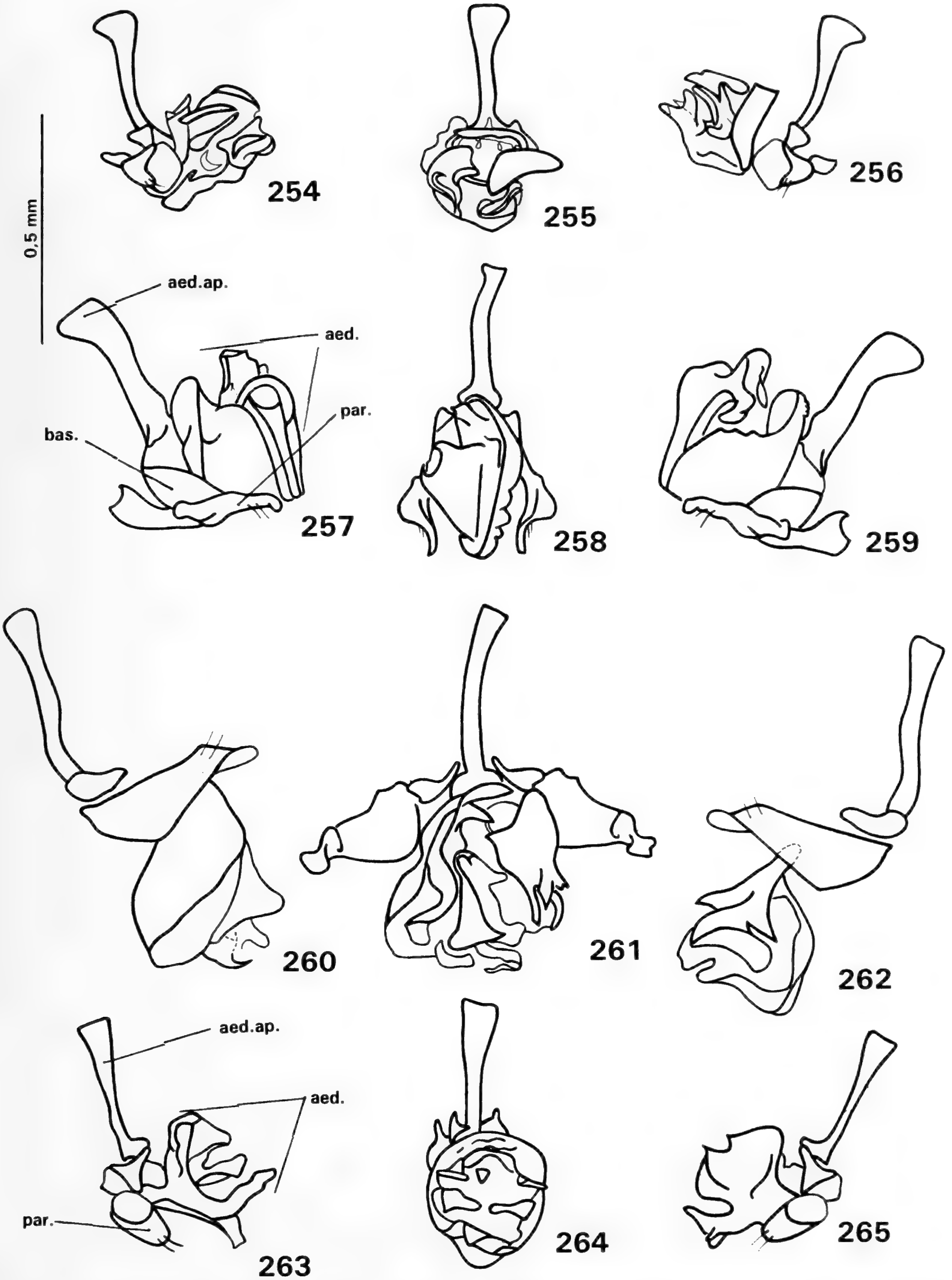
zinae the tribes Sciomyzini and Tetanocerini are monophyletic.

The tribe Sciomyzini includes *Pherbellia, Pteromicra, Calliscia, Parectinocera, Colobaea, Tetanura, Atrichomelina, Oidematops,* and *Sciomyza.*

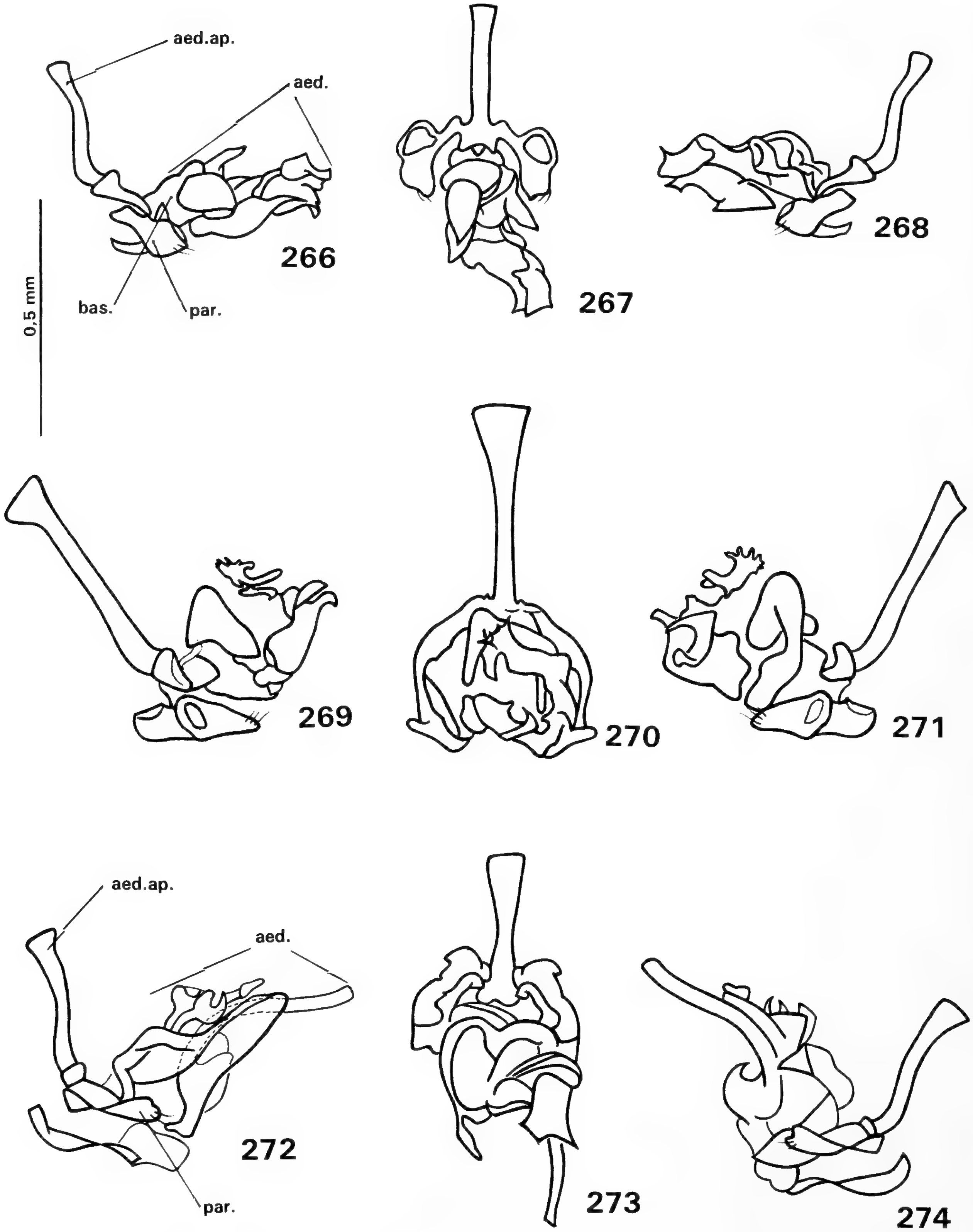
The tribe Tetanocerini includes *Antichaeta, Chasmacryptum, Coremacera, Dichetophora, Dictya, Dictyacium, Dictyodes, Ectinocera, Elgiva, Ethiolimnia, Euthycera, Euthycerina, Eutrichomelina, Guatemalia, Hedria, Hydromya, Hoplodictya, Ilione,*



Figs. 242–253. Male terminalia. 242, 245, 248, 251, Right lateral view; 243, 246, 249, 252, frontal view; 244, 247, 250, 253, left lateral view. 242–244, *Hydromya*; 245–247, *Neolimnia*; 248–250, *Euthycerina*; 251–253, *Tetanocera*. Aedeagal apodeme (aed. ap.); aedeagus (aed.); paramere (par.).



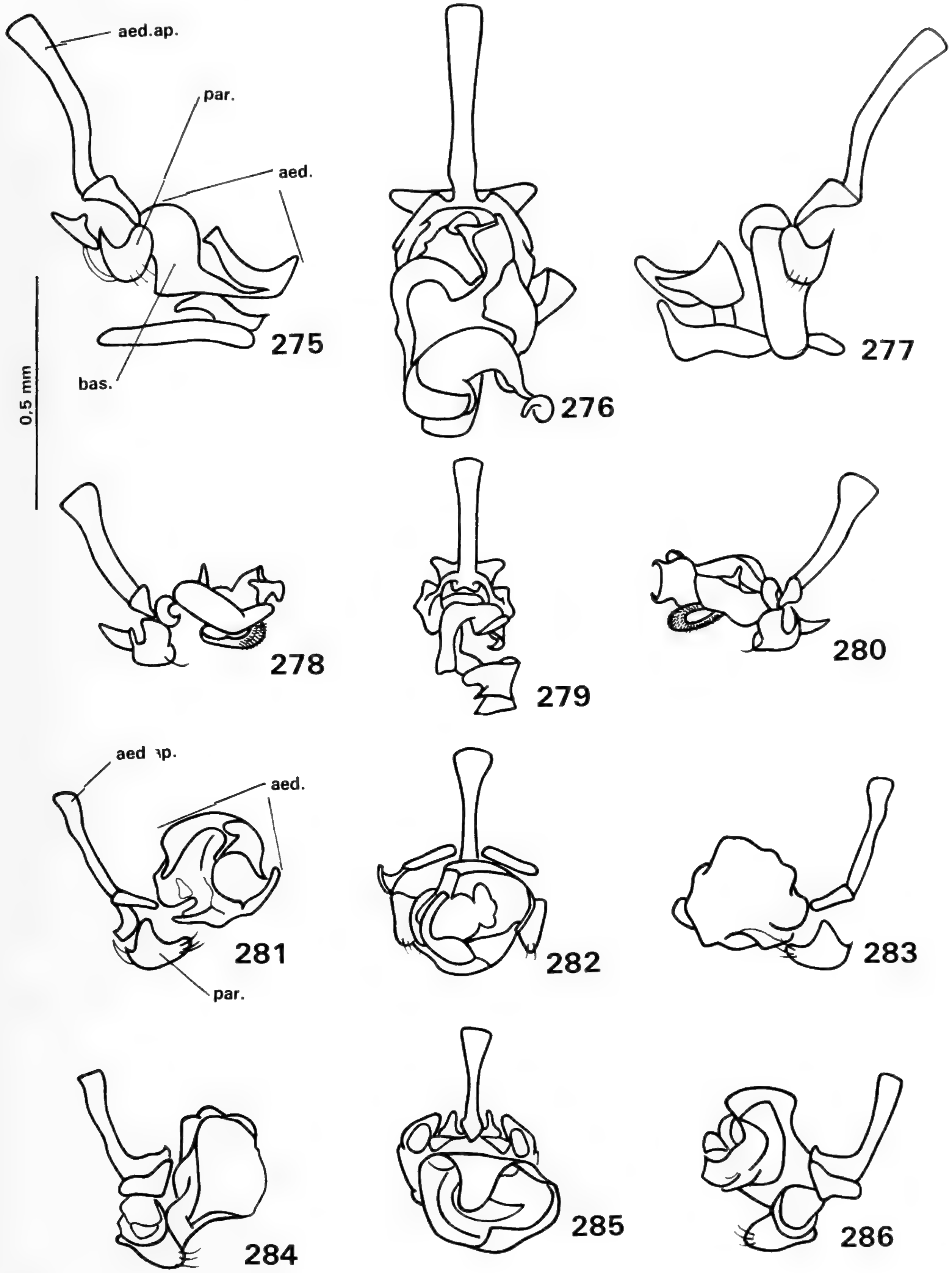
Figs. 254–265. Male terminalia. 254, 257, 260, 263, Right lateral view; 255, 258, 261, 264, frontal view; 256, 259, 262, 265, left lateral view. 254–256, *Trypetolimnia*; 257–259, *Psacadina*; 260–262, *Steyskalina*; 263–265, *Dictyodes*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).



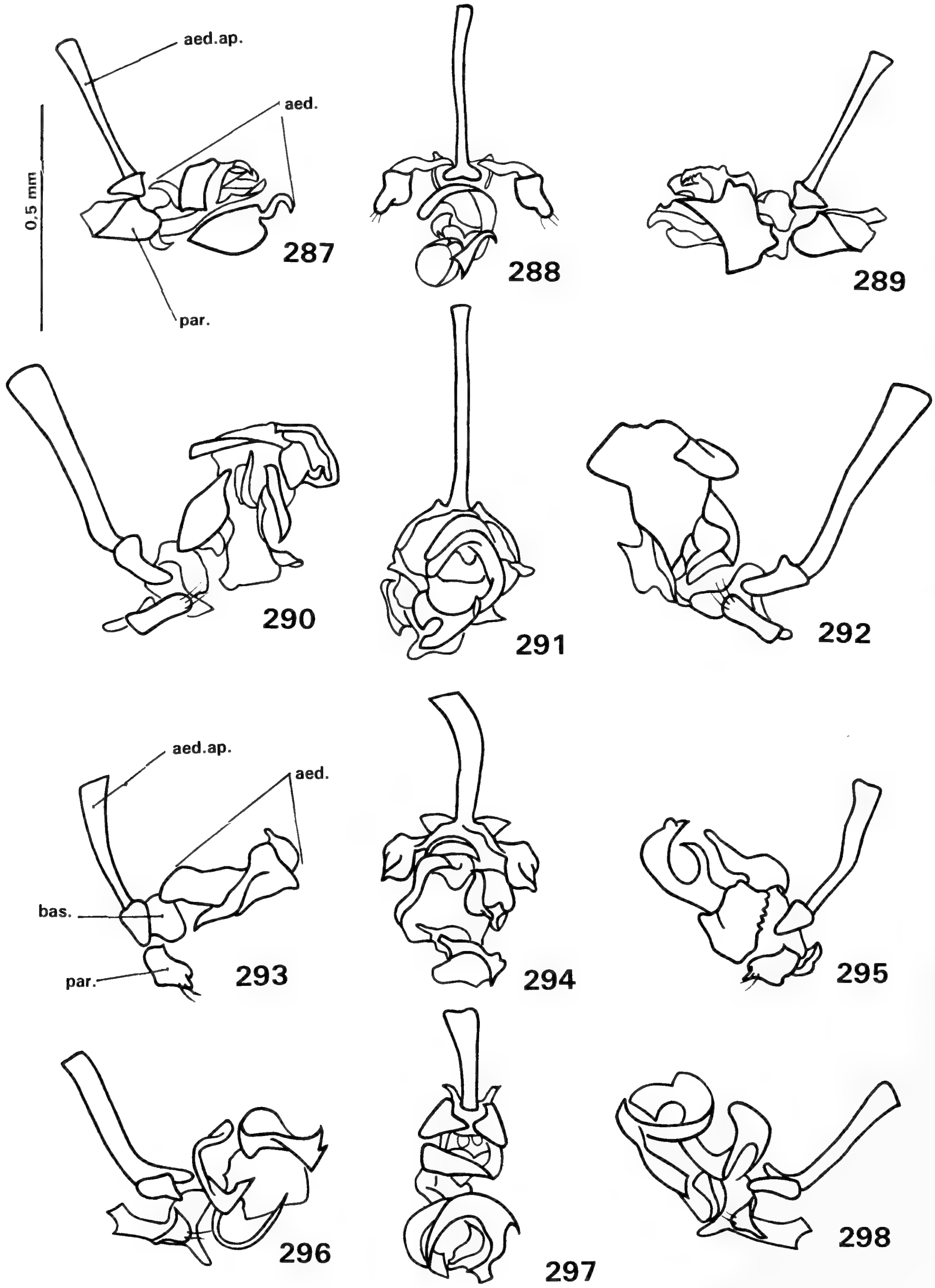
Figs. 266–274. Male terminalia. 266, 269, 272, Right lateral view; 267, 270, 273, frontal view; 268, 271, 274, left lateral view. 266–268, *Ilione*; 269–271, *Pherbina*; 272–274, *Trypetoptera*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

Limnia, Neolimnia, Perilimnia, Pherbecta, Pherbina, Poecilographa, Protodictya, Psacadina, Renocera, Sepedoninus, Sepedonella, Sepedon, Sepedomerus, Sepedonea, Shannonia, Steyskalina, Tetanocera, Tetanoceroides, Trypetoptera, Trypetolimnia, Teutoniomyia, and *Thecomyia.*

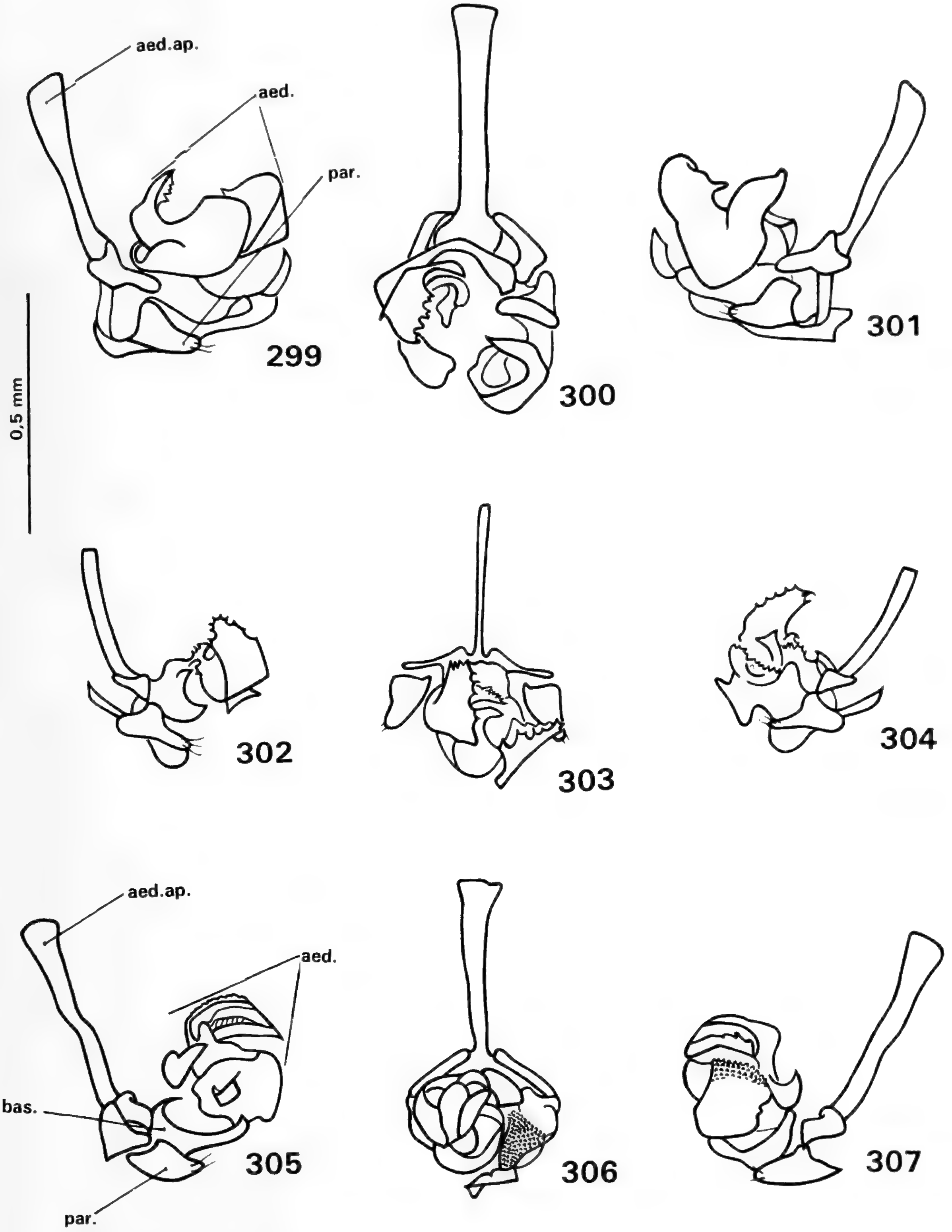
Within the Sciomyzini a monophyletic



Figs. 275–286. Male terminalia. 275, 278, 281, 284, Right lateral view; 276, 279, 282, 285, frontal view; 377, 380, 383, 386, left lateral view. 275–277, *Limnia*; 278–280, *Poecilographa*; 281–283, *Pherbecta*; 284–286, *Protodictya*. Aedeagal apodeme (aed. ap.); aedeagus (aed.); paramere (par.).



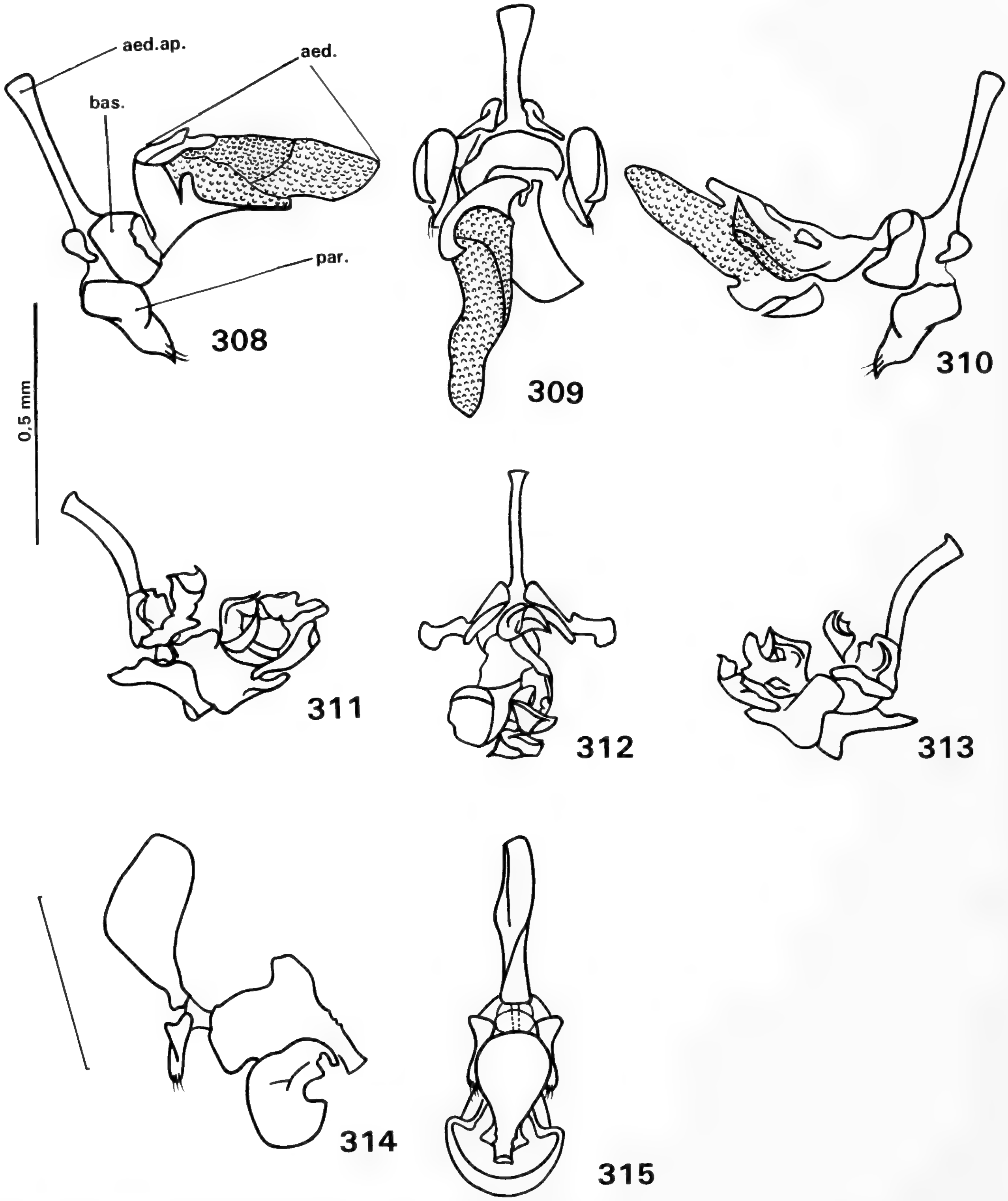
Figs. 287–298. Male terminalia. 287, 290, 293, 296, Right lateral view; 288, 291, 294, 297, frontal view; 289, 292, 295, 298, left lateral view. 287–289, *Guatemalia*; 290–292, *Elgiva*; 293–295, *Hedria*; 296–298, *Dichetophora.* Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).



Figs. 299–307. Male terminalia. 299, 302, 305, Right lateral view; 300, 303, 305, frontal view; 301, 304, 306, left lateral view. 299–301, *Coremacera*; 302–304, *Dictyacium*; 305–307, *Euthycera*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

group was formed by the genera *Colobaea, Tetanura, Atrichomelina, Oidematops* + *Sciomyza.* In this group there is the subgroup formed by *Atrichomelina, Oidematops* + *Sciomyza.*

The groups of *Shannonia* + *Perilimnia* and *Hoplodictya* + *Dictya,* at the base of Tetanocerini, are monophyletic. Three other major groups of genera are formed within the Tetanocerini: the first by *Eu-*



Figs. 308–315. Male terminalia. 308, 311, 314, Right lateral view; 309, 312, 315, frontal view; 310, 313, left lateral view. 308–310, *Ethiolimnia*; 311–313, *Thecomyia*; 314, 315, *Sepedoninus*. Aedeagal apodeme (aed. ap.); basiphallus (bas.); aedeagus (aed.); paramere (par.).

thycerina, Psacadina Enderlein (1933), *Steyskalina, Tetanocera,* and *Trypetolimnia,* the second by the genera *Dictyodes, Ilione, Pherbina, Trypetoptera, Limnia, Poecilographa,* and *Pherbecta* + *Protodictya,* and the third by *Guatemalia, Elgiva, Dichetophora, Hedria, Coremacera, Dictyacium, Euthycera, Ethiolimnia, Teutoniomyia, Thecomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus* + *Se-*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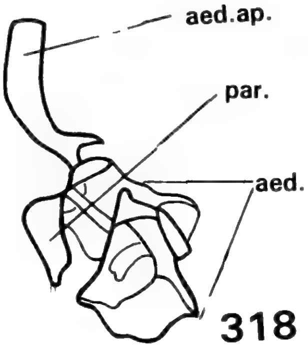

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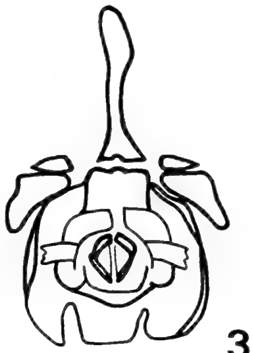
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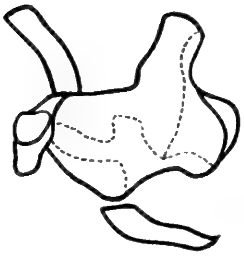
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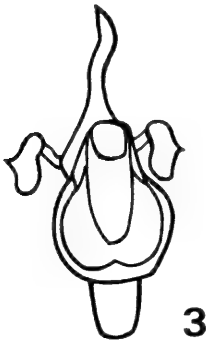
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Figs. 316–322. Male terminalia. 316, 318, 320, 322, Right lateral view; 317, 319, 321, frontal view. 316, 317, *Sepedonella*; 318, 319, *Sepedon*; 320, 321, *Sepedomerus*; 322, *Sepedonea*. Aedeagal apodeme (aed. ap.); aedeagus (aed.); paramere (par.).

pedonea. Within the last group the genera *Coremacera, Dictyacium,* and *Euthycera* form a monophyletic clade without any resolution of their phylogenetic relationships; and the group of *Ethiolimnia, Teutoniomyia, Thecomyia, Sepedoninus, Sepedonella, Sepedon, Sepedomerus* + *Sepedonea* is monophyletic.

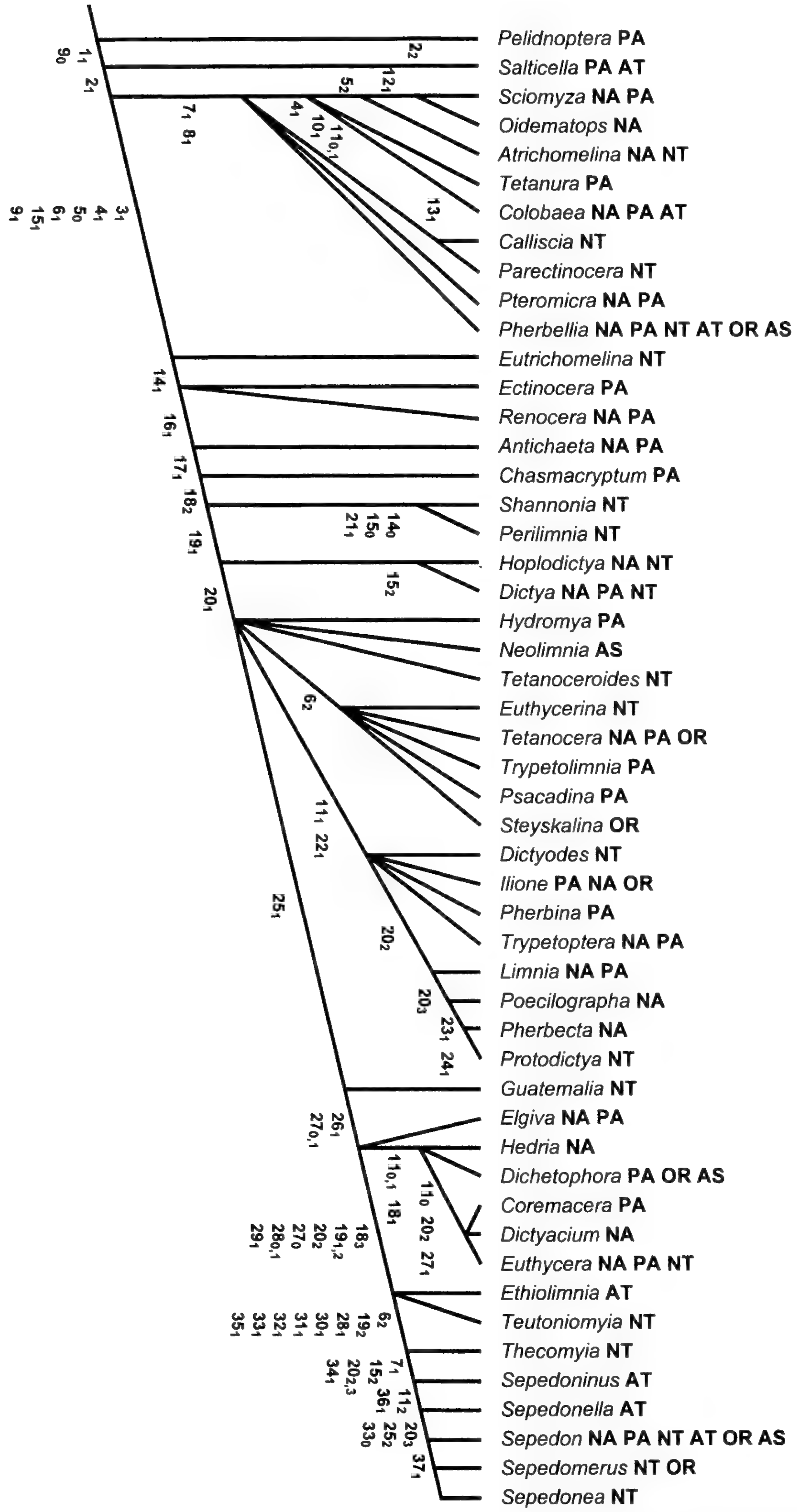

Fig. 323. Consensus cladogram. Outgroup *Pelidnoptera.* 37 characters. Consistency index: 0.60. Retention index: 0.88. Regions: AT, Afrotropical; AS, Australian; NA, Nearctic; NT, Neotropical; OR, Oriental; PA, Palearctic.

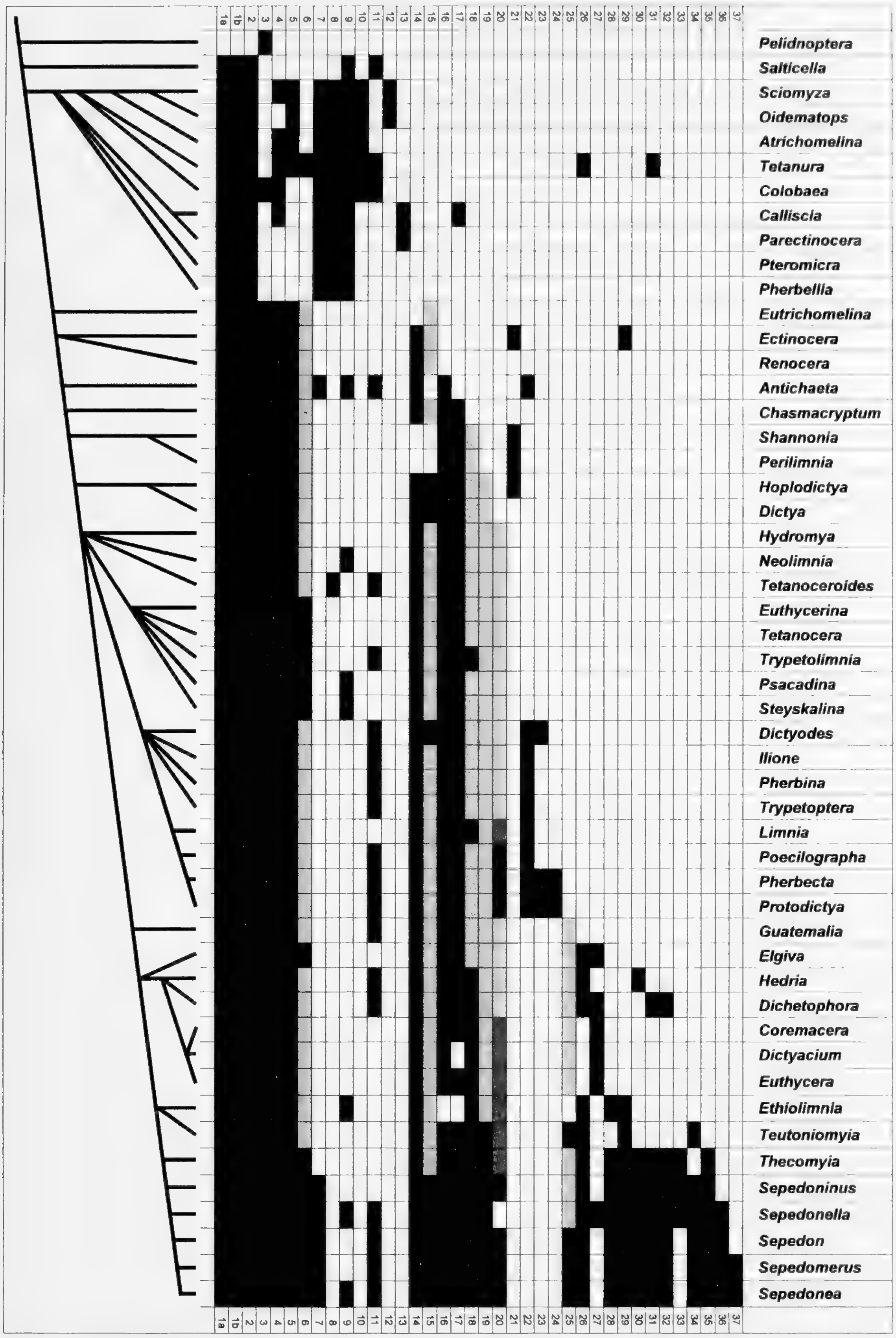

Fig. 324. Arrangement of character states among genera of Sciomyzidae. White = plesiomorphic condition; gray (light and dark) = intermediate and relatively more apomorphic conditions for multistate characters (progressing from light gray to dark gray); black = apomorphic condition.

Acknowledgments

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BMNH	The Natural History Museum, London, England
DZUP	Coleção de Entomologia Pe. J. S. Moure, Department of Zoology, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil
MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil
UCR	University of California, Riverside, California, U.S.A.
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

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Appendix 1.

List of genera and type species used in the analysis.

Antichaeta analis Meigen, 1830
Atrichomelina pubera (Loew), 1862
Calliscia calliscelles (Steyskal), 1963
Chasmacryptum seriatimpunctatum Becker, 1907
Colobaea bifasciella (Fallén), 1820
Coremacera marginata (Fabricius), 1775
Dichetophora obliterata (Fabricius), 1805
Dictya umbrarum (Linnaeus), 1758
Dictyacium ambiguum (Loew), 1864
Dictyodes dictyodes (Wiedemann), 1830
Ectinocera borealis Zetterstedt, 1838
Elgiva cucularia (Linnaeus), 1767
Ethiolimnia platalea Verbeke, 1950
Euthycera chaerophylli (Fabricius), 1798
Euthycerina vittithorax Malloch, 1933
Eutrichomelina fulvipennis (Walker), 1837
Guatemalia straminata (Wulp), 1897
Hedria mixta Steyskal, 1954
Hoplodictya setosa (Coquillett), 1901
Hydromya dorsalis (Fabricius), 1775
Ilione albiseta (Scopoli), 1763
Limnia unguicornis (Scopoli), 1763
Neolimnia repo Barnes, 1976
Oidematops ferrugineus Cresson, 1920
Parectinocera neotropica Becker, 1919
Perilimnia albifacies Becker, 1919
Pherbecta limenitis Steyskal, 1956
Pherbellia punctata (Fabricius), 1791
Pherbina coryleti (Scopoli), 1763
Poecilographa decora (Loew), 1864
Protodictya chilensis Malloch, 1933
Psacadina disjecta Enderlein, 1939
Pteromicra glabricula (Fallén), 1820
Renocera pallida (Fallén), 1820
Salticella fasciata (Meigen), 1830
Sciomyza simplex Fallén, 1820
Sepedomerus macropus (Walker), 1849
Sepedon sphegea (Fabricius), 1775
Sepedonea lindneri (Hendel), 1932
Sepedonella nana Verbeke, 1950
Sepedoninus planifrons Verbeke, 1950
Shannonia meridionalis Zuska, 1969
Steyskalina picta Ghorpadé and Marinoni, 1999
Tetanocera elata (Fabricius), 1781
Tetanoceroides mesopleuralis Malloch, 1933
Tetanura pallidiventris Fallén, 1820
Teutoniomyia plaumanni Hennig, 1952
Thecomyia longicornis Perty, 1833
Trypetolimnia rossica Mayer, 1953
Trypetoptera punctulata (Scopoli), 1763

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Review of the chewing louse genus *Abrocomophaga* (Phthiraptera: Amblycera), with description of two new species

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Abstract.—The South American chewing louse *Abrocomophaga chilensis* Emerson & Price has, since its description, remained the sole known member of the amblyceran family Abrocomophagidae. We herein provide a redescription of the species as well as descriptions and illustrations for two new species of *Abrocomophaga*: *A. emmonsae* off *Cuscomys ashaninka* Emmons from Perú and *A. hellenthali* off the degu, *Octodon degus* (Molina), from Chile. After our reevaluation of the status of the family Abrocomophagidae, we consider it a synonym of the family Gyropidae.

Resumen.—Desde su descripción original, el piojo sudamericano *Abrocomophaga chilensis* Emerson & Price, ha permanecido como el único miembro conocido de la familia Abrocomophagidae, perteneciente a los amblíceros. En este trabajo presentamos una redescripción de dicha especie y además descripciones e ilustraciones de dos especies nuevas del género *Abrocomophaga: A. emmonsae* parásito de *Cuscomys ashaninka* Emmons proveniente del Perú y *A. hellenthali* parásito del degu, *Octodon degus* (Molina), de Chile. Después de reevaluar el status de la familia Abrocomophagidae, la consideramos como sinónimo de la familia Gyropidae.

Emerson & Price (1976) described a distinctive new taxon of South American chewing louse, *Abrocomophaga chilensis,* and placed it in a new monotypic family, the Abrocomophagidae. All known specimens of this louse were found on a single chinchilla rat, *Abrocoma bennetti* Waterhouse, from Chile. Since the original description, little has been written about this enigmatic and phylogenetically important amblyceran (Emerson & Price 1985), almost certainly because no new information was available. We recently obtained series of *Abrocomophaga* from two other South American rodent hosts; these lice represent two new species in this genus. With the addition of these two new species, we reevaluate the status of the family Abrocomophagidae and the genus *Abrocomophaga.* Our purpose here is to describe and illustrate these new species and to establish the synonymy for the family Abrocomophagidae.

Family Gyropidae Kellogg

Gyropidae Kellogg, 1896:68. Type genus: *Gyropus* Nitzsch.

Abrocomophagidae Emerson & Price, 1976:425. Type genus: *Abrocomophaga* Emerson & Price. New synonymy.

The features associated with the species of Gyropidae and the relationship of this family to other members of the suborder Amblycera have been accurately treated by Clay (1970) and will not be repeated here.

In her treatment of the amblyceran Phthiraptera, Clay (1970) followed the organization presented by Ewing (1924) in recognizing the Gyropidae as being divided into three subfamilies: (1) the Gyropinae with six pairs of abdominal spiracles (on III–VIII) and at least one pair of legs having a modified tarsal claw strongly adapted for clasping hair; (2) the Gliricolinae with only five pairs of abdominal spiracles (on III–VII) and legs with a single greatly reduced tarsal claw; and (3) the Protogyropinae with six pairs of abdominal spiracles (on III–VIII) and all legs having a single unmodified tarsal claw.

The establishment of the family Abrocomophagidae by Emerson & Price (1976) was based primarily on the fact that *Abrocomophaga chilensis,* the sole member of this new family, had an unmodified tarsal claw on each leg and only five pairs of abdominal spiracles, a combination of characters seen in no other gyropid louse. However, as our understanding of character evolution has matured over the years, we have come to the conclusion that these differences are of generic-level rather than familial-level significance. In fact, the main difference between the Abrocomophagidae and the monotypic Protogyropinae was that the former had only five pairs of abdominal spiracles (on III–VII), whereas the latter had six pairs (on III–VIII). Because the number of abdominal spiracles in the Gyropidae varies from the primitive six pairs to a reduced state of five pairs, it is our feeling now that this difference is not of familial significance and that the Abrocomophagidae should be considered a synonym of the family Gyropidae (subfamily Protogyropinae) as delineated by Clay (1970). A discussion of other features associated with the Abrocomophagidae and *Abrocomophaga* may be found in Emerson & Price (1976). Lakshminarayana (1976) presented a thorough review of the suprageneric classification of the Phthiraptera and gave a listing of the superfamily, family, subfamily, and tribe names proposed to that time.

Genus *Abrocomophaga* Emerson & Price

Abrocomophaga Emerson & Price, 1976: 425. Type species: *Abrocomophaga chilensis* Emerson & Price.

This genus is separated from others in the family Gyropidae (and suborder Amblycera) in having known representatives with all legs having an unmodified tarsal claw and the abdomen with only five pairs of spiracles.

Abrocomophaga chilensis Emerson & Price

Abrocomophaga chilensis Emerson & Price, 1976:426. Type host: *Abrocoma bennetti bennetti* Waterhouse.

Male.—Emerson & Price (1976) provide a full illustration in Fig. 5 and two aspects of the male genitalia in Figs. 3 and 4. Head with numerous medium-length setae on dorsal and ventral surfaces; without heavy dorsal seta near antennal base. Pronotum with 10–14 setae; prosternum with 5–7 setae, mesosternum with 8–10. Metanotum with 10 setae, including 6 longer median setae and each side laterally with 1 long, 1 short seta; metasternal plate with 12–14 setae. Abdominal tergal setae: I, 4; II, 6–8; III, 8–10; IV, 10–12; V, 11–13; VI, 11–14; VII, 10–12; VIII, 6–9. Terga III–VII each with small faint median pigmentation; V–VIII each with median pair of shorter setae recessed posterior to main row. Posterior margin of each of pleura II–VIII with 1 very long and 1 adjacent short heavy seta. Last tergum with 2 short, 1 very long seta on each side. Abdominal sternal setae: II, 7–9; III, 9–12; IV, 11–15; V, 12–14; VI, 10–13; VII, 9–11. Sterna IV–VII each with small faint median pigmentation. Subgenital plate with 7 or 8 medium to short median setae. Genitalia with only ill-defined weak mesosomal sclerites associated with sac and with blunt apical tip of parameres. Dimensions (in mm): temple width, 0.19–0.20; head length, 0.16–0.18; prothorax width, 0.15–0.16; metathorax width, 0.18–

0.20; abdomen width at segment V, 0.30–0.31; genitalia width, 0.08; genitalia length, 0.17–0.20; genitalia paramere length, 0.06–0.07; total length, 0.94–0.98.

Female.—Emerson & Price (1976) provide a full illustration in Fig. 2 and one of the ventral terminalia in Fig. 1. Head and thorax as for male, abdomen differing as follows. Tergal setae: IV, 9–11; V, 10–12; VI, 10–13; VII, 9–12. All setae on terga V–VIII aligned in row. Last tergum with 2 very long setae on each side, in addition to 2 shorter setae. Sternal setae: II, 8–10; III, 10–13; IV, 11–13; V, 11–14; VI, 11–13; VII, 8–11. Subgenital plate with 9–11 medioanterior setae and convex posterior margin bearing median fringe of small spicules. Anal fringe ventrally of 5 + 5 and dorsally of 3 + 3 longer lateral setae, with few minute median setae in each row. Dimensions (in mm): temple width, 0.20–0.22; head length, 0.17–0.20; prothorax width, 0.16–0.17; metathorax width, 0.19–0.20; abdomen width at segment V, 0.32–0.35; anus width, 0.07–0.08; total length, 1.07–1.14.

Material.—10 male, 10 female paratypes of *Abrocomophaga chilensis,* ex *Abrocoma bennetti bennetti,* Chile.

Remarks.—This species is recognized by both sexes with consistently small dimensions, including narrow head and abdomen, and their abdominal tergal and sternal setal counts; the female with a narrow anus; and the male with unique genitalia and a small recessed pair of abdominal tergal setae on each of V–VIII. Type deposited in the NMNH.

Emerson & Price described *Abrocomophaga chilensis* on the basis of a large series of specimens from a single host individual of *Abrocoma bennetti bennetti* from Chile collected by Robert E. Martin. We can now provide more specific information on the type host and type locality. The type host collected by Robert E. Martin on 2 November 1974 bears his field number 1105 and is deposited in the Recent mammal collection at the Field Museum in Chicago as FMNH 119794 with locality information as follows: Chile: Santiago Province; 10 km W of Til Til [Tiltil; 1000 m]. The host was an adult female.

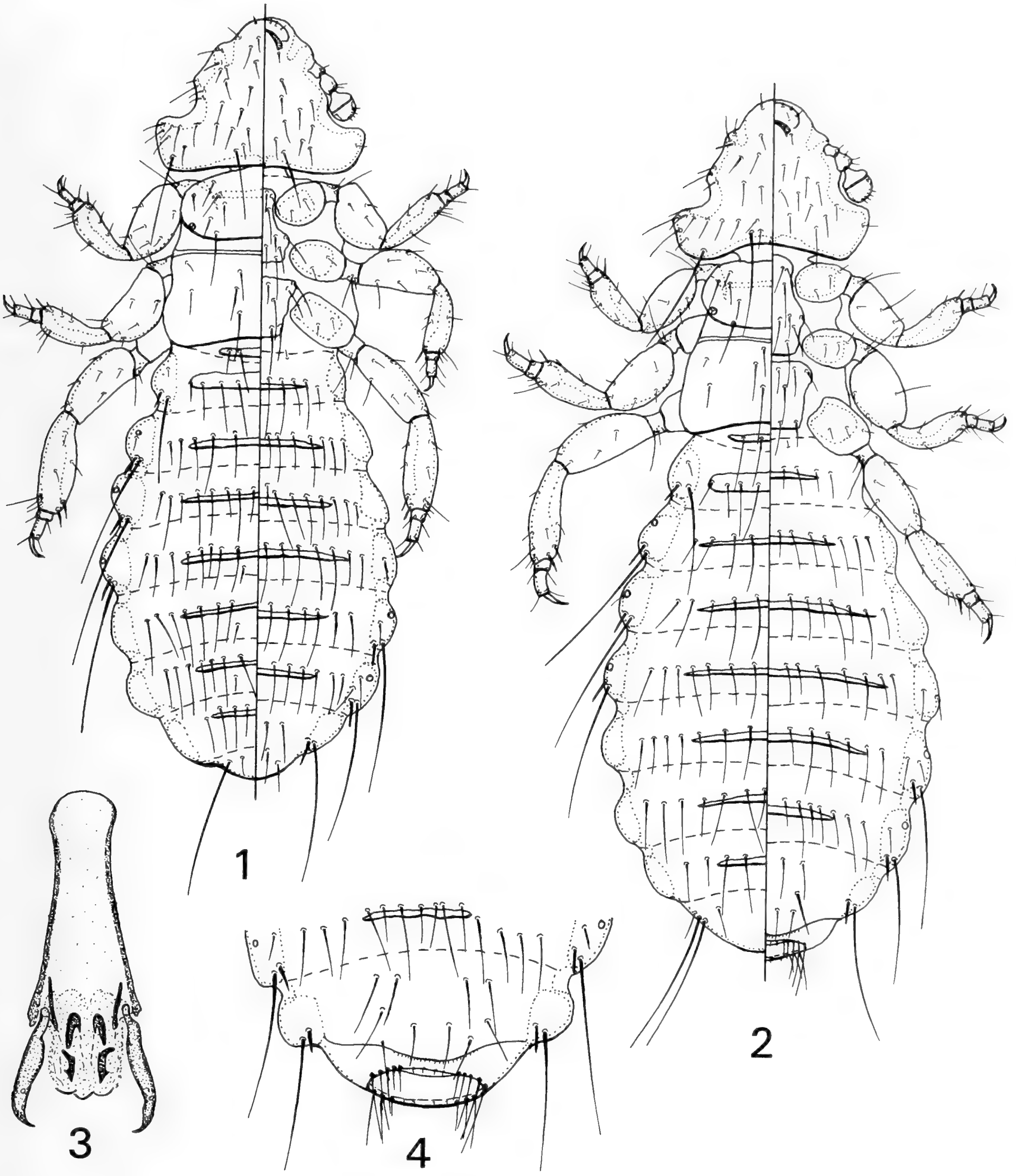
Abrocomophaga emmonsae, new species
Figs. 1–4

Type host.—*Cuscomys ashaninka* Emmons.

Male.—As in Fig. 1. Differing from *Abrocomophaga chilensis* as follows. Abdominal tergal setae: IV, 14; V, 18; VI, 14; VII, 16. Terga I–VIII each with small median faintly pigmented area; V–VII each with median pair of shorter setae recessed posterior to main row. Abdominal sternal setae: II, 10; III, 14; IV, 16; V, 15; VI–VII, 12. Sterna II–VII each with lightly pigmented median area. Genitalia (Fig. 3) with prominent inwardly curved sharply pointed parameres and conspicuous associated mesosomal sclerites as shown. Dimensions (in mm): temple width, 0.26; head length, 0.20; prothorax width, 0.19; metathorax width, 0.26; abdomen width at segment V, 0.40; genitalia width, 0.09; genitalia length, 0.20; genitalia paramere length, 0.06; total length, 0.98.

Female.—As in Fig. 2. Differing from *Abrocomophaga chilensis* as follows. Abdominal tergal setae: IV, 12–13; V, 12–16; VI, 13–18; VII, 13–16. Abdominal sternal setae: II, 8–11; III, 11–15; IV, 13–17; V, 13–16; VI, 12–18; VII, 11–14. Ventral terminalia as in Fig. 4. Dimensions (in mm): temple width, 0.26–0.27; head length, 0.20–0.22; prothorax width, 0.19–0.20; metathorax width, 0.23–0.26; abdomen width at segment V, 0.41–0.47; anus width, 0.09–0.10; total length, 1.06–1.16.

Type material.—Holotype male, ex *Cuscomys ashaninka,* Perú: Cuzco, Cordillera Vilcabamba (11°39′36″S, 73°38′31″W) el. 3350 m, 15 June 1997, coll. Louise H. Emmons #1359; in collection of the Museo de Historia Natural, Universidad Nacional de San Marcos, Lima, Perú, MUSM 12715 ♀. Paratypes: 6 females, same data as holotype; in collections of the Universidad Na-



Figs. 1–4. *Abrocomophaga emmonsae:* (1) Dorsal-ventral male; (2) Dorsal-ventral female; (3) Male genitalia; (4) Ventral female terminalia.

cional de San Marcos and the National Museum of Natural History, Washington, D.C.

Etymology.—This new species is named in honor of Louise H. Emmons, National Museum of Natural History, Smithsonian Institution, who collected the host and enthusiastically encouraged the junior author to examine it for ectoparasites. Her survey efforts in South America have greatly contributed to our understanding of this fauna and her field guides to Neotropical mammals have created a broader understanding of the rainforest for both the public and students of all ages, and have certainly contributed to conservation efforts.

Remarks.—Although this new species is close to *Abrocomophaga chilensis,* both sexes are readily separable by their consistently larger dimensions, including broader head and abdomen, and their larger number of abdominal tergal and sternal setae; the female with the broader anus; and the male with the recessed pair of setae on only abdominal terga V–VII and with unique genitalia that have the distinctive mesosomal sclerites and acutely pointed parameres.

Abrocomophaga hellenthali, new species
Figs. 5–8

Type host.—*Octodon degus* (Molina).

Male.—As for *Abrocomophaga chilensis* except as follows. Head (Fig. 6) with heavy dorsal seta near antennal base. Abdomen (Fig. 5) with tergal setae: II, 5–6; III, 6–7; IV–V, 7–8; VI–VII, 8; VIII, 5–6. Terga I–VII each with small faint median pigmentation; V and VII each with median pair of shorter setae recessed posterior to main row. Posterior margin of each of pleura II–VIII with short slender seta adjacent to very long seta. Last tergum with 1 long, 3–4 short setae on each side. Abdominal sternal setae: II, 6; III, 8–9; IV, 9–10; V, 8–10; VI, 7–8; VII, 6. Sterna II–VII each with small faint median pigmentation. Genitalia (Fig. 7) with numerous conspicuous spinelike mesosomal sclerites associated with sac and with sharply pointed apical tip of parameres.

Dimensions (in mm): temple width, 0.23–0.26; head length, 0.18–0.20; prothorax width, 0.17–0.18; metathorax width, 0.22–0.23; abdomen width at segment V, 0.38–0.41; genitalia width, 0.08–0.09; genitalia length, 0.19–0.21; genitalia paramere length, 0.07; total length, 0.83–0.88.

Female.—Head and thorax as for male, abdomen (Fig. 8) differing as follows. Tergal setae: VIII, 6–7. All setae on terga V and VII aligned in row. Last tergum with 2 very long setae on each side, in addition to 2 shorter setae. Sternal setae: II, 6–8; VI, 8–9; VII, 6–7. Subgenital plate with 9–11 medioanterior setae and convex posterior margin bearing median fringe of small spicules. Anal fringe as for *Abrocomophaga chilensis.* Dimensions (in mm): temple width, 0.24–0.26; head length, 0.19–0.20; prothorax width, 0.17–0.19; metathorax width, 0.22–0.26; abdomen width at segment V, 0.43–0.47; anus width, 0.09–0.10; total length, 0.94–0.98.

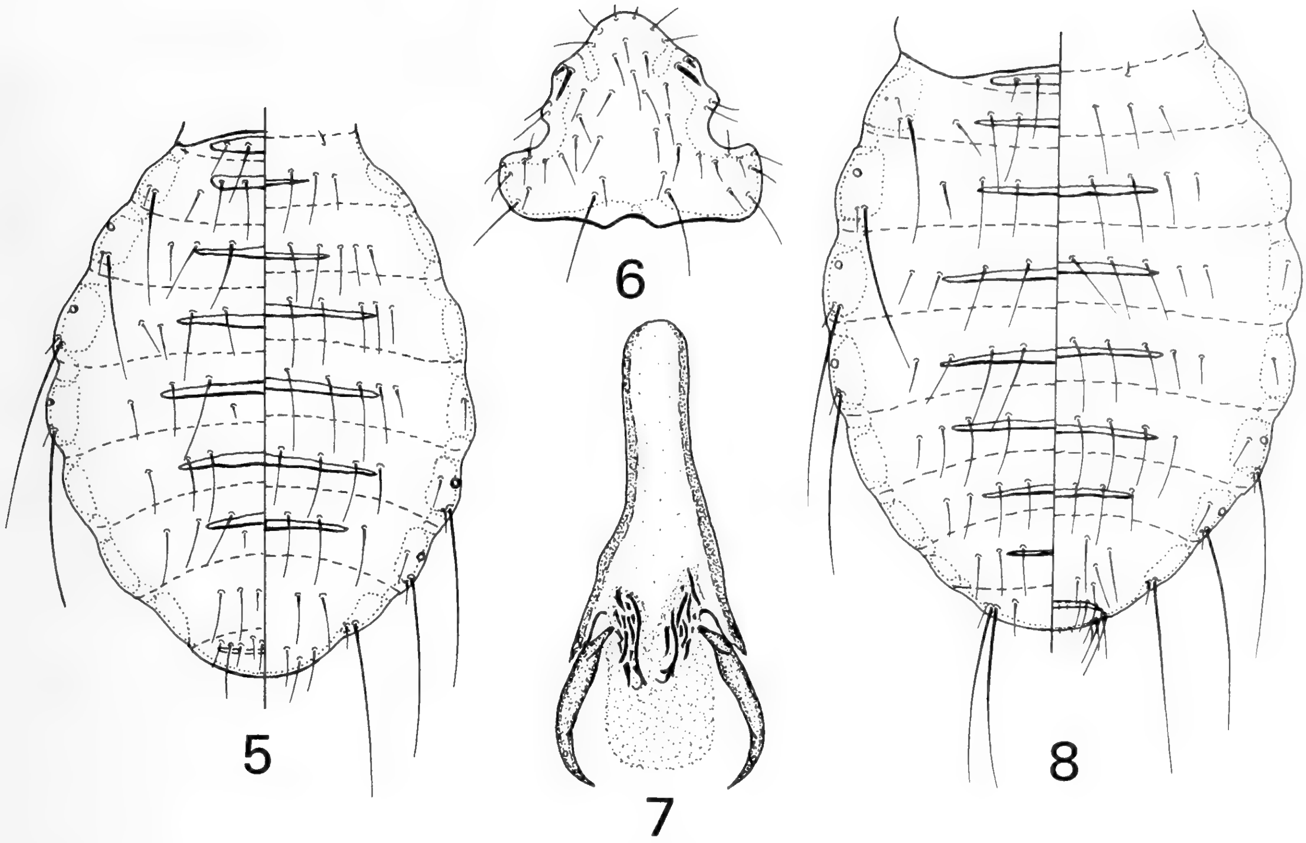
Type material.—Holotype male, ex *Octodon degus,* Chile: Santiago, Santiago, 2.5 km NE of Cerro Manquehue, Trappist Monastery, 9 July 1975, coll. Robert E. Martin #1222 (FMNH 119614 ♀); in collection of the K. C. Emerson Entomology Museum, Oklahoma State University, Stillwater. Paratypes: 2 males, 3 females, same data as holotype; 1 female, same except 1 August 1975, Robert E. Martin #1235 (FMNH 119756 ♂); 1 male, 1 female, same except 27 April 1976, Robert E. Martin #1432 (FMNH 119639 ♂); all in same collection as holotype.

Etymology.—This species is named for Ronald A. Hellenthal, University of Notre Dame, in recognition of his strong interest in chewing louse taxonomy and his many years of cooperative studies with RDP.

Remarks.—This species is separated from the other two of the genus by both sexes having large dimensions, including a broad head and abdomen, a heavy dorsal preantennal head spine, a short slender seta adjacent to the very long seta on each of pleura II–VIII, and a consistently small number of abdominal tergal and sternal setae; the female with a broad anus; and the male with a recessed pair of setae only on abdominal terga V and VII and with unique genitalia that have a distinctive assemblage of spinous mesosomal sclerites and acutely pointed parameres.

Discussion

The caviomorph rodent family Octodontidae contains 6 genera and 11 living spe-



Figs. 5–8. *Abrocomophaga hellenthali:* (5) Dorsal-ventral male abdomen; (6) Dorsal male head; (7) Male genitalia; (8) Dorsal-ventral female abdomen.

cies, all with very restricted Andean or pre-Andean ranges; *Octodon degus* is the most widely distributed species. With the discovery of *Cuscomys ashaninka,* the caviomorph family Abrocomidae now contains two Recent genera and a total of five species (Emmons 1999). Both families occupy a diverse array of high-elevation habitats, and their geographic ranges overlap broadly in southern South America. The relationships between the Abrocomidae and Octodontidae have been the subject of debate. The abrocomids were historically treated as a subfamily of the Echimyidae and more recently as either a subfamily of the Octodontidae or as a closely related family in the superfamily Octodontoidea following Reig (1986) and Carleton (1984). However, Glanz & Anderson (1990) suggested that the abrocomids are more closely aligned with the chinchillas and may belong in the superfamily Chinchilloidea.

Where accurate records are available, we have found gyropid lice to be extremely host-specific ectoparasites (Price & Timm 1997), with speciation of lice closely paralleling speciation in their mammalian hosts. The various species in a louse genus are almost always restricted to the various species of a host genus or to very closely related genera of hosts. Our discovery of the two new species of *Abrocomophaga* described herein, although clearly supporting the host specificity we observe in gyropids, is odd in that closely related species of lice are found on different families of rodents. Two of the species of *Abrocomophaga* now known—*A. chilensis* and *A. emmonsae*—are apparently host-specific parasites of abrocomid rodents (*Abrocoma bennetti* and *Cuscomys ashaninka,* respectively) and one species—*A. hellenthali*—is apparently a host-specific parasite of an octodontid rodent (*Octodon degus*). Because only three species are known in the genus *Abrocomophaga* and the genus is only known from five separate host individuals in three separate genera, it is premature to attempt to reconstruct a phylogeny for the group.

Naturally occurring transfers (host switching) of parasitic lice between nonrelated hosts is not common, but has been documented in both mammals and birds (Paterson et al. 1999). Nest sharing between different species of mammals is rare in nature; however, sequential use of tree hole nests by birds is widespread. Timm (1983) postulated that the broad host distributions of species and genera seen in many lineages of bird lice are in part due to host transfers that might occurred during the evolutionary history of the groups. Mammal lice exhibit greater host specificity because opportunities for lice to colonize new host taxa are rare. Although nest sharing by different species of rodents is exceedingly rare, it has been well documented for *Octodon degus* and *Abrocoma bennetti* in Chile. In a field study with marked individuals, Fulk (1976) found *O. degus* and *A. bennetti* regularly to share burrows and even the same nests. In excavating nests, he found female *A. bennetti* with their own infants as well as infant degus. Correspondingly, female *O. degus* also had both species of young in their nests. Fulk (1976:504) considered nest sharing a common behavior in these two species, and suggested "This practice may be mutualistic, each animal contributing to the survival of the other's young."

Although we don't know that nest sharing occurs between *Octodon degus* and *Abrocoma bennetti* throughout their range, the fact that it does occur demonstrates how an ancestral *Abrocomophaga* could be transferred from one host family to another. With only three species of *Abrocomophaga* known to date, we cannot differentiate between the hypotheses that the current distribution of species we see on the rodent families Abrocomidae and Octodontidae are historically shared or relatively recent host transfers. When additional species of *Abrocomophaga* from other abrocomid and octodontid hosts are known, we may be able to address whether the Abrocomidae or the Octodontidae, or perhaps a common ancestor, represent the ancestral host for this enigmatic and poorly known group of lice.

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We thank Louise Emmons and Linda Gordon, National Museum of Natural History, Washington, D.C., for allowing us to remove specimens of lice from mammal specimens housed at the National Museum, thereby making the discovery of *Abrocomophaga emmonsae* and other new species possible. Larry Heaney and Bruce Patterson made our work at the Field Museum possible and productive. Robert Anderson examined specimens of *Abrocoma* for us as well as translated our Abstract into Spanish for the Resumen included herein. Rob Anderson, Barbara Clauson, Louise Emmons, Marcela Gómez-Laverde, and Ricardo Palma provided valuable assistance on earlier drafts of this manuscript. This manuscript has been approved for publication by the Director, Oklahoma Agricultural Experiment Station, Stillwater.

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A new species of the genus *Cubacubana* (Insecta: Zygentoma: Nicoletiidae) from a Mexican cave

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Abstract.—A new cavernicolous species of the genus *Cubacubana* (Zygentoma: Nicoletiidae) is described. This species is probably more distant from any other species of this genus described until now.

The genus *Cubacubana* was originally described with three cavernicolous species from Cuba (Wygodzinsky & Hollinger 1977), although Espinasa (1999b) has proposed that one of the species is of the genus *Anelpistina* (Silvestri, 1905). In Wygodzinsky's paper, he asserted that the Mexican fauna of free-living and cavernicolous Nicoletiines is very rich and quite possibly species of *Cubacubana* will also be found on the mainland. Later another *Cubacubana* species was described from Aruba island (Mendes 1986) and finally a species was described from México, *C. mexicana* (Espinasa, 1991), thus fulfilling Wygodzinsky's prediction. Further exploration of caves in México has shown that organisms of the genus *Cubacubana* are actually abundant (Espinasa 1989).

The new species has a series of characters that permit us to define it as a cave adapted troglobite such as the overall large size, enlarged appendages, and surface crawling as opposed to occurring under rocks. Its presence in at least two different cave localities can be explained because they are within the same karstic area and probably are a single underground system (Diamant-Adler 1991).

Materials and Methods

Detailed descriptions of the caves can be found in the "Tepeyollotli" bulletins of the SMES speleological society (Diamant-Adler 1991). Organisms collected were crawling on the cave's floor. They were placed into a vial with 96% ethanol. Dissections were made with the aid of a stereo microscope and the different parts of the body were mounted in fixed preparations with Hoyer's solution. All illustrations were made with aid of a camera lucida attached to a compound microscope.

Types were deposited in the following collection: LESM-DB-MEX (Laboratory of Ecology and Systematic of Microarthropods. Department of Biology, Faculty of Sciences, UNAM. México D.F.). Catalog number: ZYG-5.

Cubacubana asymmetrica, new species
Figs. 1A–G, 2A–F

Type material.—México, Puebla State, Coyomeapan municipality, Tepepa, "TP4-13" Cave (780 meters deep and more than 5 kilometers long). Ex soil, 23 Dec 1990, L. Espinasa col. Male holotype, two male paratypes and five female paratypes.

Other localities: México, Puebla State, Coyomeapan municipality, Huitzilatl, "Xaltégoxtl" Cave (60 meters deep and more than 2 kilometers long). Ex soil, 3 Jan 1991, R. Espinasa col. Two males and two females.

Description.—Maximum body length 22.5 mm. Maximum length of antennae 34 mm, of caudal appendages 35 mm. When complete, antennae measure 3× length of body and caudal appendages 2× length of body. General color light yellow to white. Macrochaetae simple or forked.

Head with approximately 5 + 5 macrochaetae on border of insertion of antennae. Antennae of male with 83 preserved articles; distal articles very slender and long, with internal sensory organs similar to *C. negreai* (Wygodzinsky & Hollinger, 1977). Basal article of antennae in males without projections. Pedicellus of antennae of male elongate as shown in Fig. 1B, with clusters of unicellular glands arranged in 5 groups. In adults, right pedicellus bigger than left and longer than basal article (Fig. 1B–C). Female basal articles of antennae simple. Mouthparts very elongate (Figs. 1A and 2A); galea almost as long as lacinia (Fig. 2A), with 2 apical conules of different width (Fig. 2B). Two teeth on lacinia and on bigger tooth's base, an extra very small hyaline tooth. Labial palp long and slender, apical article one and a half times longer than wide and subtriangular (Fig. 1A). Labium and 1st article of labial palp with macrochaetae. Mandibles with 4 macrochaetae, without small pegs on the bigger tooth. Legs elongate; hind tibia approximately 8–9 times longer than wide. Leg chaetotaxy as in *C. mexicana* (Espinasa, 1991). Claws of normal size.

Cerci of male with a very short basal article, a very long 2nd one bearing numerous spines, followed by numerous short articles of simple chaetotaxy. In adults, the very long article is slightly curved and with spines, all inserted on tubercles and roughly of the same size and form (Fig. 1D–E). The spine row does not reach base of article. Female cerci simple.

Thorax with short macrochaetae: 2 + 2 on anterior border of pronotum, 3 + 3 macrochaetae on nota's lateral borders, and 1 + 1 submedian distinct macrochaetae apart from several setae of varied sizes on nota's posterior borders.

Urotergite X of both sexes with a small degree of prominence and posterior part short in length, approximately one fifth its width, with a shallow emargination (Fig. 1G), posterior angles with a few macrochaetae of varied sizes, length of inner macrochaetae almost equal to distance between them.

Abdominal terga and sterna as in other members of genus. Abdominal sterna II–VII subdivided into coxites and sternite. Sterna VIII and IX of male entire. Urosternum III and IV of male without modified coxites. Urosternum VIII of male shallowly emarginate on posterior margin, angles of emargination pointed to slightly rounded. Urosternum IX of male straight behind, without modifications (Fig. 1F). Stylets II–VIII with two macrochaetae and an extra subapical pair. Stylets IX larger than others, with four macrochaetae and the extra subapical pair. Terminal spine with small teeth. In males and females styles IX without spines.

Penis and parameres as shown in Fig. 1F. Parameres very short, broaden slightly at base on inner face, and attaining only ½ of stylets IX. Surface of parameres with short setae, apical portion with numerous very short setae. Subgenital plate of female subelliptic or parabolic slightly rounded, slightly longer than wide. Ovipositor surpassing apices of stylets IX by a distance equal to ¼ the length of stylets (Fig. 2F). Gonapophyses with approximately 17 articles.

Post-embryonic development as in Tables 1–2, Figures 1D–E and 2C–F. Length of body can be obtained from the length of hind tibia according to the next formula:

$$\text{Length of body} = (5.57)\ \text{length of hind tibia} + 1.65 \pm 3$$

Etymology.—asymmetrica = Asymmetric. Makes reference to the asymmetric size of pedicellus in males, the right one being longer than the left.

Remarks.—*Cubacubana asymmetrica* can be differentiated from other members of the subfamily Cubacubaninae by the following characters: Species of genus *Texo-*

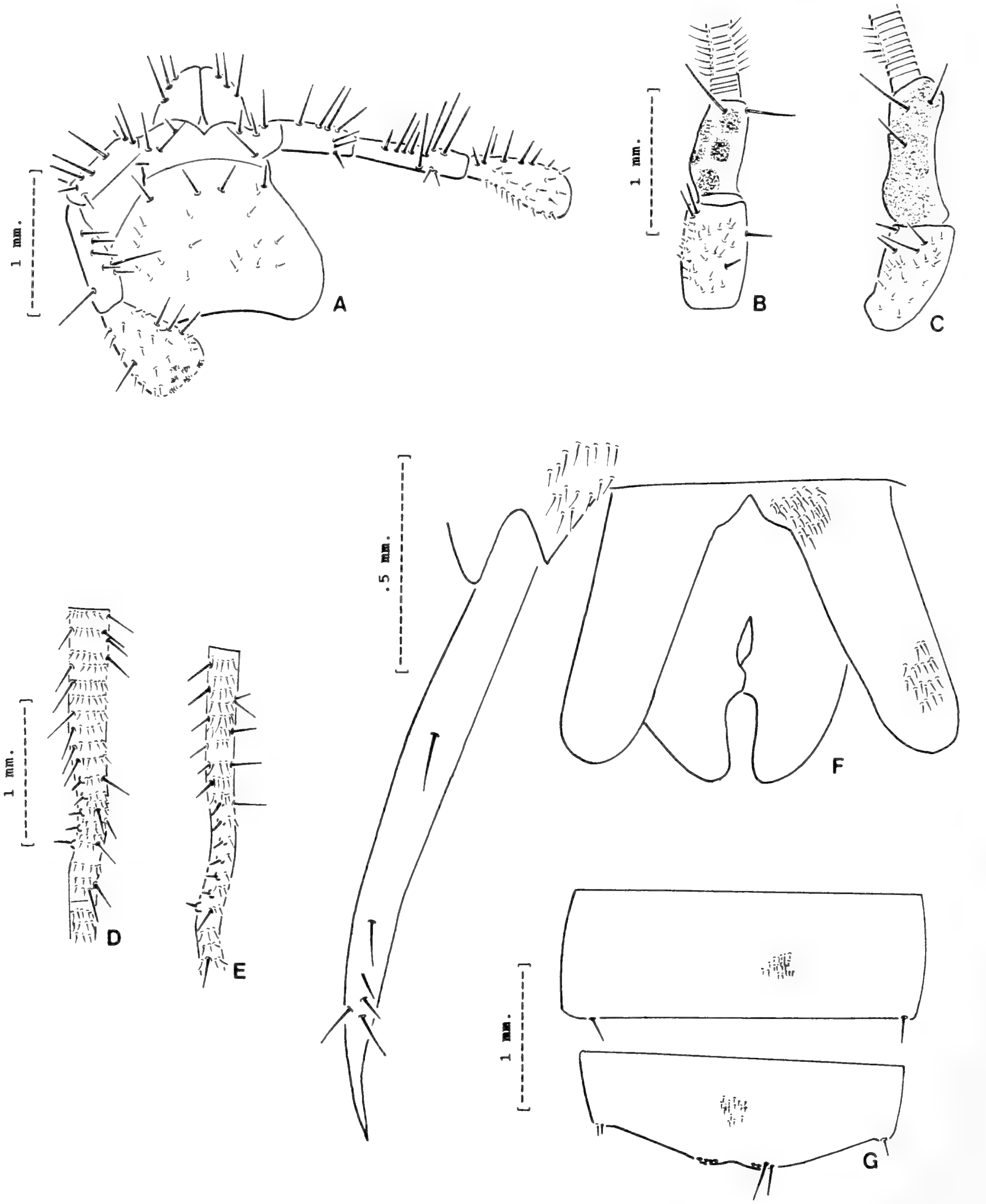

Fig. 1. *Cubacubana asymmetrica* n. Sp.: A, labium with palp; B, Male. Basal portion of left antenna; C, Male. Basal portion of right antenna; D, Juvenile male. Basal portion of cercus with five spines; E, Adult male. Basal portion of cercus with seven spines; F, Male. Genital area; G, Urotergum X.

reddellia (Wygodzinsky, 1973) or *Squamigera* (Espinasa, 1999a), have scales, which are lacking in *Cubacubana. Allonicoletia* (Mendes, 1992) lacks stylets in urosternite II, which are present in *Cubacubana. Neonicoletia* (Paclt, 1979) has a rugged endopodium, absent in *Cubacubana. Prosthecina* (Silvestri, 1933), has a submentum with conspicuous lateral lobes bearing numerous glandular pores, absent in Cubacubana.

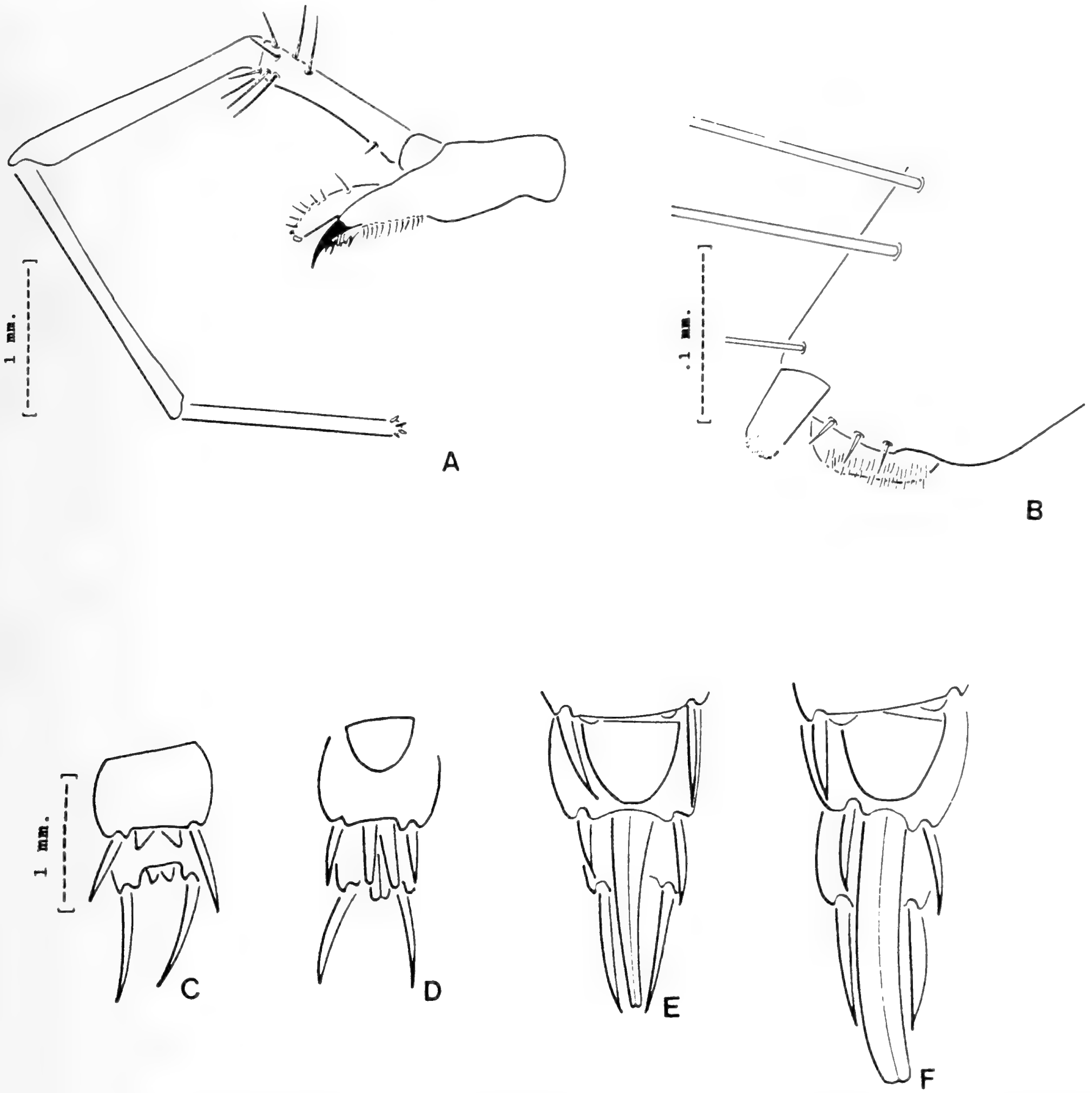

Fig. 2. *Cubacubana asymmetrica* n. Sp.: A, Maxilla; B, Apical portion of maxilla; C–F, Post-embryonic development of female. Ovipositor and subgenital plate. Length of ovipositor in Table 2 as follows: C = −3/2, D = −1, E = 0, F = ¼.

Most species of *Anelpistina,* have articulated submedian appendages in urosternite IV of males, which are absent in *Cubacubana.* From the two species of *Anelpistina* that lack such appendages; *A. decui* (Wygodzinsky & Hollinger, 1977) and *A. inappendicata* (Espinasa, 1999b), and from the described species of *Cubacubana*; *C. ramosi* (Wygodzinsky, 1959), *C. negreai* (Wygodzinsky & Hollinger, 1977), *C. arubana* (Mendes, 1986), and *C. mexicana* (Espinasa, 1991), *C. asymmetrica* differs by the posterior part of urotergite X, which is short in length (one fifth the width of the urotergite), while in the other species it is longer (approximately one half to one third). Males are also differentiated by long pedicellus (twice or more long than wide) and also by the asymmetry of adults, in which right pedicellus is bigger than left.

Cubacubana asymmetrica can be further differentiated from *C. mexicana,* the only

Table 1.—Post-embryonic development of male *Cubacubana asymmetrica.*

MALES: Length Hind tibia mm	Length both pedicellus		Spines in III urosternum		Emargination urosternum VIII			Sensory cones urosternum IX		Spines in stylets IX		Parameres vs. stylets IX				Spines in Cerci (Fig. 1D–E)		
	Equal	Unequal	No	Yes	No	Small	Big	No	Yes	No	Yes	No	1/3	1/2	3/4	No	5	7
Cave of "TP4-13"																		
1.50	+		+		+			+		+		+				+		
2.74	+		+			+		+		+				+			+	
3.10		+	+			+		+		+				+				+
3.18		+	+			+		+		+				+				+
Cave of "Xaltégoxtl"																		
2.74	+		+			+		+		+				+			+	
2.88	+		+			+		+		+				+				+

Table 2.—Post-embryonic development of female *Cubacubana asymmetrica.*

FEMALES: Length hind tibia mm	Ovipositor surpassing apex stylets IX (Fig. 2C–F)			
	−3/2	−1	0	1/4
Cave of "TP4-13"				
1.74		+		
3.45				+
3.45				+
3.49				+
Cave of "Xaltégoxtl"				
1.76	+			
2.89			+	
3.16				+

other Mexican *Cubacubana* species described, by its longer antenna (three times the length of the body instead of one and a half), caudal appendages (two times the length of the body instead of slightly more than one), maxillary palp (distal article 11 or more times longer than wide instead of less than ten) and legs (hind tibia approximately eight to nine times longer than wide instead of six). Furthermore males do not have spines or cones on urosternum III and IX or on styles IX. Gonapophyses of females have fewer articles (approximately 17 instead of 22).

Cubacubana asymmetrica shares characteristics present in other genera, such as the curvature of cerci of *Prosthecina addititia* (Wygodzinsky, 1951), or some type of asymmetry in the pedicellus as in *Coletinia subterranea* (Silvestri, 1902) and *Coletinia asymetrica* (Bach de Roca et al., 1985). These characters are probably the result of convergent evolution.

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Three new species of bathyal cidaroids (Echinodermata: Echinoidea) from the Antarctic region

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Abstract.—Two new species of *Aporocidaris, A. eltaniana* and *A. usarpi,* and one new species of *Notocidaris, N. lanceolata,* are described from material collected during United States Antarctic Research Program expeditions in the 1960's. All three species occur in the bathyal zone near or south of the Subantarctic Convergence. Gonopore sizes and peristomial morphology suggest that these species are sexually dimorphic and that the females can brood direct-developing young. However, only one of the *Aporocidaris* species was found to harbor embryos on the peristomial membrane.

In the mid- to late 1960's, Dr. Richard H. Chesher, at the Museum of Comparative Zoology at Harvard (MCZ), studied echinoid material collected under the auspices of the United States Antarctic Research Program (USARP). The USARP, which began in 1955, included trawling and dredging expeditions by ships in the vicinity of Antarctica (Fig. 1). Material collected by the U.S. National Science Foundation Research Vessel R/V *Eltanin* is of particular importance to this paper. Dr. Chesher identified numerous USARP echinoids, in the process discovering several new species. In some cases, he proposed manuscript names and indicated type specimens for new species (for example, see David & Mooi 1990), but he was unable to continue systematic work after 1967, thereby leaving these names and manuscripts unpublished. Chesher's cidaroid research was incorporated into a dissertation (Fell 1976), and two of the species described below were covered in this work. As a result, several putative types for which no names have been published are deposited in the National Museum of Natural History (NMNH)-the major repository of echinoid collecting during the USARP, and in the MCZ. Here, we publish these names for the first time.

Antarctic cidaroids are represented by approximately 20 species in 5 genera, and all belong to the subfamily Ctenocidarinae. With one or two exceptions, the ctenocidarines are restricted to the Antarctic and Subantarctic regions and are among the most diverse of the Antarctic echinoids. Although their taxonomy was hugely advanced in Fell (1976), an exact count of valid taxa is difficult, given the uncertain specific and subspecific status applied to the variants. We are currently engaged in a databasing project that will result in a comprehensive overview of all Antarctic echinoids, including cidaroids, and it was this review that prompted the work on the taxa described herein.

Much of the Antarctic cidaroid fauna still requires revision in a modern context. For example, the only recent attempt (Smith & Wright 1988) to resolve phylogenetic relationships among any of the cidaroids concentrated on Cretaceous forms, and did not deal with Antarctic taxa. Phylogenetic relationships among the different genera and species are still speculative and will remain

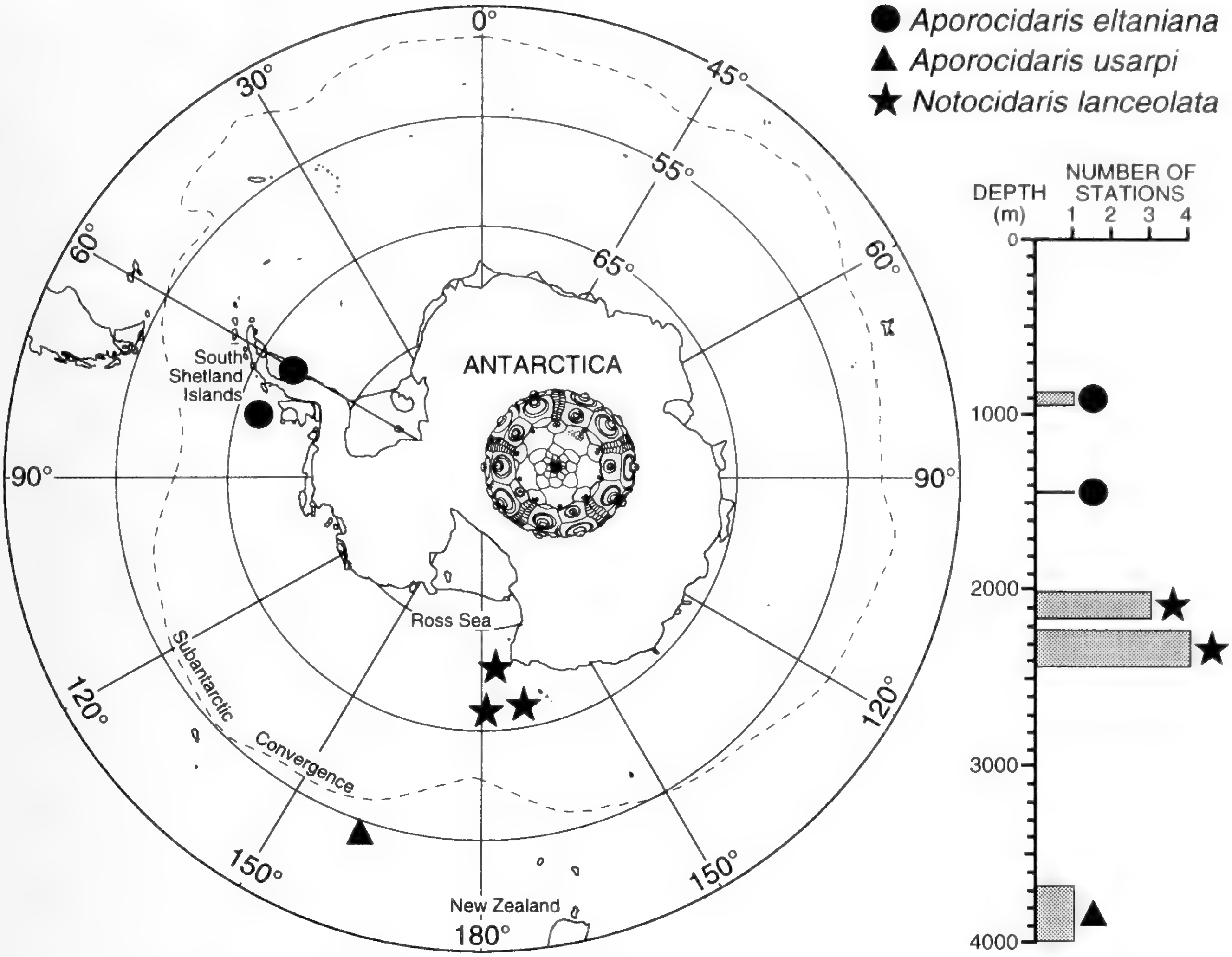

Fig. 1. Collecting localities and recorded depths (graph at right) for *Aporocidaris eltaniana* new species, *A. usarpi* new species, and *Notocidaris lanceolata* new species. Number of stations refers to the number of R/V *Eltanin* stations that for a given species fall within the depth range indicated by the height of the shaded box.

so until a more complete knowledge of the taxonomy is established. The lack of consistent, well-delineated features as well as detailed analyses of morphological variation makes the Antarctic cidaroids a particularly difficult group, as evidenced by the almost unusable keys provided by previous major revisions such as Mortensen (1928). In addition, material is often rare, and several taxa are represented only by juveniles, or have not been collected since they were first described from single or very few individuals. Therefore, determination of terminal taxa to be used in phylogenetic analysis is in its infancy, and any effort to place the taxa described here in an evolutionary context is premature.

Jackson (1912) and Smith (1984) provided excellent comparative overviews of cidaroid morphology. Cidaroids are very easy to separate from other types of regular urchins. Each interambulacral plate bears a single, large, perforate primary tubercle supporting a primary spine that is strongly differentiated from the secondary spines covering the rest of the test. Primaries are many times larger than secondaries, and much more robust. The shafts of adult cidaroid primary spines are unique not only among all spines on a cidaroid, but also among echinoids in general in completely lacking an epithelial layer. These spines are often invested with various epizoans such as sponges, serpulids, bryozoans, and small mollusks. Each primary is encircled by a palisade of much shorter secondary spines called scrobiculars that can be appressed to the base of the primary spine.

In contrast to other regular echinoids, cidaroid ambulacra are very narrow relative to the interambulacra. The ambulacral plates are arranged in two simple columns, each of which bears a single tube foot pore (usually bipartite), and one to several small secondary spines. The ambulacral series continue to the mouth on the peristomial membrane, and the number of peristomial ambulacrals can be helpful in discriminating certain Antarctic taxa. The perignathic girdle consists of interambulacral processes called apophyses. The Aristotle's lantern of Antarctic species is typical for cidaroids, and does not vary enough to form the source of characters that could be used to distinguish the taxa.

Although it is relatively easy to recognize a cidaroid, a confounding feature of the taxonomy within the group is conservatism in plate architecture and overall form of the test. However, the cidaroids more than compensate for this conservatism in diversity of primary spine morphology. The taxa described in this paper exemplify the fact that many cidaroid species cannot be identified without information on the primary spines. Both scrobicular and non-scrobicular secondary spines can also be useful in diagnosing Antarctic cidaroids.

Cidaroids are epibenthic and inhabit various environments from sandy and stony bottoms in littoral zones to gravels and muds of sub-littoral regions. They are also common in the deep-sea on muddy bottoms of bathyal slopes or abyssal plains to 5000 meters, and they constitute a significant part of the benthic community at these depths. Many, if not all, of the Antarctic cidaroids are direct developers, as suggested by the fact that in almost every species, a subset of adults presumed to be females have greatly enlarged gonopores. Fell (1976) and Lockhart et al. (1994) recorded that many species also brood their young in and around "marsupia" created by the more or less sunken peristome, a feature of which we make special note in the following descriptions. Because the presence of brooded young is correlated with enlarged gonopores, and because large gonopores are known to signify females in other echinoids, we also use the presence of enlarged gonopores and marsupia to infer gender in adult specimens.

Upon occasion, primary spines of Antarctic cidaroids also support a very poorly understood parasite, *Echinophyces mirabilis* Mortensen & Rosenvinge, 1909. The occurrence of this parasite is correlated with some modifications of the infected echinoid's morphology and a delay in the appearance and change in position of the gonopores. The mechanism by which a parasite of a more or less biologically inert external feature such as the cidaroid spine can affect the expression of gonads and gonopores is totally unknown and clearly deserves further study. It is surprising that virtually no research beyond the original description and that of Mortensen & Rosenvinge (1910) has been done on this unusual phenomenon. Fell (1976), Jangoux (1987), and Pearse & Cameron (1991) have summarized what few data exist, finding that *Echinophyces* is found only in *Ctenocidaris* Mortensen, 1910 and *Rhynchocidaris* Mortensen, 1909. We report on the results of our as yet unsuccessful search for evidence of this parasite in the new species, in the hope that future studies might be able to use even these negative data.

Order Cidaroida L. Agassiz, 1835

Family Cidaridae Gray, 1825

Genus *Aporocidaris* A. Agassiz & Clark, 1907

Diagnosis.–Ctenocidarine cidarids with a large apical system which can be as much as 75% of the horizontal diameter of the test. Apical system often significantly domed or convex. Mid-interambulacral regions usually with a slightly depressed, naked interradial suture.

Remarks.–Mortensen (1928) considered four nominal species in the genus *Aporocidaris,* but he emphasized the "exceedingly slight" differences between 3 of them: *A. antarctica* Mortensen, 1909, *A. fragilis* A. Agassiz & Clark, 1907, and *A. milleri* (A. Agassiz, 1898). Fell (1976) proposed synonymy of these 3 species under *A. milleri* but suggested a new species, *A. eltaniana.* In an unpublished manuscript, Chesher recognized yet another species, *A. usarpi.* We introduce the latter names to the published literature for the first time.

Aporocidaris eltaniana, new species
Fig. 2

Aporocidaris eltaniana.—ex Fell, 1976: 211, figs. 7, 8j–k, name used in unpublished thesis.

Diagnosis.—Apical system as much as 68% of test diameter. Aboral primary tubercles large and markedly transversely oval at ambitus. Aboral primary spines cylindrical, 1 to 1.5 times test diameter, mostly smooth or with small bumps arranged in longitudinal rows; tip blunt, or slightly concave. Oral primary spines with conspicuous thorns along lateral edges of shaft. Preserved specimens dark brown, primary spines whitish, secondary spines beige to light brown. Other characters as for *Aporocidaris.*

Description.—The test is about half the height of the horizontal diameter, but the height of the apical system is quite variable and can add as much as 20% to the overall height of the coronal part of the test. The largest recorded size of the specimens examined is about 45 mm in horizontal diameter of the test. The holotype is 29.3 mm in diameter, 16.9 mm high, has an apical system diameter of 15.6 mm and a peristome diameter of 12.5 mm.

The ambulacra are almost straight (Fig. 2A, B), particularly on the oral surface, and their tuberculation is of the usual *Aporocidaris* pattern (Fig. 2E). There is no naked area along the perradial suture. The inner and outer pore of each podial pore pair are divided by a well-developed "bridge" of stereom (Fig. 2E).

The interambulacra have about one more plate in each series than *A. milleri* of similar size. The crowding of the plates into the relatively flat corona, and the size of the tubercles between the ambitus and the peristome cause the tubercles to be compressed into horizontally oriented ovals (Fig. 2B). The scrobicular tubercles are more than twice the diameter of the other secondary tubercles, and surround each primary tubercle except where the oval outlines of the primaries touch (Fig. 2D). The interradial suture is conspicuously sunken in larger specimens (Fig. 2D).

The apical system is large (about 60% of the horizontal diameter on average), and almost flat or only slightly domed in most specimens. However, a few exceptional individuals have a strongly arched apical region that can account for over a fifth of the total height of the test. The genital plates are large, with scattered secondary tubercles. In males, the gonopores are small and close to the outer edges of the genital plates (Fig. 2A). In several of the specimens, the gonopores are large, forming notches that in extreme cases can extend part way along the interradial suture separating the interambulacral plates adjacent to the genital. Like Fell (1976), we have assumed these specimens to be females. The gonopores first appear in specimens as small as 16 mm in test diameter. Ocular plates are only about a third the area of the genitals, and the ocular pores are surrounded by a circular ridge that seems to be most pronounced in the males (Fig. 2A). Tuberculation is not dense, and restricted to the central parts of the plates over the majority of the apex (Fig. 2A).

The peristome is just over 55% of the test diameter in small specimens, but becomes smaller in larger individuals (approximately 40% of the test diameter), relative to test diameter. The peristome itself is somewhat sunken around its periphery, notably in the interambulacral regions. Seven to 8 pairs of ambulacral plates continue onto the peristome in larger specimens, and there are

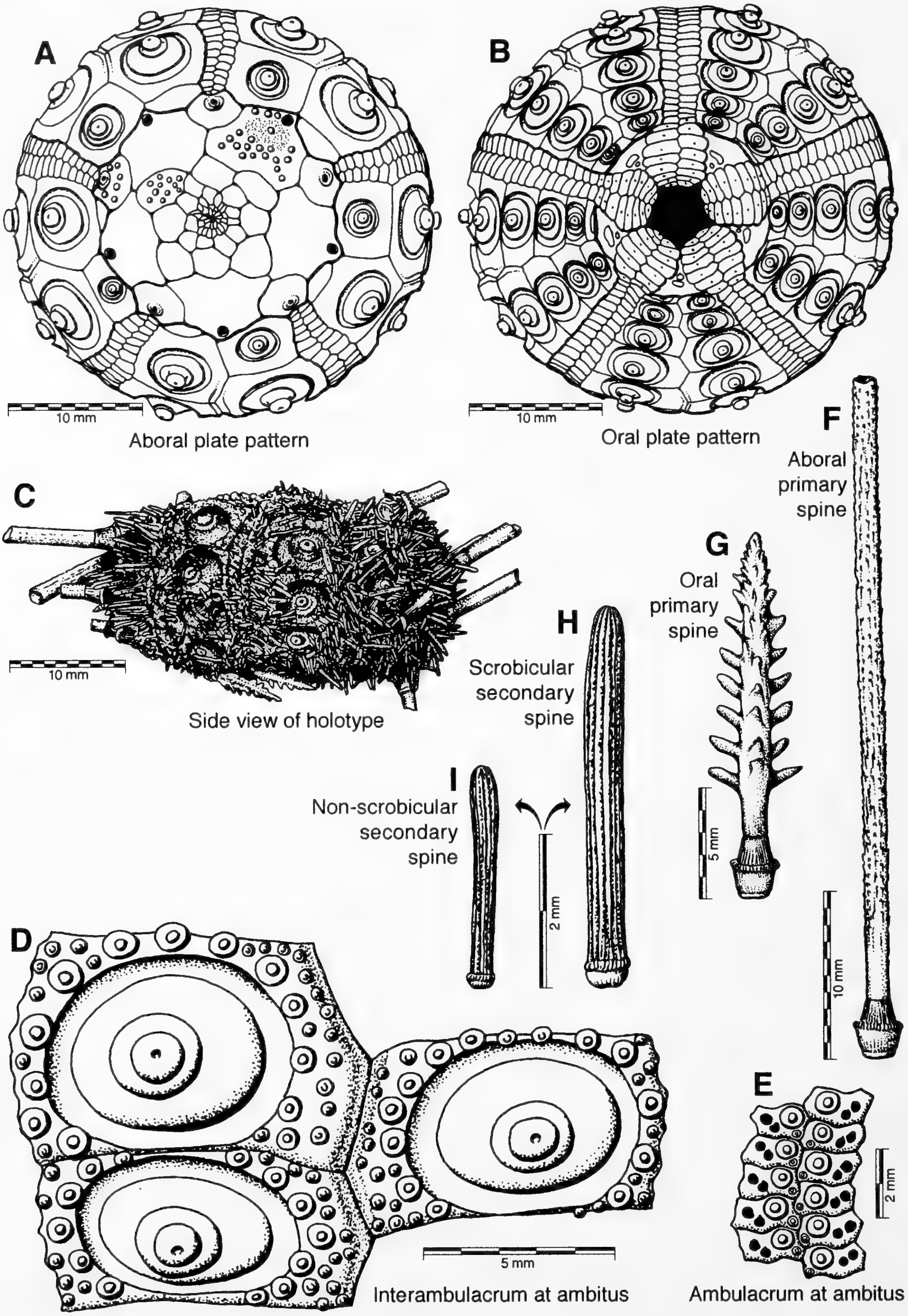

Fig. 2. *Aporocidaris eltaniana* new species. C drawn from holotype (NMNH E48122); A, B, D–I drawn from paratypes in lot NMNH E11161. For A and B: mouth, anus, and gonopores in solid black; podial pores omitted; secondary tubercles shown only for single genital, ocular, and periproctal plates, but omitted elsewhere, including coronal plates.

only 2 or 3 small scales in each interradial region (Fig. 2B).

The longest aboral primary spines found (on the almost intact specimens in NMNH E11161) are approximately 1.5 times the test diameter and rod-like with blunt or slightly concave tips and large milled rings (Fig. 2F). The surface of the shaft is smooth proximally, but bears small, longitudinally aligned, blunt spinules for more than 80% of its length out to the tip (Fig. 2F). The flat areas between the longitudinal rows are covered with a variously developed fibrous and anastomosing calcareous meshwork. The oral primaries are strongly curved towards the peristome, and bear well developed thorns that project laterally, but become smaller towards the tip of the spine. There is often another row of shorter thorns along the distal part of the shaft (Fig. 2G). The more or less cylindrical scrobicular spines are blunt, but not club-shaped (Fig. 2H). The non-scrobicular secondaries are much shorter than the scrobicular spines and sometimes slightly curved near the almost imperceptibly swollen tip (Fig. 2I).

The small globiferous pedicellariae are rare, but appear simply to be half-sized versions of the larger type. The stem of a globiferous pedicellaria is thick, and straight. Neither the valves nor stem are otherwise distinctive among *Aporocidaris* species (Mortensen 1928).

Types.—Holotype NMNH E48122, extracted from NMNH E11161, R/V *Eltanin* Cruise 6, Station 432 (Fig. 2C). Paratypes NMNH E11161 (3 dry specimens, one dissected lantern), E11188 (17 dry specimens, including 3 less than 10 mm in horizontal test diameter), E11212 (dry spines only), E11290 (more than 60 dry specimens), E14597 (2 specimens greater than 28 mm in test diameter, the largest of which is a female with more than 12 young urchins brooded on the peristome, 1 specimen 14.3 mm in horizontal test diameter, and 16 specimens less than 10 mm in test diameter, all in alcohol), MCZ 8406 (1 dry specimen). The holotype was chosen because it retained significant spine cover (Fig. 2C). The paratypes in NMNH E11161 were used to make the drawings of plate architecture so as not to disturb what spination remains on the holotype.

Etymology.—Named for U.S. National Science Foundation R/V *Eltanin.* The species name was first coined in an unpublished doctoral thesis by Fell (1976), and we introduce the name here in recognition of that first usage.

Distribution.—*A. eltaniana* is known only from the type series, which was collected from two R/V *Eltanin* stations (Cruise 4, Station 138; Cruise 6, Station 432) at two distinct localities, both in the region of Livingston Island in the South Shetland Islands, between 884 and 1437 m depth (Fig. 1).

Biology.—The gonopores in females may reach 1.8 mm in diameter. One female (NMNH E14597), 43.4 mm in horizontal test diameter, had more than a dozen juvenile urchins in the marsupium along the sunken edge of the peristomial margin. An exact count of the juveniles was impossible without damaging the adult specimen. Most of the young were obscured by oral primary and secondary spines that folded over to screen the deepest parts of the marsupium in the interambulacral areas proximal to the edge of the coronal plates. One of the largest of the juveniles was 2.2 mm in horizontal test diameter, and all of the brooded young possessed primary spines, the longest of which were approximately 2.0 mm long. These observations suggest that juveniles of *A. eltaniana* develop directly from relatively large eggs which are moved into, and then develop in a peristomial marsupium. None of the specimens appear to be infected by *Echinophyces.* Nothing is known of the preferred bottom type, but the gut contents of one specimen are made up of light gray silt containing small fragments of thin mollusk shells.

Remarks.—The greatly enlarged apical system and the naked, sunken area along the interradius indicate that the new species is an *Aporocidaris. A. eltaniana* is most similar to *A. milleri,* but is distinct from all *Aporocidaris* in possessing strongly developed thorns on the oral primary spines. The dramatic difference between the relatively smooth, cylindrical aboral primaries and the thorny oral primaries is unmatched in the genus, if not within the Antarctic cidaroids in general.

Aporocidaris usarpi, new species
Fig. 3

Diagnosis.—Apical system as much as 70% of test diameter in adults. Aboral primary spines cylindrical, 1 to 1.5 times test diameter, with small, irregularly distributed or only slightly aligned bumps distally. Neck of aboral primaries glossy, porcellaneous, and markedly swollen in larger specimens. Oral primary spines flattened with lateral, diametrically opposed, serrated keels that are widest just distal to neck and taper towards spine tip. Scrobicular spines fine, small, closely spaced, and not strongly differentiated from the non-scrobicular spines. Both types of secondary spines slightly club-shaped. Preserved specimens beige, primary spines white, secondary spines light beige. Other characters as for *Aporocidaris.*

Description.—The test is only moderately flattened. The height of small specimens is just over 50% of the horizontal diameter, but in larger specimens, the height is greater (up to 75% of the horizontal diameter), almost 15% of which can be in the form of the domed apical system (Fig. 3C). The largest specimen is just over 40 mm in horizontal diameter. The holotype is 35.2 mm in diameter, 23.4 mm high, has an apical system diameter of 23.0 mm and a peristome diameter of 15.2 mm.

The ambulacra are almost straight (Fig. 3A, B), particularly on the oral surface, and their tuberculation is of the usual *Aporocidaris* pattern, with smaller secondary tubercles adjacent to the perradial suture, and slightly larger ones just distal to those (Fig. 3E). There is no naked region along the perradius. In the holotype and the largest of the paratypes (NMNH E11059), the "bridge" between the pore pairs on each ambulacral plate is incomplete so that the pores are connected via a constricted passage between the pores (Fig. 3E). This condition is rare, if not unique among Antarctic cidaroids.

The interambulacral plates are high. Aborally, the primary tubercles do not occupy the entire height of the plate so that the aboral primary tubercles retain their round outlines. However, adjacent to the peristome, the tubercles are more crowded, and tend to compress slightly into transverse ovals (Fig. 3B). The scrobicular tubercles are not strongly differentiated in size from the non-scrobicular secondaries, which are small and closely spaced everywhere outside the primary tubercle except along the interradius, where tubercles are lacking (Fig. 3D). This distinct naked area is adjacent to each interradial suture and occupied by a shallow furrow that, in larger specimens, sends branches circumferentially along sutures separating plates in each of the two interambulacral columns (Fig. 3D).

The apical system is large, ranging from just over 50% of the test diameter in juveniles to over 70% of the diameter in the largest adults. In the juveniles, the apical region tends to be almost flat. It is distinctly domed in adults, with considerable irregular inflation of the centers of some of the larger apical plates (particularly the genitals), especially in the specimen identified as a female. The genital plates are large relative to the other plates in the apical system. In the largest paratype, which appears to be a female, the gonopores can be as much as 2.4 mm in diameter and in some cases occupy shallow clefts along the interradial suture (Fig. 3A). The gonopores are present in the holotype, which appears to be a male, but are not evident in the larger of the 2 small paratypes in NMNH E11059, which is 13.9 mm in diameter. Ocular plates are only about a quarter the area of the genitals, and the ocular pores are surrounded by a prominent circular ridge (Fig. 3A). The tuberculation on both oculars and genitals is fine and dense, and tends to cover the entire plate surface almost to the suture (Fig. 3A).

The peristome is sunken around its periphery, and in the region of half the test diameter. Each perradial region bears 8 or 9 plates in each ambulacral column, and there are two relatively large scales in each interradial portion of the membrane (Fig. 3B).

The longest aboral primary spines are approximately 1 to 1.5 times the horizontal diameter of the test, although even the best examples are worn or broken so that the nature of the tips cannot be ascertained. Distal to the neck, the shaft is cylindrical and rod-like, and invested with irregularly spaced to only partially aligned, short, blunt spinules or bumps that arise from the smooth, porcellaneous surface. The neck is most peculiar in that it is greatly swollen in primary spines of larger specimens, and completely unadorned with spinules. The surface of the swelling is smooth, porcellaneous and glossy, and increases the diameter of the spine by a factor of 2 at its widest point (Fig. 3F). In juvenile specimens, the neck is also porcellaneous but only slightly swollen, suggesting that the vase-like shape of the swelling becomes more prominent with age. The oral primary spines are only slightly curved towards the peristome, and bear diametrically opposing flanges or keels along the lateral sides of the shaft. The edges of these keels are finely serrated, and the keels themselves are widest proximally, tapering towards the relatively blunt spine tip to give the entire spine a dagger-like appearance (Fig. 3G). The surface of the oral primaries is smooth and shiny, but not as glossy as the aboral primaries. The almost cylindrical scrobicular spines are blunt and very slightly swollen towards the tip (Fig. 3H). Scrobicular secondaries are only slightly longer than the non-scrobicular secondary spines (Fig. 3I). Both types of secondaries are club-shaped.

The valves of the large globiferous pedicellariae are less than 1 mm in length, and very similar to those of other *Aporocidaris* (Mortensen 1928). The smaller globiferous were not detected.

Types.—Holotype NMNH E11134, R/V *Eltanin* Cruise 14, Station 1212 (Fig. 3C, F–I). Paratypes NMNH E11059 (3 dry specimens, one dissected lantern, and one almost perfect, loose spine), E14603 (1 specimen in alcohol). The holotype was chosen because it retained some spines (Fig. 3C). Plate architecture was drawn from one of the largest of the paratypes in NMNH E11059 to avoid further damage to the holotype.

Etymology.—The name "*A. usarpi*" was originally used by Dr. Richard Chesher in his identifications of USARP material now housed the NMNH (see above), and it is clear from notes placed with that material that he intended to publish the species in a manuscript that never saw press. We retain Chesher's suggested name in honor of his recognition of the distinctiveness of this taxon.

Distribution.—*A. usarpi* is known only from a single R/V *Eltanin* locality (Cruise 14, station 1212) from a mid-ocean point far to the southeast of New Zealand and north of the Ross Sea (Fig. 1) at a depth of between 3678 and 3935 m.

Biology.—Nothing is known of the habitat preferences of *A. usarpi,* and appropriate specimens could not be sacrificed for gut content observations. There is some sexual dimorphism. The putative female has greatly enlarged gonopores (up to 2.4 mm in diameter) relative to the putative male, suggesting direct development in this species. None of the specimens had young retained on the test, although the peristomial edge is slightly sunken in such a way as to suggest the same type of marsupia seen in other species bearing young on the peristome. None of the specimens show obvious signs of *Echinophyces* infection, but the paucity and condition of the material prevent us from ruling out the occurrence of the parasite in *A. usarpi.*

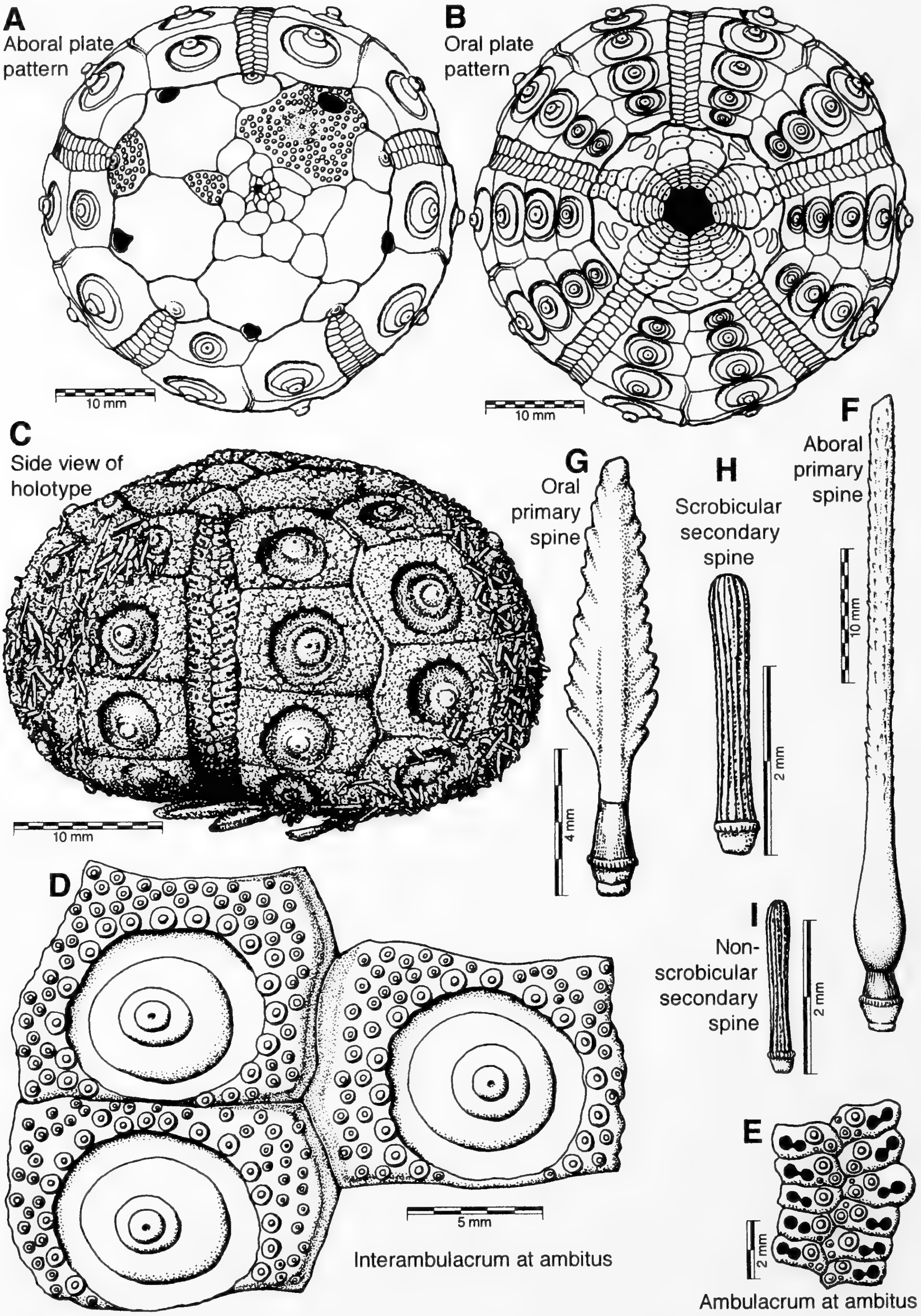

Fig. 3. *Aporocidaris usarpi* new species. C, F–I drawn from holotype (NMNH E11134); A, B, D, E drawn from paratypes in lot NMNH E11059. Conventions for A and B as in Fig. 2.

Remarks.—The greatly enlarged apical system and the naked, sunken area along the interradius indicate that the new species is an *Aporocidaris.* The species is readily distinguished from all other *Aporocidaris* by the peculiar swelling of the neck in the primary spines, and the extreme glossiness of both this swelling, and the shaft of the spines between the distal spinules. The absence of stereom bridges separating the members of the podial pore pairs has not been previously reported for any ctenocidarine taxa, let alone other *Aporocidaris.* Both the holotype and the largest of the paratypes exhibit this feature, but the two smallest specimens (below 14 mm horizontal diameter) have clearly divided pores, suggesting that the unification of the pores progresses with ontogeny, and is a derived feature of adult *A. usarpi.*

Genus *Notocidaris* Mortensen, 1909

Diagnosis.—Oral primary spines spear- or dagger-shaped. Aboral primaries rod-like and cylindrical to flattened and spatulate, with large lateral expansions distally. Spines smooth or spiny, but when present, spinules restricted to proximal part of shaft. Proximal surface of spines occasionally with coating of anastomosing hairs. Scrobicular secondary spines simple and slender (but not as fine or densely distributed as in *Aporocidaris*), not distinct in shape from other secondary spines. Interradial sutures naked, but not sunken. Apical system about 60% of horizontal diameter.

Remarks.—Mortensen (1928) listed 4 species in the genus: *N. gaussensis* Mortensen, 1909, *N. hastata* Mortensen, 1909, *N. mortenseni* (Koehler, 1900), and *N. platyacantha* (H. L. Clark, 1925). Another species, *N. remigera* Mortensen, 1950 was described after Mortensen's monograph of the cidaroids was published. We do not consider the entity *N. platyacantha* var. *contracta* Koehler, 1926 to be a valid taxon. Therefore, we attribute 5 full species to *Notocidaris,* all from Antarctic and Subantarctic waters, and all distinguished by features of the aboral primary spines. It should be noted that the range of variation recorded for each species can be extremely large and spine characteristics can overlap for species such as *N. remigera* and *N. mortenseni.* Therefore, biogeographic and bathymetric data, as well as other parts of the descriptions must also be used to make positive determinations.

Notocidaris lanceolata, new species

Fig. 4

Notocidaris lanceolata.—ex Fell, 1976: 195; figs. 7, 8f-g, name used in unpublished thesis

Diagnosis.—Aboral primary spines coarsely thorned at their base, with thorns arranged irregularly, and becoming greatly reduced in size and aligned towards tip. Spines keeled in two orthogonal planes in cross section, yielding lance-like appearance, spine tapering slightly towards relatively blunt tip. Longest spines about 2 times horizontal diameter of test in most specimens. Apical system varying from flat to arched. Test of preserved specimens beige to ochre, primary spines beige with shiny purplish-beige neck, secondary spines beige. Other characters as for *Notocidaris.*

Description.—The largest recorded horizontal test diameter is 36 mm. The height is between 50% and 60% of the test diameter. The holotype is 32.5 mm in horizontal diameter and 19.4 mm high.

The ambulacra are straight on the oral surface, with some slight sinuousness aborally (Fig. 4A, B). There are one or two secondary tubercles perradial to the podial pores, and two or three much smaller secondary tubercles next to the perradial suture (Fig. 4E). There is no naked region along the perradius. The inner and outer pore of each podial pore pair are divided by a well-developed "bridge" of stereom (Fig. 4E).

The aboral interambulacral plates are high and the primary tubercles are circular. Orally, the plates are not as high and the tubercles are compressed into transverse ovals (Fig. 4B). There are 7 or 8 plates in each column in a specimen about 50 mm in diameter. The scrobicular tubercles are in general only slightly differentiated from the non-scrobicular secondaries, which are abundant and closely spaced except along the interradial suture, where tubercles are lacking (Fig. 4D). There is no sunken area along the interradial suture.

The apical system is usually about 60% of the test diameter in larger specimens, and can range from being flat, as in the holotype, to domed. The gonopores are restricted to the genital plates and do not significantly invade the adjoining interambulacra. The females have enlarged gonopores. The oculars are large and circumferentially elongated so that they are much wider than they are high, and about half the surface area of the genital plates (Fig. 4A). The ocular pore is encircled by a prominent ridge and the tuberculation is fine and evenly distributed across each plate in the apical system except directly adjacent to the sutures (Fig. 4A).

The peristome is only slightly sunken at its periphery, and approximately 45% of the test diameter. There are 7 or 8 plates in each ambulacral column on the peristome of larger specimens, and as many as 5 small, irregularly shaped scales in each interradial portion of the membrane (Fig. 4B).

The ambital and aboral primary spines can be up to 2 times the diameter of the test and tapered. Several complete examples remain attached to the holotype (Fig. 4C). Near the base, the spine is adorned with irregularly arranged, prominent thorns and serrations which diminish sharply in size about 30% of the spine's length away from the base, giving way to strongly aligned, distal rows of spinules (Fig. 4F). Although the cross-section of the spine is broadly circular, usually there are also well-developed keels set almost orthogonally to each other along the distal part of the spine. The degree to which these keels are developed varies among specimens and even on an individual, but the basal thorns seem to be a constant feature. Basally, the spine can bear a surface coat of anastomosing hairs similar to that seen in some *Aporocidaris*. The oral primaries are differ from the aboral primaries in lacking strongly developed keels except laterally, where they can also be strongly serrated (Fig. 4G), particularly in specimens with thorny aboral primaries. The oral primaries adjacent to the peristome are very small and dagger- or arrowhead-shaped, with somewhat less distinctly serrated keels. In specimens with reduced keels on the aboral primaries, the oral primaries are less dagger-shaped, and more oval in outline. The scrobicular spines are slightly pointed (Fig. 4H). The non-scrobicular secondary spines are smaller, particularly in the ambulacra (Fig. 4I).

As in most ctenocidarines, the globiferous pedicellariae come in two sizes, both of which are quite long and slender in *N. lanceolata,* though not diagnostically so. The valves can be just over 1 mm long in the larger form.

Types.—Holotype MCZ 8336, R/V *Eltanin* Cruise 32, Station 2110 (Fig. 4C). Paratypes NMNH E21865 (3 dry specimens), E21866 (1 dry specimen), E22004 (1 specimen in alcohol), E22005 (5 specimens in alcohol), E22006 (3 specimens in alcohol). We decided to retain the holotype designated in Fell (1976) to avoid confusion, and also because the specimen has exemplary spine cover (Fig. 4C). Drawings of spines and plate architecture were made from the paratypes to avoid damaging the holotype.

Etymology.—In his thesis, Fell (1976) attributed the name to Richard Chesher, who recognized the distinctiveness of the new taxon in a manuscript that was never published. Chesher based the name on the keeled, lanceolate spines.

Distribution.—Known from 7 R/V *Eltanin* stations (Cruise 27, Stations 1867, 1926, 1929; Cruise 32, Stations 2002, 2108, 2110, 2129) at three distinct localities in the

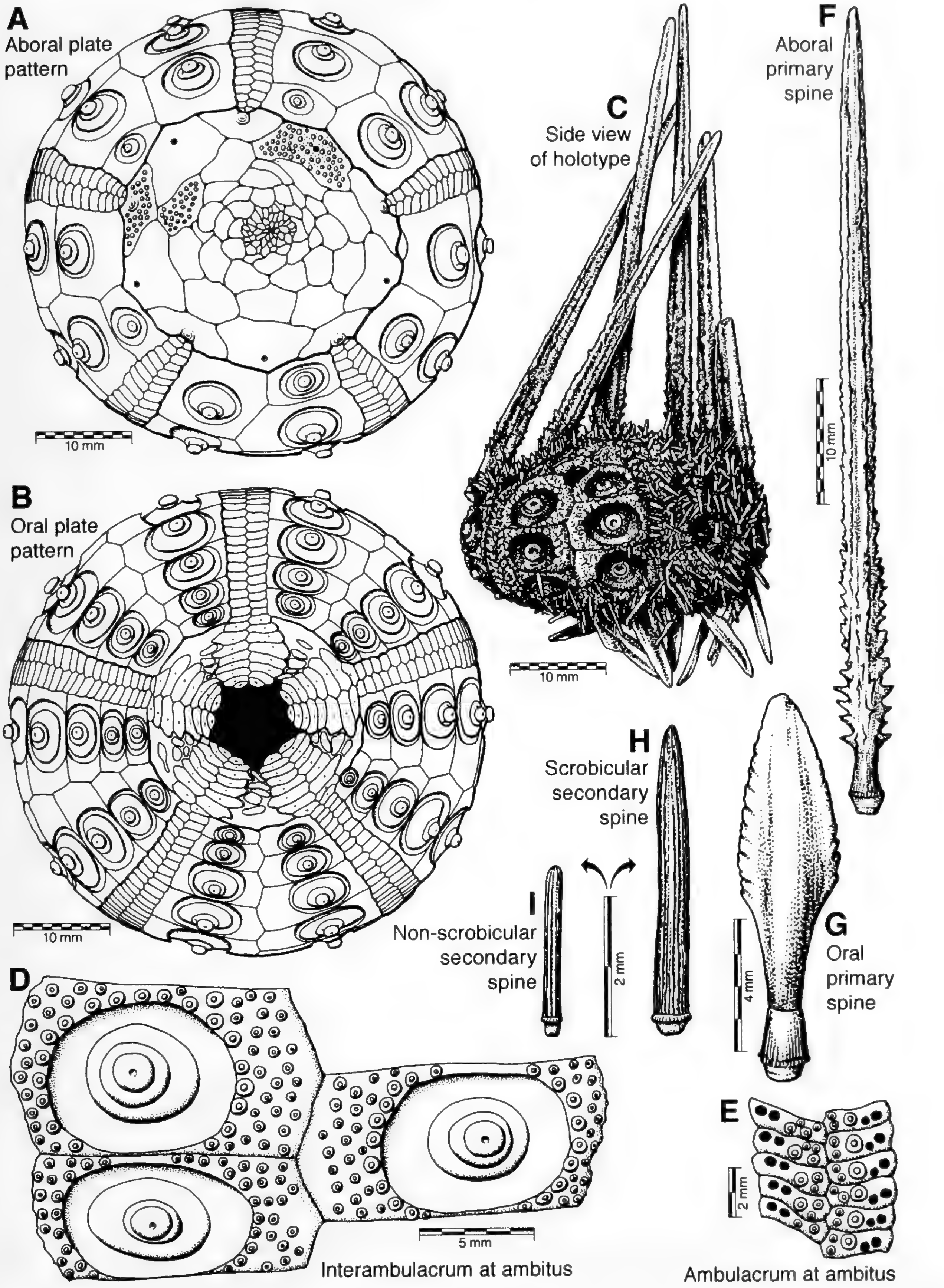

Fig. 4. *Notocidaris lanceolata* new species. C drawn from holotype (MCZ 8336); A, B, D, E drawn from paratypes in lot NMNH E21865; F–I drawn from paratype (NMHH E 21866). Conventions for A and B as in Fig. 2.

Ross Sea between 2005 and 2421 m (Fig. 1).

Biology.—The spines seem remarkably free of epizoans. The preferred habitat is unknown. Some specimens, which could be females, have enlarged gonopores, but no broods have been observed. No evidence of *Echinophyces* infection could be detected.

Remarks.—As noted by Fell (1976:197), the species was based on a specimen rescued by Dr. Merrill Foster from "material intended for disposal overboard" and later turned over to Chesher, who selected it as a potential type. The holotype, in having primaries that are thorny and strongly lanceolate, is close to one end of a range that includes forms in which the keels can be almost absent. As Fell (1976:197) indicated, "were it not for the range of intermediates between fluteless [unkeeled] and fully fluted [keeled] specimens obtained at two stations, one would not believe they were of a single species". Typical *N. lanceolata* may be most easily confused with particularly thorny *N. hastata,* especially since they inhabit the same environments, while variants of *N. lanceolata* with greatly reduced keels on the spines may be confused with *N. gaussensis.* In addition, the surface coating of anastomosing hairs between the thorns and keels near the base of the spine can cause some confusion with *Ctenocidaris,* particularly if this feature alone is used to sort material. Because *N. lanceolata* occurs, on average, almost 1000 m deeper than *N. gaussensis* and virtually all *Ctenocidaris,* available depth data should help to provide initial clues in identification.

Acknowledgments

We would like to thank Cynthia Ahearn (National Museum of Natural History) for her patience and helpfulness throughout our endless inquiries and loan requests and Chris Mah of the California Academy or Sciences (California Academy of Sciences) for digging out distant data. Fred Collier (Museum of Comparative Zoology) provided invaluable information concerning the type of *N. lanceolata.* We are also grateful for the editorial comments of John Pearse and Dave Pawson. Mooi's research was supported by an American Philosophical Society General Research grant. This paper is a contribution of the theme "Signal morphologique de l'Évolution" of the UMR CNRS 5561 "Biogéosciences."

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A new species of *Pristigaster,* with comments on the genus and redescription of *P. cayana* (Teleostei: Clupeomorpha: Pristigasteridae)

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Abstract.—A new species of the hitherto monotypic genus *Pristigaster* (Clupeiformes: Pristigasteridae) is described for the Amazon basin. *Pristigaster whiteheadi,* new species, is distinguished from its only congener, *P. cayana,* by the presence of pelvic fins; the lack of caudal-fin filaments; the different angle between the predorsal bones and the vertebral column; the presence of 36–39 vertical scale rows (40–47 in *P. cayana*); and the presence of 18–20 horizontal scale rows (21–26 in *P. cayana*). *Pristigaster cayana* is redescribed, and its occurrence in French Guyana is questioned.

Resumo.—Uma nova espécie do gênero até então monotípico *Pristigaster* (Clupeiformes: Pristigasteridae) é descrita para a bacia Amazônica. *Pristigaster whiteheadi,* espécie nova, distingue-se de *P. cayana* pela presença de nadadeiras pélvicas; ausência de filamentos nos lobos da nadadeira caudal; o ângulo diferente entre os ossos pré-dorsais e a coluna vertebral; a presença de 36–39 fileiras verticais de escamas (40–47 em *P. cayana*); e a presença de 18–20 fileiras horizontais de escamas (21–26 em *P. cayana*). *Pristigaster cayana* é redescrita e sua ocorrência na Guiana Francesa é questionada.

The Clupeomorpha is a highly diverse group of teleosts, containing over 350 recent and over 150 fossil species (Grande 1985, Nelson 1994). The group is one of the most important fisheries resources worldwide, and their phylogenetic relationships within teleosts have been a matter of intense debate in recent years. For the past two decades, following the original suggestion by Patterson & Rosen (1977), Clupeomorphs were placed as the sister group to the Euteleostei. More recently, Clupemorpha have been proposed as sister group to Ostariophysi, a hypothesis supported by molecular data (Van Le et al. 1993, Patterson 1994) and morphological characters (Lecointre & Nelson 1996, Johnson & Patterson 1996, Arratia 1997).

Clupeomorphs are a demonstrably monophyletic group (Grande 1985) including basal fossils as the extinct genera *Diplomystus* and *Armigatus,* and the extinct order Ellimmichthyiformes. Recent clupeomorphs are all in the order Clupeiformes, itself divided into suborders Denticipitoidei (with a single species from African freshwaters) and Clupeoidei (all other recent clupeiforms). Clupeoids comprise three superfamilies: Engrauloidea (with a single family, Engraulididae), Clupeoidea (with families Chirocentridae and Clupeidae) and Pristigasteroidea (with families Pristigasteridae and Pellonidae).

The pristigasteroid family Pellonidae includes the central and South American genera *Chirocentrodon, Neoopisthopterus, Pellona, and Pliosteostoma.* The Pristigasteridae, in turn, comprises the Central and

South American *Odontognathus* and *Pristigaster,* the South American and Indo-Pacific *Opisthopterus* and the Indo-Pacific *Raconda.* The genus *Ilisha* could not be demonstrated monophyletic by Grande (1985), most of its species forming a polytomy at the base of Pristigasteroidea.

Pristigaster is the most peculiarly-shaped of all pristigasteroids, with an extremely deep body resembling characiforms of the genera *Gasteropelecus* and *Thoracocharax.* So far a single species, *P. cayana,* is recognized in the genus. All other proposed names have been shown to be either invalid or junior synonyms of that species (Whitehead 1973, 1985). However, Whitehead (1985) suggested that a second species might exist. Stimulated by Whitehead's original suggestion, we undertook a detailed examination of available material of *Pristigaster,* and concluded that indeed there is a second diagnosable species in the genus, still undescribed. In this paper, we formally name and diagnose the new species and redescribe *P. cayana.*

Methods and materials.

Morphometric measurements were all point-to-point, taken with calipers, recorded to the nearest 0.1 mm and expressed as percentages of standard length, except for subunits of the head, expressed as percentages of head length. Counts and measurements were made on the left side of the specimens, whenever possible, according to Whitehead (1985), except for horizontal rows of scales (counted between dorsal-fin origin and anal-fin origin), vertical rows of scales (counted from origin of pectoral fin to caudal base), and scales around caudal peduncle (number of horizontal scale rows). Principal caudal-fin rays included all branched rays plus one unbranched ray in each lobe. Counts for each lobe, upper first, are separated by a slash. Vertebral counts were taken from radiographs and cleared and stained specimens and the terminal "half centrum" is included. Specimens were dissected to determine sex by an incision on the right side of the abdomen to expose the gonads. Tooth counts include sockets in cases where the actual tooth has fallen off. Within the meristic information given here, figures for holotype are provided in parentheses.

Figures associated with specimen lists in species descriptions are, first, number of specimens examined in respective lot, and second, range of SL's in mm.

Specimens cleared and counterstained for bone and cartilage were prepared by a modified version of the method of Taylor & Van Dyke (1985). Descriptive accounts follow the general organization in Whitehead & Teugels (1985), the most complete anatomical survey of a clupeomorph available to date. Synonymic lists include only those references in which the species referred to can be reliably identified as either *P. cayana* or *P. whiteheadi.*

Specimens examined in this work are deposited in the following institutions: AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; FMNH, Field Museum of Natural History, Chicago; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MZUSP, Museu de Zoologia, Universidade de São Paulo, São Paulo.

Pristigaster whiteheadi, new species

Figs. 1, 2B

Pristigaster cayana (not Cuvier); Whitehead, 1985:301 (in part, only specimens with pelvic fins); Whitehead & Bauchot, 1985:24 (in part, only specimens with pelvic fins); Stewart, Barriga & Ibarra, 1987:21 (specimen examined).

Holotype.—MZUSP 52963 (female, 83.4 mm SL). BRAZIL: Amapá, Rio Araguari, Ferreira Gomes, collected by M. Goulding, January–February, 1984.

Paratypes.—Brazil: MZUSP 30341 (2, 76.5–83.4), same data as holotype. Amazonas; MZUSP 11391 (8, 57.5–67.7, 2 of which cleared and counterstained), AMNH 227329 (1, 52.2), USNM 351306 (1, 62.0), FMNH 107783 (1, 56.5), Rio Içá, Santo Antônio do Içá; MZUSP 11392–393 (2, 69.4–73.0), Rio Solimões, above mouth of Jutaí; MZUSP 11394–403 (10, 43.5–76.2), Rio Solimões, Fonte Boa; MZUSP 27597 (1, 62.00, Rio Solimões, Município de Benjamin Constant; MZUSP 18694 (3, 29.4–40.0), Rio Solimões, Lago Janauacá and vicinity; MZUSP 52950 (2, 22.0–25.0), Rio Solimões, 3°10′57″S, 67°56′31″W; MZUSP 6600 (1, 70.0), Lago Manacapuru; MZUSP 18512 (1, 67.0), mouth of Rio Ituxi; MZUSP 18516 (1, 70.0), mouth of the Paciá; INPA 8555 (21, 18.0–66.6, 3 of which cleared and stained), Paraná do Tapurá, near mouth of Rio Madeira; MZUSP 6220 (1, 84.0), Rio Negro, Igarapé Jaraquí, above Manaus; MZUSP 52951 (1, 39.0), Rio Jauaperi, 1°34′54″S, 61°28′48″W; MZUSP 52952 (2, 57.7 and 67.0), Rio Negro, 1°33′48″S, 61°33′02″W; MZUSP 49597 (3, 28.3–37.3), Rio Acre, above Boca do Acre; MZUSP 7625 (1, 67.0), Rio Amazonas, Paraná do Mocambo, above Parintins; BMNH 1897.12.1.197–199 (3, 62.8–65.0), Rio Juruá; MZUSP 52949 (21, 47.0–86.0), Rio Japurá, Paraná do Japurá, 3°09′12″S, 64°46′54″W; MZUSP 52962 (1, 63.3), Rio Amazonas, 1°54′S, 55°31′W; MZUSP 52948 (5, 35.5–76.0), Rio Madeira, below Nova Olinda; MZUSP 52958 (1, 36.0), Rio Madeira, 3°33′37″S, 58°59′49″W; MZUSP 52957 (1, 34.0), 3°33′18″S, 58°59′57″W, MZUSP 52959 (1, 41.0), 3°29′21″S, 58°51′38″W, MZUSP 52960 (1, 30.5), 3°26′44″S, 58°49′49″W, MZUSP 52961 (4, 30.5–41.0), 3°33′S, 58°55′W, Rio Madeira, Paraná do Urucurituba. Roraima: MZUSP 11404 (1, 33.0), Rio Branco, 20 kilometers below Boiaçu. Pará: MZUSP 52953 (1, 28.0), 1°35′S, 52°11′W, MZUSP 52954 (7, 50.0–55.0), 1°27′S, 52°03′W, Rio Amazonas, Furo do Urucuricaia; MZUSP 5493 (1, 85.0), Rio Trombetas, Oriximiná; MZUSP 52955 (1, 53.7), 1°29′S, 52°5′W, MZUSP 52956 (8, 22.3–66.5), 1°36′S, 52°12′W, Rio Amazonas, below Rio Xingu. ECUADOR. FMNH 101946 (1, 89.0) 0°49′S, 75°31′W, Río Tiputini, near mouth in Río Napo and Quebradas).

Diagnosis.—Distinguished from its only congener, *P. cayana,* by the following features: 1—presence of pelvic fins; 2—absence of filaments on upper and lower lobes of caudal fin; 3—vertical scale rows 36–39 (40–47 in *P. cayana*); 4—horizontal scale rows 18–20 (21–26 in *P. cayana*); 5—supraneurals (predorsal bones) gradually less sloped posteriorly, posterior one nearly perpendicular to vertebral column (supraneurals all equally sloped in *P. cayana*). Most specimens of the new species can also be distinguished from *P. cayana* by lower gill raker counts (18–21, versus 21–25 in *P. cayana*) and by lower anal-fin ray counts (41–48 versus 44–53 in *P. cayana*).

Description.—Meristic and morphometric data are presented in Tables 1 and 2. For a general aspect of the fish, refer to Fig. 1. Body highly compressed, ventral profile of body extremely expanded and convex, its anterior region (at isthmus) almost perpendicular to longitudinal axis of fish. Five protruding predorsal supraneurals strongly inclined anteriorly. The entire abdominal region, from isthmus to anal-fin origin, bordered by a series of 29–34 (holotype 31) abdominal scutes, gradually more prominent posteriorly. Scutes anterior to vertical through pectoral-fin base mostly imbedded in soft tissue, those posterior to that point protruding markedly beyond abdominal profile resembling a series of translucent hooks. Pelvic-fin origin usually over 25th scute (as in holotype), rarely over 24th or 26th scutes.

Snout blunt, always shorter than orbital diameter. Mouth subterminal and turned dorsally, its lower jaw protruding beyond upper. Maxilla extending slightly posterior to vertical through anterior margin of eye. Teeth conical, minute, disposed in a single irregular row in both jaws and highly variable in number, becoming more numerous with growth. Premaxillary teeth 8 (in spec-

Table 1.—Selected meristic features of *Pristigaster cayana* and *P. whiteheadi.*

	Pristigaster cayana				*Pristigaster whiteheadi*				
	n	Range	Mean	*SD*	*n*	Holotype	Range	Mean	*SD*
Branched dorsal-fin rays	79	12–13	12.177	0.384	95	12	11–13	12.053	0.305
Branched pectoral-fin rays	79	10–12	10.848	0.622	95	10	9–11	10.537	0.522
Branched pelvic-fin rays					95	3	3–4	3.137	0.346
Branched anal-fin rays	73	44–53	48.096	2.076	93	44	41–48	44.258	1.436
Gill rakers	77	21–25	22.208	0.848	95	21	18–21	19.895	0.722
Horizontal rows of scales	55	21–26	23.182	1.090	35	—	18–20	19.114	0.631
Vertical rows of scales	39	40–47	43.077	1.797	18	—	36–39	38.222	0.878
Scales around caudal peduncle	18	15–16	15.833	0.383	9	—	13–15	14.556	0.726
Premaxillary teeth	58	9–23	16.862	3.322	78	14	8–18	11.962	1.970
Maxillary teeth	62	18–80	53.871	14.140	84	63	14–64	40.000	11.600
Dentary teeth	49	5–14	9.408	2.188	53	9	5–9	7.132	1.301
Ventral scutes	75	30–35	32.013	1.257	92	31	29–34	31.065	0.849
Vertebrae	7	42–44	43.428	0.728	7	—	43–44	43.286	0.488

imens <44 mm SL) to 18 in larger specimens (holotype 14). Maxillary teeth 14 (in 22 mm SL specimen) to 64 (in 79 mm SL specimen) (holotype 63). Dentary teeth 6 (at 43 mm SL) to 9 in larger specimens (holotype 9). Eyes very large, round in external aspect. Pupil extremely large relative to eye size, its diameter almost 60% that of orbit. Adipose eyelid weakly developed in young, but covering most of iris in adults.

Gill cover rounded in profile, with continuous membranous margin concealing a marked depression on posterior margin of opercle. Dorsal limit of gill opening slightly ventral to horizontal at dorsal margin of eye. Gill rakers slender, closely set and conspicuous, their number increasing with growth, ranging from 18 (at 22 mm SL) to 21 (at 83 mm SL) (holotype 21) on lower part of first branchial arch and from 8 to 12 (holotype 11) on upper part.

Table 2.—Morphometrics of *Pristigaster cayana* and *P. whiteheadi.* Standard length is expressed in mm; measurements 1 to 12 are proportions of standard length; 13 to 16 are proportions of head length.

	Pristigaster cayana				*Pristigaster whiteheadi*				
Character	*n*	Range	Mean	*SD*	*n*	Holotype	Range	Mean	*SD*
Standard length	79	23.5–142.0	66.68	—	95	83.4	22.0–86.0	56.12	—
1. Body depth	78	0.38–0.65	0.550	0.041	95	0.56	0.42–0.58	0.534	0.031
2. Predorsal length	79	0.39–0.48	0.421	0.014	95	0.43	0.40–0.48	0.425	0.017
3. Prepectoral length	78	0.23–0.31	0.271	0.012	95	0.27	0.24–0.31	0.272	0.013
4. Prepelvic length					95	0.59	0.48–0.61	0.571	0.025
5. Preanal length	78	0.57–0.70	0.649	0.023	95	0.67	0.54–0.71	0.657	0.024
6. Caudal peduncle depth	79	0.08–0.11	0.096	0.008	95	0.09	0.07–0.12	0.098	0.007
7. Head length	79	0.25–0.31	0.287	0.010	95	0.29	0.25–0.32	0.286	0.012
8. Dorsal-fin base	79	0.12–0.16	0.138	0.009	95	0.12	0.12–0.17	0.145	0.012
9. Dorsal-fin length	72	0.24–0.33	0.283	0.020	94	0.26	0.24–0.32	0.289	0.018
10. Anal-fin base	78	0.42–0.53	0.486	0.026	95	0.44	0.42–0.50	0.467	0.016
11. Pectoral-fin length	79	0.17–0.28	0.250	0.016	95	0.23	0.16–0.26	0.230	0.015
12. Pelvic-fin length					94	0.04	0.02–0.07	0.048	0.006
13. Snout length	79	0.18–0.26	0.223	0.021	95	0.25	0.21–0.29	0.247	0.015
14. Eye diameter	79	0.33–0.44	0.393	0.022	95	0.40	0.34–0.45	0.399	0.023
15. Interorbital width	79	0.12–0.21	0.176	0.016	95	0.20	0.18–0.25	0.205	0.013
16. Upper jaw length	79	0.41–0.57	0.486	0.033	95	0.49	0.43–0.53	0.479	0.019

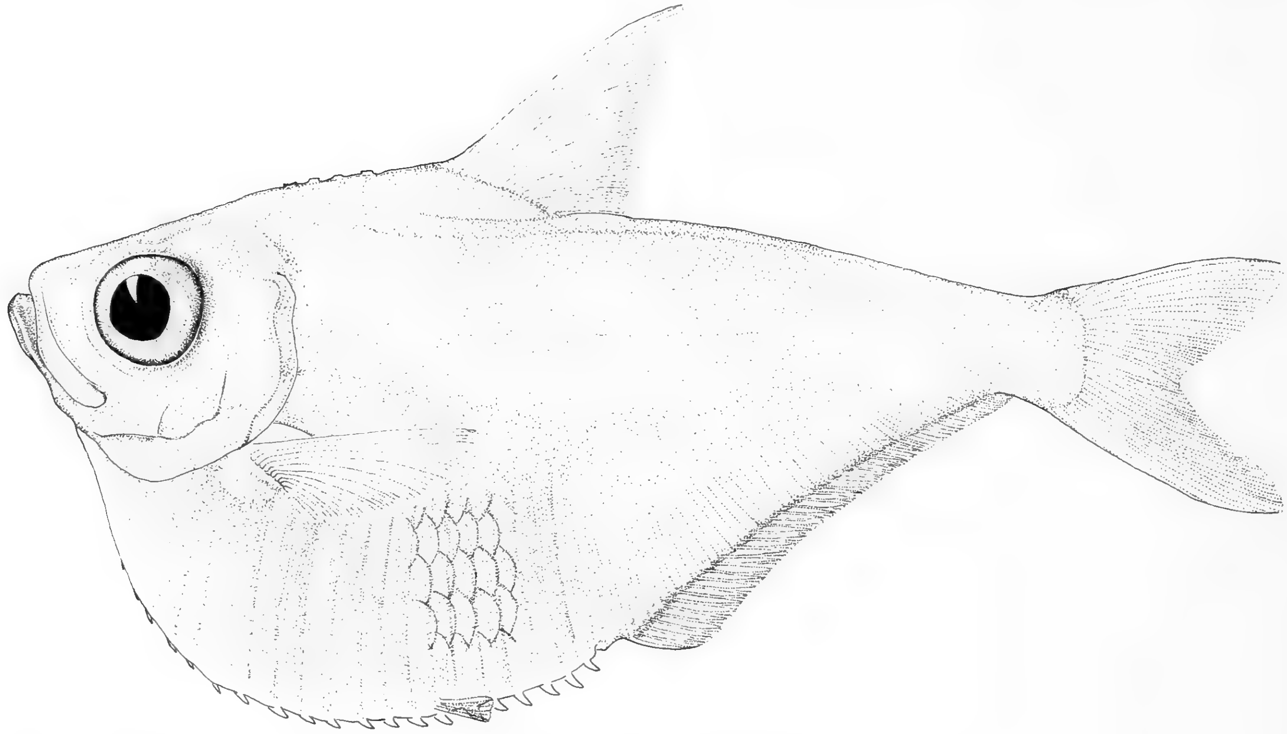

Fig. 1. *Pristigaster whiteheadi,* new species, holotype, MZUSP 52963, 83.4 mm SL.

Dorsal fin triangular when extended, pointed dorsally; origin located on anterior half of SL, and anterior to vertical through anal-fin origin. Dorsal-fin rays iii+(12)–13, third ray (unbranched) longest, twice as long as fin-base. Pectoral-fin origin located at middepth of body, slightly dorsal to ventral margin of gill cover and slightly anterior to its posterior margin. Pectoral-fin length shorter than HL, its posterior tip, when adpressed to body, reaching beyond vertical through dorsal-fin origin. Pectoral-fin rays i+(10)–11. Axillary scale present on region dorsal to pectoral-fin base, extending for approximately 20% of fin. Pelvic fins minute, length spanning approximately the space of three consecutive abdominal scutes, with origin located nearly at ventral margin of body, at vertical through posterior tip of pectoral fin. Pelvic-fin rays i+3+i. Anal fin long and low, its origin slightly posterior to vertical through posterior end of dorsal-fin base. Anal-fin rays ii–iii+41–47 (holotype ii+44); rays progressively shorter posteriorly. Tips of last anal-fin rays reaching base of inferior caudal-fin basal fulcra. Caudal fin deeply forked, lower lobe slightly longer than upper. Caudal-fin rays 10/9. Vertebrae 43 or 44.

Scales large (approximately same size as pupil) and cycloid, covering all of body, and easily detachable, rarely preserved in their entirety. Vertical scales rows 36–39. Horizontal rows 18–20. Scale covering extending to midlength of middle caudal-fin rays. Entire anal-fin base rimmed by row of small scales (about half as large as remaining body scales).

Pigmentation in alcohol.—Dorsum, snout and upper part of sides brown. Remainder of body silvery due to heavy deposits of guanine (which tend to disappear after extended preservation). Narrow concentrations of dark melanophores on upper and lower lips, and sometimes anterior portion of chin. Region corresponding to neurocranium dark, due to brain pigment visible through translucent skull bones. Scattered dark chromatophores along entire dorsum and upper sides, more concentrated along dorsal-fin base and dorsal part of caudal peduncle. A middorsal dark spot is sometimes present anterior to dorsal fin (as

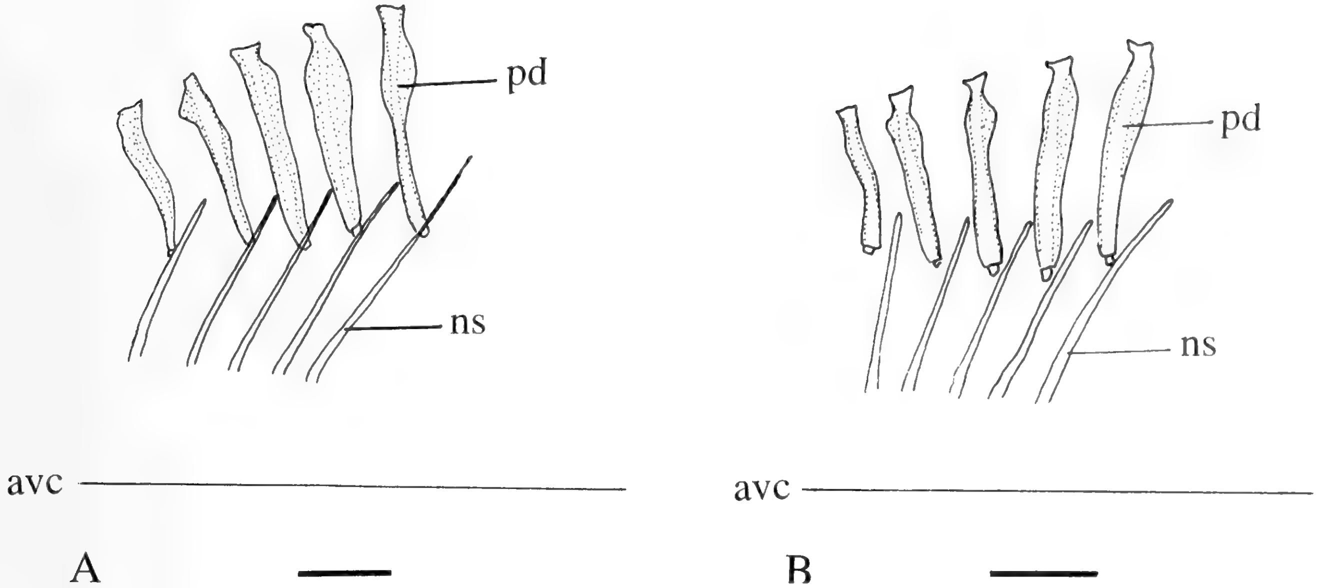

Fig. 2. Predorsal bones and corresponding neural spines in lateral view, anterior to left. A—*Pristigaster cayana,* MZUSP 30338; B—*P. whiteheadi,* n. sp., paratype, INPA 8555; Abbreviations: pb—predorsal bone, ns—neural spine, avc—main axis of vertebral column. Scale bars = 1 mm.

in holotype). Myosepta visible but not outlined by dark pigmentation. Fins hyaline, except for faint rows of melanophores along outer rays of caudal fin and a few scattered isolated melanophores on dorsal fin.

Etymology.—The name of this species is a posthumous tribute to Peter J. P. Whitehead, who contributed more than any other individual to the knowledge of clupeomorph fishes, also for first suggesting that there might be two different species in *Pristigaster.*

Distribution.—Brazil and Ecuador, in the following river basins: Rio Solimões/Amazonas, Rio Trombetas, Rio Branco, Rio Japurá, Rio Negro, Rio Madeira, Rio Juruá, Rio Araguari (State of Amapá, Brazil) and Río Napo.

Pristigaster cayana Cuvier, 1829
Figs. 3, 4

Pristigaster cayanus Cuvier, 1829: pl. 10, fig. 3; 1829:321 (name only, American seas); Valenciennes, 1847 (redescription of holotype).

Pristigaster argenteus Schinz, 1822:300 (based on Cuvier's figure; nomen oblitum).

Pristigaster lichtensteinii Jarocki, 1822: 322, fig. 3 (based on Cuvier's figure, reproduced; nomen oblitum).

Pristigaster triangularis Stark, 1828:408 (based on Cuvier's figure; nomen oblitum).

Pristigaster martii Agassiz, *in* Spix & Agassiz, 1829:55, pl. 24a (Amazon); no pelvic fins; post-dates *cayanus* by a month or so (see Whitehead & Bauchot, 1985); Amaral-Campos, 1941:187; Whitehead & Myers, 1971; Le Bail et al., 1983.

Pristigaster americanus Guérin-Menéville, 1844:33, pl. 57, fig. 3 (Atlantic coast of South America).

Pristigaster phaeton Valenciennes, 1847: 338 (Amazon); no pelvic fins (see Whitehead & Bauchot, 1985).

Pristigaster cayana; Myers, 1956 (validity of *P. cayanus* Cuvier as of 1829; emmendation of specific name to agree with feminine gender of genus); Hildebrand, 1964 (synonymy of *cayana, phaeton* and *martii*); Whitehead, 1964:428, fig. 108 (synopsis); 1967:100, 102 (types of *cayana* and *phaeton*); 1973a:85 (*triangularis* a nomen oblitum; synonymy); 1985:301 (in part, only specimens without pelvic fins; synonymy, diagnosis; distribution; habitat and biology); Whitehead & Myers, 1971:487 (validity of *martii*); Whitehead & Bauchot, 1985:24 (in part, only specimens without pelvic fins; types of *cayana, phaeton*); Eschmeyer, 1998:347 (catalog and suggestion—not accepted here—that name is not available from Cuvier, 1829).

Material examined.—95 specimens (23.5–142.0 mm SL). Brazil. Amazonas: MZUSP 31032 (1, 90.0), Lago do Prato, Rio Negro, Anavilhanas; MZUSP 11389 (1, 142.0), Lago Puraquequara; MZUSP 52947 (1, 64.0), Lago Manacapuru; MZUSP 7023 (20, 52.5–74.0, 2 of which cleared and counterstained), Rio Madeira, 25 kilometers below Nova Olinda; MZUSP 11405 (1, 37.5), Rio Solimões, Ilha do Xibeco; MZUSP 9568 (1, 96.0), Manaus; MZUSP 18696 (1, 92.0), Rio Solimões, Lago Janauacá; MZUSP 52943 (1, 23.5), Rio Negro, 1°58′16″S, 61°15′42″W; MZUSP 52944 (6, 30.0–36.0), Rio Içá, 3°03′57″S, 68°04′26″W; MZUSP 52945 (1, 34.0), Rio Solimões, 2°40′15″S, 66°39′14″W; MZUSP 52946 (1, 62.2), Rio Japurá, Paraná do Japurá, 3°08′20″S, 64°46′52″W; MZUSP 1388 (1, 111.0) and 11390 (1, 86.0), Rio Juruá; BMNH 1925.10.28.5 (1, 88.9), Rio Solimões, Manacapuru. Roraima: MZUSP 30334 (1, 137.0), Rio Branco, below Xeruini; MZUSP 30335 (1, 112.0) and 30337 (1, 103.0), Rio Branco, Marará; MZUSP 30339 (2, 100.0 and 110.0), Rio Branco, Lago do Maguari; MZUSP 30340 (6, 68.3–82.5), Rio Branco, Xeruini; MZUSP 52942 (1, 105.0), Rio Branco, 1°16′59″S, 61°50′52″W. Rondonia: MZUSP 30336 (1, 81.0) and 30338 (29, 33.0–66.0, 3 of which cleared and counterstained), Rio Madeira, Calama. Pará: MZUSP 5560 (2, 72.0 and 73.5), Lago Ururiá, Oriximiná; MZUSP 5668 (1, 82.5), Lago Puru, Oriximiná; MZUSP 8280 (1, 97.0), Rio Trombetas, Oriximiná; MZUSP 5689 (1, 72.0), Rio Trombetas, mouth of Lago Paru. Mato Grosso: MZUSP 17030 (1, 29.0), Rio Araguaia, Santa Terezinha; MZUSP18627 (2, 116.0 and 126.0), Rio Araguaia, Lago Dumbá. PERU. Loreto: FMNH 71264 (1, 100.0), mouth of Río Tigre, 80 miles SW of Iquitos; MZUSP 15217 (1, 83.0), Cocha Aguajal, Río Amazonas, Iquitos: MZUSP 15216 (2, 83.0 and 88.0), Río Marañon, Nauta; Pucallpa: MZUSP 18557 (1, 47.0), Río Ucayali.

Diagnosis.—See diagnosis of *P. whiteheadi.*

Description.—Meristics and morphometrics are presented in Tables 1 and 2. Body form and disposition, shape and arrangement of abdominal scutes (30–35 in number) as in *P. whiteheadi.*

Shape, size and position of snout, eye, pupil, adipose eyelid, mouth, maxilla and also shape, arrangement and number of teeth as in *P. whiteheadi.* Number of teeth also increasing with growth. Premaxillary teeth 9 (in specimens <25 mm SL) to 23 in larger specimens. Maxillary teeth 18 (in 23.5 mm SL specimen) to 80 (in 105 mm SL specimen). Dentary teeth 7 (at 54 mm SL) to 14 in larger specimens.

Shape of gill cover, gill membrane and shape and disposition of gill rakers and position of dorsal limit of gill opening as in *P. whiteheadi.* Number of gill rakers also increasing with growth, ranging from 21 (at 45 mm SL) to 25 (at 110 mm SL) on lower part of first branchial arch and from 9–12 on upper part.

Pelvic fins absent. Position, shape and size of all other fins and axillary scale identical to those of *P. whiteheadi.* Dorsal-fin rays iii+12–13. Pectoral-fin rays i+10–12. Anal-fin rays ii–iii+44–53. Caudal-fin rays 10/9. Tips of dorsalmost two branched upper lobe caudal-fin rays elongated into filament twice as long as first principal ray (unbranched) in a specimen 100 mm SL. Tips of eighth and ninth lower lobe caudal-fin rays also prolonged into a shorter lower lobe filament about one-third as long as tenth (unbranched) ray in same specimen.

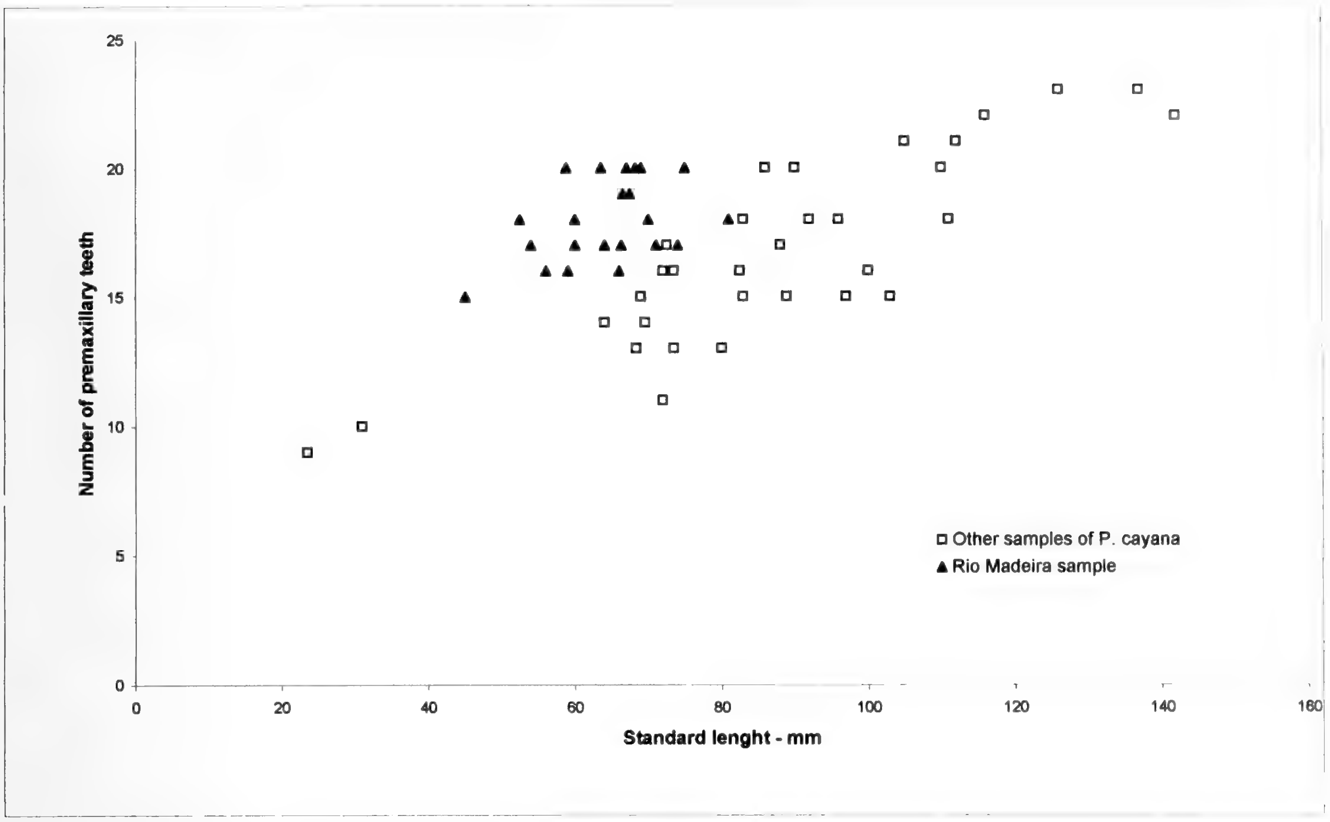

Fig. 3. Size-dependent variation of the number of premaxillary teeth in *P. cayana.*

Upper and lower caudal-fin filaments frequently broken in preserved specimens. Vertebrae 43–44.

Size, shape and distribution of cycloid scales on body and fins as in *P. whiteheadi.* Vertical scale rows 40–47. Horizontal rows 21–26.

Pigmentation in alcohol.—As in *P. whiteheadi.*

Distribution.—Nearly coincident with that of *P. whiteheadi,* with which it is sympatric in most localities of the Amazon Basin, but extending further south into Rio Araguaia, State of Mato Grosso, Brazil. The locality associated with the holotype of the species is reported as Cayenne, French Guiana (Whitehead 1967). This information is not provided in the original accounts on the species by Cuvier, which state simply "seas of America". Other reports on the type-locality have inferred it from the species name (e.g., Myers 1956). Representatives of *Pristigaster* have never been collected again in French Guiana, in any of the surveys of the area (e.g., Le Bail et al. 1983, Planquette et al. 1996, also P. Keith, pers. comm.). The genus has also not been reported from surrounding areas, like Guyana, Suriname or the Orinoco basin. We strongly suspect that the Cayenne locality is erroneous, and may simply reflect a port of shipment or an intermediate post en route between South America and France, in which the material studied by Cuvier may have remained temporarily.

Remarks.—The sample from Rio Madeira differs from remaining ones in number of premaxillary teeth (Fig. 3), but no other meristic or morphometric difference was found between that population and others throughout the range of the species. In the absence of additional significant differences we prefer to consider the higher number of premaxillary teeth in the Rio Madeira sample as populational variation.

Notes on the name P. cayana.—The history of the names associated with the species referred to here as *Pristigaster cayana* is rather complicated. The first reference to the species was done in Cuvier (1816), as

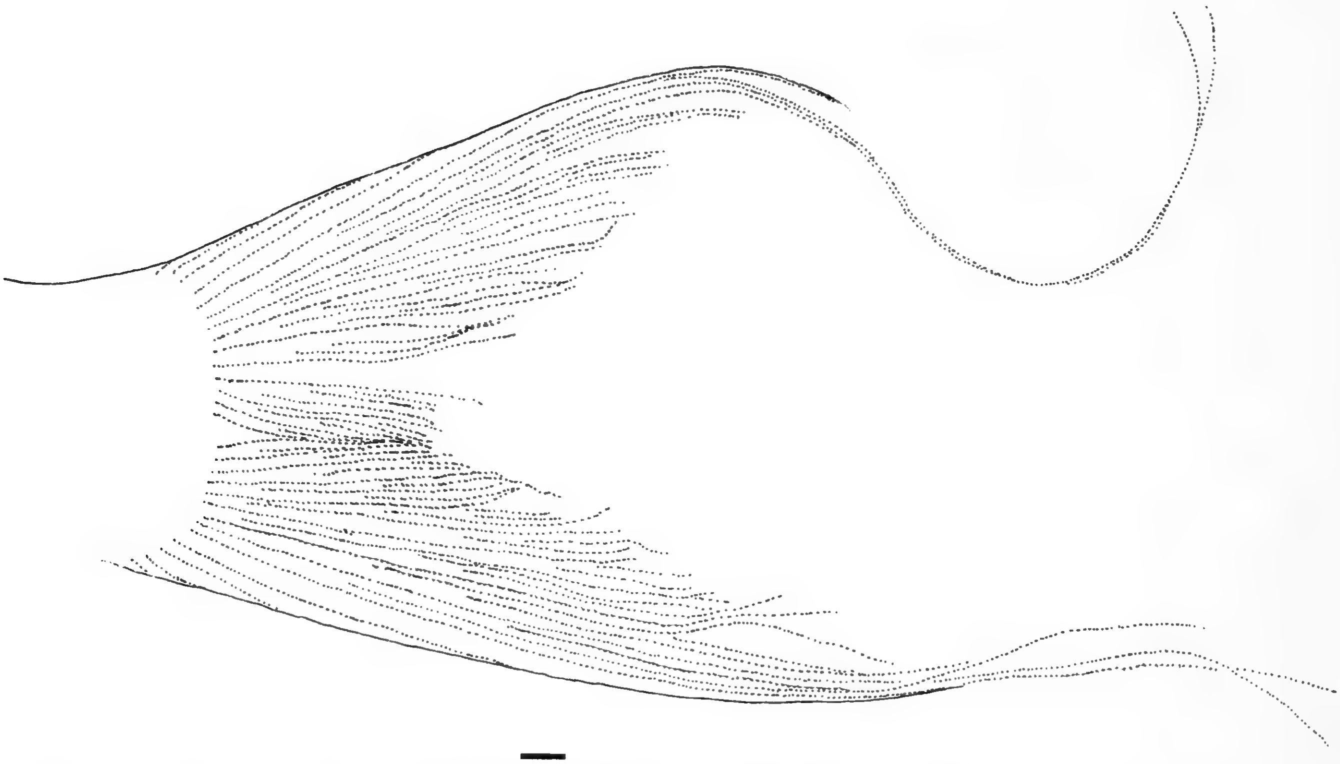

Fig. 4. *Pristigaster cayana,* MZUSP 30340; caudal fin in lateral view, showing filaments. Scale bar = 1 mm.

an illustration associated with the genus name only. In 1829, Cuvier proposed the name *cayanus* for the species figured in 1816, in what is clearly a valid species description as was shown by Myers (1956). The species name therefore must date from 1829, and it precedes the validly described *P. martii* by a month or so (Whitehead 1985:301). Various other names (*argenteus, lichtensteinii* and *triangularis*) were proposed between 1816 and 1829, all on the basis of the same illustration in Cuvier (1816). We consider all of these names to qualify as nomina oblita according to the International Code of Zoological Nomenclature (ICZN, 1985, Art. 79c). They have never been used subsequently as the valid names for the species, and the junior synonym, *cayanus,* has certainly been used in more than 10 publications by more than five authors in the intervening period (e.g., Valenciennes 1847, Günther 1868, Jordan & Evermann 1896, Norman 1923, Ihering 1930, Myers 1956, Whitehead 1967, 1973, 1985; Whitehead & Bauchot 1985).

Discussion

As demonstrated in this paper, in spite of the overall similarity in body shape and pigmentation, *Pristigaster cayana* and *P. whiteheadi* are clearly distinct and diagnosable through several morphological features. When suggesting the recognition of a second species of the genus, Whitehead (1985) and Whitehead & Bauchot (1985) based their observations on just a few specimens and did not notice some of the striking differences we found. In the diagnostic features of *P. cayana,* Whitehead (1985) described the pelvic fins as usually absent, indicating that presence or absence could vary within the species. At the same time, however, the author considered that one species without pelvic fins and high gill raker counts (22–24, usually 23) could possibly be different from a species bearing pelvic fins with lower gill raker counts (19–20, usually 20). Results of our study reveal that presence of pelvic fins is indeed diagnostic. They exist only in *P. whiteheadi* and are consistently present from the smallest to the largest individual of both sexes. Gill raker counts overlap to a certain extent, but there is a significant mean difference (see Table 1) between the two species. Other differences pointed out in the diagnosis of *P. whiteheadi* leave little doubt that there are indeed two separate species in *Pristigaster.* None of the various other names applied to *P. cayana* (see synonymy above) could possibly have been based on the new species. They either were based on Cuvier's 1816 illustration or clearly mentioned the absence of pelvic fins in specimens examined.

The two *Pristigaster* species share the highly peculiar expanded morphology of the abdomen, to a degree which distinguishes them from all other recent clupeiforms. Not only the depth, but also the shape of the abdominal expansion (abruptly emerging nearly vertically from gular region) are obviously apomorphic conditions not seen elsewhere in other recent clupeomorphs, and strongly suggest that *Pristigaster* is monophyletic. These characteristics are associated with a host of internal-anatomical modifications not yet studied in detail, and which will be the subject of a forthcoming paper.

Sexing of most of the specimens of both species examined did not reveal any obvious sexual dimorphism. It also tested the validity of our interspecific diagnostic characters by showing that the differences were not simply due to sexual dimorphism.

Acknowledgments

We thank Efrem Ferreira and Paulo Petry (INPA), Tony Gill and Oliver Crimmens (BMNH), and Barry Chernoff and Mary-Anne Rogers (FMNH), for the loan of material under their care. We are also grateful to Philippe Keith for information regarding collections in French Guyana. The manuscript benefited from reviews by Fábio Di Dario, Lance Grande, Thomas Munroe and an anonymous reviewer. Research funding for both authors is provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; individual grants) Projeto PRONEX, and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP).

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113(1):249–263. 2000.

A new species of *Apogon* (Perciformes: Apogonidae) from the Saya de Malha Bank, Indian Ocean, with redescriptions of *Apogon regani* Whitley, 1951, *A. gardineri* Regan, 1908, and *A. heraldi* (Herre, 1943).

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Abstract.—A new species of fish, *Apogon quartus,* known only from the Mascarene Plateau, is described. It is related to *Apogon poecilopterus* Cuvier *in* Cuvier and Valenciennes, 1828, *Apogon carinatus* Cuvier *in* Cuvier & Valenciennes, 1828, and *Apogon queketti* Gilchrist, 1903, recently treated by Gon (1996) as members of the subgenus *Jaydia* Smith, 1961. *Apogon quartus* can be distinguished from these three species by having a single predorsal scale, 18 total (13 well developed) gill rakers on the first arch, and a single dark spot, perhaps appearing as an ocellus in life, on the body just behind the opercle flap. Six additional nominal species are added to the 10 valid (19 nominal) species treated by Gon in *Jaydia.* Three of these names, *Apogon argyrogaster* Weber, 1909, formerly in *Siphamia, Apogon melanopus* Weber, 1911, and *Apogon fuscomaculatus* Allen & Morrison, 1996, are valid species. The holotype of *Apogon heraldi* (Herre, 1943) redescribed here, is a synonym of *A. poecilopterus. Apogon fuscovatus* Allen, 1985 was determined to be a synonym of *A. melanopus* by Allen & Morrison (1996) The other name, *Apogon tchefouensis* Fang, 1942, may be synonymous with one of the species Gon treated but is not placed with certainty. Character overlaps between the subgenus *Jaydia* and other *Apogon* subgenera, particularly the largest subgenus *Ostorhinchus* Lacépède, 1802, are briefly examined. Virtually all derived characters of *Jaydia* grade into *Ostorhinchus.* Two rare species *Apogon regani* Whitley, 1951 and *Apogon gardineri* Regan, 1908 only known from the Mascarene Plateau are redescribed from new material. Both belong with the *Apogon nigripinnis* Cuvier *in* Cuvier and Valenciennes, 1828, complex of species.

The Russian vessel *Vityaz* made trawl stations along the Saya de Malha Bank during 1989 collecting fishes. Two of these collections contained a new species and a specimen of *Apogon regani* Whitley, 1951. The new species was first identified as an *Apogonichthys* Bleeker, 1854c, based on the mostly smooth preopercle edge and the slightly rounded caudal fin. An examination of internal and external characteristics led to the conclusion that this specimen is an *Apogon* Lacépède, 1802. Some characters are held in common with species in the subgenus *Jaydia* recently treated by Gon (1996). The ten species of *Jaydia* have the fourth dorsal spine longer than any other dorsal spine, variable serrations on preopercular edges, rounded or truncated caudal fins, and some have bioluminescent organs. Gon and Allen (1998) included another new species, *Apogon photogaster* in *Jaydia.* A review of additional nominal species with possible relationships to the new species yielded six names, *Apogon argyrogaster* Weber, 1909, (previously in *Siphamia* Weber, 1909, see Lachner 1953, p.

416), *Apogon melanopus* Weber, 1911, *Apogon tchefouensis* Fang, 1942, *Apogon heraldi* (Herre, 1943), *Apogon fuscovatus* Allen, 1985 and *Apogon fuscomaculatus* Allen & Morrison, 1996.

Specimens of all the above species have been most frequently taken by trawls, often in deeper waters. Fishes in *Jaydia* have body shapes ranging from elongate more slender forms, *Apogon truncatus* Bleeker, 1854e, to *A. melanopus* a deeper body form with an emarginate caudal fin typical of most *Apogon.* Smith (1961) based *Jaydia* on *Apogon ellioti* Day, 1875, now recognized as a synonym of *A. truncatus* a slender species with a rounded caudal fin and having bioluminescent activity.

In the process of trying to locate more material of the new species, specimens of two deep-dwelling species from the Nazareth Bank near Cargados Carajos Shoals (St. Brandon) described by Regan (1908) were found. Randall and van Egmond (1994) reported *Apogon punctatus* Regan, 1908, (=*Apogon regani* Whitley, 1951) taken in a trawl from the Seychelles. No material of *Apogon gardineri* Regan, 1908, has been reported since the original description, but deep dives by J. E. Randall during 1979 in Mauritius yielded two specimens. It is likely that more material will be only slowly forth coming. Both of these species are regarded as endemics of the Mascarene Plateau.

Methods

Methods of taking and recording meristic data and measurements are given in Fraser & Lachner (1985). All measurements are in millimeters to the nearest 0.1 mm. All proportions are based on standard length and all material is reported by standard length rounded to the nearest millimeter, except for the primary type material. All x-ray photographs are in data files maintained by the author. The acronyms used in the lists of materials to designate institutions and collections cited, follow general usage given in Leviton et al. (1985) and Eschmeyer (1998).

Apogon quartus, new species

Figs. 1 & 2

Material examined.—Holotype: USNM 307688; (49.8); Indian Ocean, Saya de Malha Bank, 11°05′00″S, 62°02′00″E; *Vityaz* Cr. 17; Sta 2808; 8 Jan 1989; 58–61 m.; X-ray.

Comparative material.—*Amia albomarginata* Holotype: USNM 68402; (83.6); Philippines, Cavite; X-ray. *Apogon arafurae* Holotype: BMNH 1879.5.11.141; (90.0); Arafura Sea. *Apogon argyrogaster* Syntypes: ZMA 101075; (34.9–47.5); New Guinea, west coast; Siboga sta 164; 32 m. BPBM 32628; (15.5–48.3); New Guinea, Nagada Harbor; 18 Nov 1987; 30 m; X-ray. *Apogon bilaciniatus* Lectotype: ZMA 101280; (46.2); Indonesia, Lombok. *Apogon ellioti* Paralectotype?; ZSI 1905; (77.7, 96.0 mm TL); India, Madras; X-ray. Paralectotype?; AMS B.8226; (77.3, 98.1 mm TL); India, Madras; X-ray. *Apogon fuscovatus* Holotype: WAM P14397; (94); Australia, Darwin; 4 Sep 1965. Paratypes: WAM P14516–17; (83–85); Australia, N. of Darwin; 9 Sep 1965. WAM P 28316-001; (66); Australia, Darwin; 10 Sep 1965. *Apogon glaga* Syntype: RMNH 5614 (71.9, ~93 mm TL); Indonesia. *Apogon hungi* Neotype: USNM 340009; (76.4); Mozambique Channel. *Jaydia hungi* Holotype: MNHN 1965-711 (94.3); Egypt, Gulf of Suez. *Apogon lineatus* Lectotype: RMNH 70a; (62.4); Japan. USNM 71240; (64.6); Japan, Shimizu Suruga; Albatross; 1906; female. USNM 32586; (56.3); China, 35°55′49″N, 120°21′29″E; 25 Jul 1993; female. *Amia melas* [=*Apogonichthys melanopterus*] Holotype: ANSP 47491; (~35.2 head distorted); Philippine Islands. *Apogon melanopus* WAM P 14963; (100); Australia, Darwin; 4 Sep 1965. *Apogon modestus* Holotype: RMNH 5579; (61.9); Indonesia, Java. *Apogon nigricans* Syntype: ZSI 1872; (55.0, 71+ TL) India, Madras; X-ray. *Apo-*

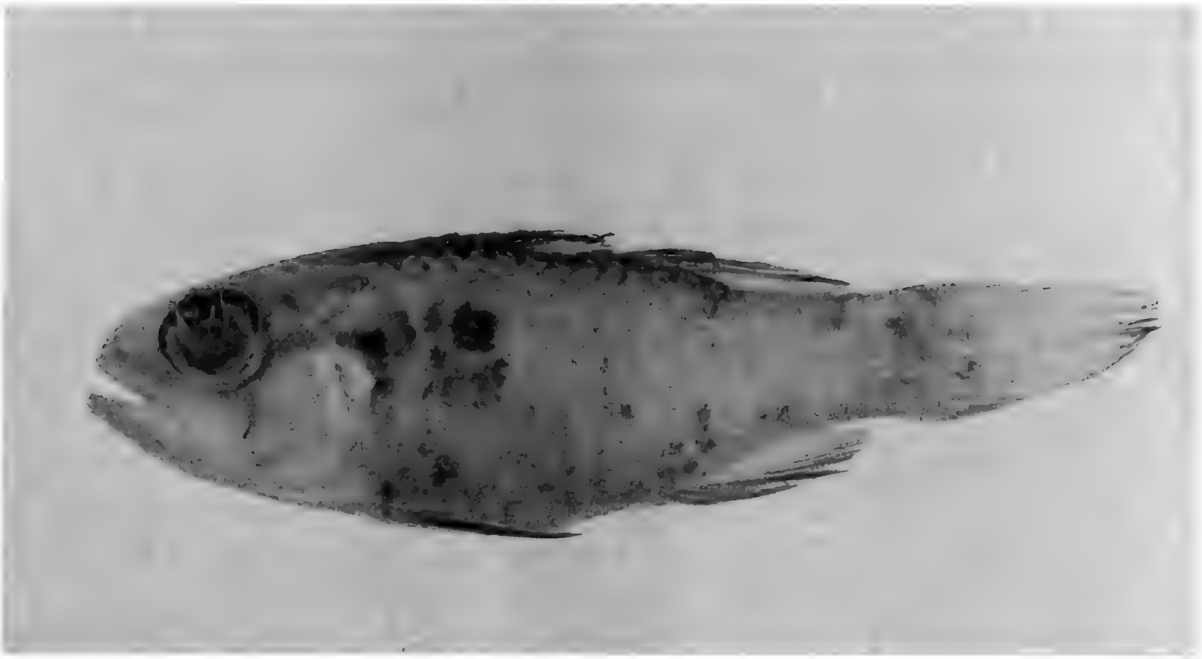

Fig. 1. The holotype of *Apogon quartus* from the Saya de Malha Bank, Indian Ocean, 49.8 mm SL.

gon novaeguineae Holotype: MNHN 8695; (56.5); New Guinea. *Apogon photogaster* Paratype: USNM 348214; (43.3); Papua New Guinea, Madang Lagoon; 21 Oct 1996; 18–23 m; X-ray. *Apogon poecilopterus* Holotype: RMNH 214; (79.0); Indonesia, Java. *Apogon queketti* Syntypes: SAM 11657; (75.1); South Africa, Natal; X-ray. SAM 11658; 5(44.1–77.4); same data; X-ray. *Jaydia smithi* Paratypes: ZMH 5034; 5(12.7–46.3); *Amia striata* Holotype: USNM 68403; (67.2); Philippines, Luzon; female; X-ray. Paratypes: USNM 93410; 11(39.2–66.2); same data; X-ray. Somalia, Gulf of Aden; X-ray. *Apogon striatodes* Holotype: USNM 213408; (55.5); Indian Ocean, Thailand. Paratypes: China, Hong Kong: CAS 160877; (57); CAS 161015; (55). Philippines, Luzon: CAS 85669; (45); Corregidor I.: CAS 32723 (46). Thailand, Gulf of Thailand: CAS 79648; (36–37); CAS 79652; (44); (CAS 82205; 8(18–59); CAS 85676; (26–30); CAS 85666; 3(28–34); CAS 85667; (19); CAS 82202; (17–47); CAS 82208; (54). *Apogon tchefouensis* Paratypes: MNHN 1941-148; (45.7); China, Shandong Prov., Tché-Fou, Ho Ting Chieh; X-ray. MNHN 1941-149; (35.0); same data; X-ray. *Apogon truncatus* Holotype: RMNH 5582; (55.4); Indonesia, Batavia (=Jakarta). *Apogon hoevenii* Syntype: RMNH 5581; (40.2, 50 mm TL, one of 6 spec. in size range, 24 spec. 25–49 mm SL); Indonesia, Ambon. USNM 261058; 8(35–39); Philippines, Siquoijor I. *Apogon* sp. USNM 349199; (48.8); Philippines, Palawan, Puerto Princesa City.

Diagnosis.—A species of *Apogon* in the subgenus *Jaydia* with 15 pectoral rays, generally smooth to crenulate preopercle edge, one predorsal scale, 18 total (13 well developed) gill rakers on the first arch, fourth dorsal spine the longest, and a single dark spot, perhaps appearing as an ocellus in life, on the body just behind the opercle flap.

Description.—For general body shape see Fig. 1. Proportions (as percentage of standard length): greatest body depth 33.5; head length 42.2; eye diameter 11.4; snout length 9.2; bony interorbital width 10.2; upper-jaw length 20.5; caudal-peduncle depth 14.8; caudal-peduncle length 21.5; first dorsal-spine length 3.4; second dorsal-spine length 9.0; third dorsal-spine length 15.7; fourth dorsal-spine length 17.9; spine in second dorsal fin 14.8; first-anal-spine length 2.4; second-anal-spine length 11.4; pectoral-fin length 21.2; pelvic-fin length 21.2.

Dorsal fin VII–I,9; anal fin II,8; pectoral fin 15–15; pelvic fin I,5; principal caudal rays 9 + 8; number of simple pored lateral-line scales unknown, series extending from posterior edge of posttemporal to caudal fin; transverse scale rows above lateral line 2; transverse scale rows below lateral line ~4; median predorsal scales 1, the lateralis system extending well onto the nape as a raised semi-translucent fleshly area of about seven striations or rows with many small papillae; number of circumpeduncular scale rows unknown; total gill rakers 18, well developed 13, 3+2 upper arch, 11+2 lower arch.

Villiform teeth in wide band on premaxilla; wide band grading to two rows on dentary; one to two rows on palatine and one to three rows on vomer; none on ectopterygoid, endopterygoid or basihyal.

Vertebrae 10 + 14. Five free hypurals, one pair of slender uroneurals, three epurals, a free parhypural. Three supraneurals, two supernumerary spines on first dorsal pterygiophore. Basisphenoid present. Supramaxilla absent. Posttemporal smooth on posterior margin. Preopercular ridge smooth, posterior vertical edge smooth, ventral horizontal edge slightly crenulate with one or two spinelets at angle. Infraorbital with irregular edges, but without serrations. Scales ctenoid. Caudal fin slightly rounded. Nose and pre-interorbital area semi-translucent and slightly bulbous. No indication of bean-like bioluminescent organs associated with intestine near anus.

Life colors.—Unknown.

Preserved color pattern.—In 70% ethyl alcohol: peritoneum pale, stomach and intestine pale. Dark mark from ventral margin of eye ending near posterior edge of premaxilla, two dark lines from posterior margin of eye, upper to posttemporal, lower onto opercle ending in a ventrally directed, short mark; dark spot ocellus-like on side just behind opercle flap, with about five smaller spots positioned anteriorly and ventrally close to large spot; other melanophores on pectoral-fin base and abdomen, scattered diffuse spots on caudal peduncle behind second dorsal and above anal fin; scales above the lateral-line scales outlined with melanophores; lower third of snout dusky between upper jaw and eye; pelvic fins with spine and distal third of rays dark to tips; anal fin with dark band on spines and first three fin-rays to tip, fourth fin-ray mostly dark, distal third of next two fin-rays dark, last two fin-rays pale from base to tips; caudal fin with tips of rays dark; second dorsal-fin spine and first four fin-rays dark to tips, remaining fin-rays pale; first dorsal fin with the anterior four spines and membranes dark to their tips, remaining spines and membranes pale.

Distribution.—Known from the Indian Ocean on the Saya de Malha Bank (Fig. 2).

Etymology.—The Latin word for fourth, *quartus* in reference to the longest dorsal spine.

Remarks.—The fourth dorsal spine is the longest dorsal spine in this specimen. With additional characters including a high number of pectoral-fin rays, rounded caudal fin and preserved color pattern, this species can be placed within the broad limits of subgenus *Jaydia* revised by Gon (1996). *Apogon quartus* is the first species of this subgenus to be found on the extensive isolated shallow banks the Central Indian Ocean. Most of the species treated by Gon (1996) have a continental distribution pattern. Only a few specimens of *Apogon hungi* Fourmanior & Nhu-Nhung, 1965, and *Apogon smithi* (Kotthaus, 1970) have been reported from insular localities (Gon, 1996).

Apogon quartus appears to be most closely related to *Apogon poecilopterus* Cuvier *in* Cuvier & Valenciennes, 1828, *Apogon carinatus* Cuvier *in* Cuvier & Valenciennes, 1828, and *Apogon queketti* Gilchrist, 1903. The new species differs from *A. queketti* and *A. carinatus* by not having an ocellus in either dorsal fin. *A. poecilopterus* has more predorsal scales (4–5) and a darkish gill chamber. The ocellus-like spot on the body is unique to *A. quartus* among these species.

Apogon argyrogaster is unique among

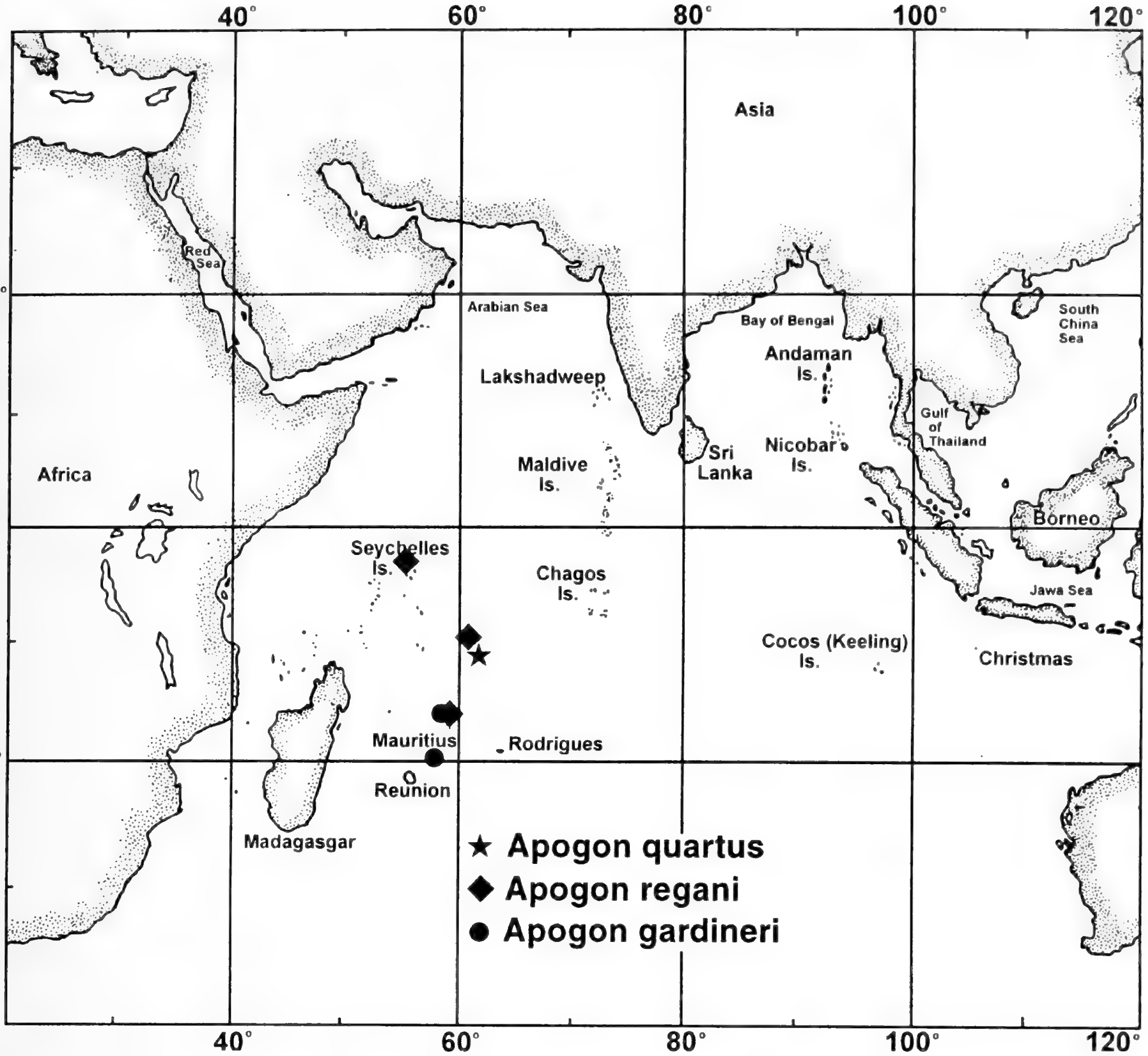

Fig. 2. Distribution of collection sites for *Apogon quartus, Apogon gardineri,* and *Apogon regani.*

species of *Apogon* with its large ventral organs (probably bioluminescent) extending on each side of the body from the breast area forward into the lower part of the mouth and backward to past the origin of the anal fin. Gon & Allen (1998) recently described *Apogon photogaster* with an externally similar bioluminescent system to *A. argyrogaster* but made no comparisons. Their name appears to be a synonym of *A. argyrogaster.* They placed *A. photogaster* in *Jaydia. Apogon argyrogaster* has faint bars on the side of its body, two predorsal scales, 8–9 well developed gill rakers in addition to the luminous organs. All are characters differing from *A. quartus.*

Apogon melanopus, with nine anal rays and an emarginate caudal fin unlike all other *Jaydia* species, is a member of *Jaydia* with the fourth dorsal spine the longest and 16–17 pectoral-fin rays. This species was described by Allen (1985) as *A. fuscovatus.* Allen & Morrison (1996) later synonymized Allen's species when describing another new species, *A. fuscomaculatus,* which they compared with *Apogon striatus* (Smith & Radcliffe *in* Radcliffe 1912). *Apogon melanopus* and *A. fuscomaculatus* differ in having higher well-developed gill rakers (15–16) and lower well-developed gill rakers (8–9) respectively and general color pattern (no ocellus-like spot in either species) from *A. quartus.*

Paratypes of *A. tchefouensis* from the

East China Sea examined by me have no discernable color patterns because of the strong brown stain on both specimens. Fang (1942) described the color in alcohol as "... uniformément brun-noirâtre." Fang (1942) described the preopercle as "Bord libre du préopercule nettement denticulé avec des dents assez fortes surtout à son angle, mais plus fines à la partie supérieure du bord postérieur." The condition of the preopercle with a smooth ridge and prominent serrations, stronger at the angle and finer ones on the posterior edge and ventral edge, suggest a different group, probably type B (but serrations more like type A on edges) of Gon's categories than with the group (type C) containing *A. quartus.* The posttemporal is serrated. Total gill raker and rudiment count on the first gill arch is 18, well-developed rakers 14 (3+2 on upper arch, 12+1 on lower arch) of the larger paratype. The smaller paratype is in poor shape and has a badly damaged head. The pectoral ray count was 15 on one side of both paratypes and 14 for the other side for the larger paratype. Palatine teeth are in one to two short rows for the larger paratype. Palatine teeth of the lectotype of *Apogon lineatus* Temminck & Schlegel, 1842, are in 4 short rows like the holotype of *Apogon striatodes* Gon, 1996, (3–4 short rows), and the holotype *A. striatus* (3–4 short rows) but not *Apogon novaeguinae* Valenciennes, 1832 with one row. Additional information about the color of the peritoneum and intestine from the holotype and paratypes may help determine whether *A. tchefouensis* is a junior synonym of either *A. lineatus* or *A. striatus* or the senior synonym of *A. striatodes.* The known distribution of the two species recognized by Gon (1996) in the East China Sea region do not appear to overlap, but he suggests the possibility for Taiwan. If distributional patterns are accurate, then the larger paratype of *A. tchefouensis* should be identified as *A. lineatus.* What ever the eventual status of *A. tchefouensis,* the paratypes can be distinguished from *A. quartus* by having serrated preopercle and posttemporal.

Fowler & Bean (1930) compared *Apogonichthys melanopterus,* their replacement name for *Amia melas* Fowler, 1918, with *Apogon carinatus.* Fowler (1918) first related his new species to *Apogon nigricans* Day, 1875, a nominal species related to, if not the same as *Apogon melas* Bleeker, 1848, with a forked caudal fin, a trace of a dark spot on the midbase of the soft dorsal fin and darkish pelvic and vertical fins. In his original description, Fowler noted that the holotype of *Amia melas* has the fourth dorsal spine longer than the third. My observation of the holotype agrees with Fowler's statement. However, the third spine is noticeably stronger (thicker) than the fourth spine unlike other species of *Jaydia. Apogon melanopterus* is consistent in some other characters with *Jaydia*: gill-raker count (3+1–11+3), some serrations on the preopercle edge and a rounded? (damaged) caudal fin, but has 14 pectoral-fin rays versus the common 15–17, rarely 14 or 18 pectoral-fin rays of *Jaydia.* This species differs from *A. quartus* in preserved color pattern (no ocellus-like spot; dorsal, pelvic, anal and caudal fins all blackish), predorsal scales (3), strong third dorsal spine and 14 pectoral rays. I cannot with certainty place *A. melanopterus* within *Jaydia* as treated by Gon.

Relationships.—The basis for the proposed monophyly of *Jaydia* will need to be re-examined because some of Gon's (1996) diagnostic features are present in other species of *Apogon.* For example, *Apogon hoevenii* Bleeker, 1854d, a more 'typical' *Apogon* with an emarginate caudal fin, serrated preopercular edge and a low pectoral ray count (12), has the fourth dorsal spine variably as its longest. The holotype of *A. melanopterus* has the fourth dorsal spine as the longest and a robust thicker third dorsal spine. One undescribed species and a related species, *Apogon moluccensis* Valenciennes, 1832, have the fourth dorsal spine as the longest in nearly all adults but not in all small individuals. The third spine in these two species is about as strong as the fourth spine, and both have forked caudal fins. The undescribed species has a darkish roof of the mouth and gill arches reminiscent of *A. poecilopterus.* An unidentified species of *Apogon,* either new or a juvenile of a species in the *Apogon diversus* (Smith & Radcliffe *in* Radcliffe, 1912) group, has strong serrations on the preopercular ridge and edges, serrated infraorbitals, a strongly fork caudal fin and fourth dorsal spine as the longest spine. Characters present in *A. melanopus* and the above species suggest that an expanded review is needed. A solid basis for the subgenus founded on the shape of the caudal fin, the length of the fourth dorsal spine, strength of the third dorsal spine, high pectoral-fin ray counts, supporting structures for the dorsal fin and other characters elucidated by Gon may grade with the examination of more species. Perhaps some of the other species of *Apogon* discussed here eventually may be shown to be closer to this species complex than to other *Apogon.* Those species treated by Gon that have bioluminescent systems are more likely to be monophyletic and may be worthy of the recognition as the subgenus *Jaydia.* There is, as yet, no clear resolution about whether these two subgenera represent monophyletic groupings within *Apogon.*

Status of *Apogon heraldi*
Fig. 3

Apogon heraldi (Herre, 1943) was described in *Mionurus,* a misspelling of *Mionorus* Krefft, 1868, as having nine anal rays. Herre compared it with two unrelated nominal species with six first dorsal spines, *Apogon bombonensis* (Herre, 1925) and *Apogon mydrus* (Jordan & Seale, 1905). There is enough information in Herre's description to determine that this species should be compared with those treated by Gon (1996), but not enough to place it with certainty. Herre did not give a figure of the type. A redescription of the type, with a figure is needed to provide comparison with the new species and with other related species.

Material examined.—*Mionurus heraldi* Holotype: SU 38263 (104.5); Philippines, Luzon I., Ragay Gulf, X-ray.

Comparative material.—See *A. quartus.*

Description.—For general body shape see Fig. 3, Range of proportions (as percentage of standard length): greatest body depth 39.4; head length 42.0; eye diameter 9.8; snout length 8.5; bony interorbital width 9.6; upper-jaw length 20.1; caudal-peduncle depth 16.7; caudal-peduncle length 20.2; first dorsal-spine length 2.4; second dorsal-spine length 7.1; third dorsal-spine length 10.9; fourth dorsal-spine length 14.1; spine in second dorsal fin 11.3; first anal-spine length 2.8; second anal-spine length 10.9; pectoral-fin length 25.4; pelvic-fin length 26.7.

Dorsal fin VII–I,9; anal fin II,8; pectoral fin 16–16; pelvic fin I,5; principal caudal rays 9 + 8; number of pored lateral-line scales unknown; number of transverse scale rows above lateral line unknown; number of transverse scale rows below lateral line unknown; median predorsal scales 4 or 5; number of circumpeduncular scale rows unknown. Gill rakers, upper arch 2 rudiments 1 well developed raker, lower arch 1 rudiment, 10 well-developed rakers, 11 well developed and 14 total.

Villiform teeth in single row anteriorly, slightly larger grading into wide band at sides of premaxilla; three rows anteriorly with one to two rows at sides of dentary, interior row slightly larger from anterior to side; one row on palatine; two rows on vomer; none on ectopterygoid, endopterygoid or basihyal.

Vertebrae 10 + 14. Five free hypurals, one pair of slender uroneurals, three epurals, a free parhypural. Three supraneurals, two supernumerary spines on first dorsal pterygiophore. Basisphenoid present. Supramaxilla absent. Posttemporal smooth on posterior margin. Preopercular ridge smooth, vertical margin smooth, horizontal margin with smooth undulations. Infraorbitals with crenulate to sharp edges. Scales ctenoid, many missing from body. Caudal fin slightly rounded. No indication of bean-like bioluminescent organs associated with intestine near anus.

Life colors.—Unknown.

Preserved color pattern.—In 70% ethyl alcohol: peritoneum silvery; intestine and stomach mostly pale with scattered melanophores; second dorsal fin with dark stripe near base, a narrow pale area above on first few rays to about fifth ray, more distally the fin-ray membranes dusky to dark with second narrow pale area, then fin rays dusky to tips; wide darkish stripe basally in anal fin, the membranes pale distally; spinous dorsal dusky distally, dark between the second and fifth spines, pale basally; pelvic and pectoral fins pale; gill chamber and gill arches dusky with melanophores; caudal fin membranes dusky with no indication of a darker margin.

Remarks.—*Apogon heraldi* has the fourth dorsal spine longest and can be grouped with Gon's type C preopercle pattern of *Jaydia.* Herre (1943) described the color of *A. heraldi* in alcohol as ". . . pale brown, with a more or less evident vertical dark-brown bar under each scale; there is a blackish spot on the upper half of the spinous dorsal, and a wide dark-brown cross-band on the second dorsal and the anal, which are otherwise clear; all but the basal part of the caudal is dusky; the pectorals and ventrals are clear". Herre's description of the teeth as "The very small conical teeth are in a single row in the lower jaw," and lack of comment about color in the oral cavity would suggest that this specimen is not *A. poecilopterus.* However, my re-examination of the holotype indicates that the dentition and the color pattern in the gill chamber are consistent with that of *A. poecilopterus.* The holotype has 14 gill rakers plus rudiments on the first gill arch, 2+1 on the upper arch and 10+1 on the lower arch, about 4 or 5 predorsal scales and 16 pectoral rays, all consistent with *A. poecilop-*

Fig. 3. The holotype of *Mionurus heraldi,* SU 38263, 104.5 mm SL from the Philippine Islands, Luzon I., Ragay Gulf.

terus. Herre (1943) reported on material of *A. ellioti* [=*truncatus*] and *A. poecilopterus* from the Ragay Gulf and *A. striatus* from Manila Bay in the same paper. *Apogon heraldi* is considered a synonym of *A. poecilopterus*. The type is a ripe female.

Apogon gardineri Regan, 1908
Figs. 2 & 4

Material examined.—Holotype: BMNH 1908.3.23.93; 39.7 mm SL; Cargados Carajos; 55 m. Other material: BPBM 24775; (41–42); Mauritius, off Flic en Flac; J. E. Randall et al.; 7 April 1979; 57 m; color photo; x-ray.

Comparative material.—*Apogon nigripinnis* Syntype: MNHN 8694; 63.4 mm SL; India, Pondicherry; Leschenault. Mozambique: Delagoa Bay: RUSI 3149; (60–76); x-ray. RUSI 3151; (67); 1938; x-ray. RUSI 3148; 4(42–84); x-ray. RUSI 3150; 4(68–74); x-ray. Palma: RUSI 3152; (69); 1 Aug 1951; x-ray. Aldabra I.: RUSI 3153; (49–53); 14 Nov 1954; x-ray. *Apogon striatus* Syntypes: MNHN 1973-41; 3(16.8–26.2); Madagascar, Nosy-Bé; x-ray. *Apogon suezii* Holotype: MNHN 5137; (50.6); Egypt, Suez; Letourneux. *Apogon taeniatus* Syntypes: MNHN 8693; (55.3–57.4); Red Sea; Ehrenberg. Kenya: RUSI 3106; (85); Malindi; 2 Oct 1952; x-ray. RUSI 3111; (94); Shimoni; 1950; x-ray. RUSI 3107; (77–83); Shimoni; Nov 1952; x-ray. RUSI 3112; 3(15–66); Shimoni; May 1951; x-ray. RUSI 3109; (76); Feb 1952; x-ray. Mozambique: RUSI 3105; (79); Pinda reef; 1950; x-ray. RUSI 3114; (49); Mocimboa de Praia; 3 Sep 1951; x-ray. RUSI 3110; (81); Inhambane; Sep 1948; x-ray. RUSI 3108; 3(59–82) Jun 1950; x-ray. Aldabra: RUSI 3113; (55); Nov. 1954; x-ray. ANSP 63868; (86); South Africa. *Apogon thurstoni* Holotype: BMNH 1889.8.17.2; (55.5); India, Madras; Day. *Apogon timorensis* Holotype: RMNH 5583; (60.8); Timor. QM I.820; 3(23–31); Australia, Darnley I. QM I. 8506; (28); Australia, Queensland, Green I. *Apogonichthyoides fraxineus* Holotype: RUSI 356; (57.7); Mozambique, Pinda Reef; 3 Sep 1956; x-ray. Paratypes (all x-rayed): Mozambique: RUSI 746; 8(42–65); Pinda Reef; 3 Sep 1956. RUSI 751; (67); Pinda Reef; Sep 1956. RUSI 762; (37–69); Pinda Reef; 23 Sep 1956. RUSI 758; (48–55); Delagoa Bay. RUSI 7409; (33); Ibo I.; Aug 1951. Zanzibar: RUSI 757; (41); 20 Sep 1952. RUSI 754; (54); 9 Sep 1952. RUSI 748; 3(52–57); 4 Sep 1952. RUSI 759; (23–24); Seychelles, Mahe I.; Sep 1954.

Diagnosis.—A species of the subgenus *Ostorhinchus* with two saddles on the body and one on the caudal peduncle, no cheek mark, a pale stomach, intestine and peritoneum, 14 pectoral-fin rays, 2 predorsal scales and 14–15 total gillrakers.

Description.—For general body shape see Fig. 4. Range of proportions (as percentages of standard lengths), holotype in parentheses: greatest body depth 38–39 (37.3); head length 42 (42.3); eye diameter 15 (13.8); snout length 8.8–9.5 (9.3); bony interorbital width 8.4–8.8 (8.6); upper-jaw length 18–20 (19.6); caudal-peduncle depth 14–16 (14.9); caudal-peduncle length 21–24 (19.4); first dorsal-spine length 3.0–3.6 (5.0); second dorsal-spine length 8.3–9.5 (9.3); third dorsal-spine length 19–20 (18.6); fourth dorsal-spine length 16–19 (18.6); spine in second dorsal fin 13–15 (13.8); first anal-spine length 3.1–4.1 (3.3); second anal-spine length 12–15 (11.8); pectoral-fin length 21–24 (20.1); pelvic-fin length 23–27 (23.4).

Dorsal fin VII–I,9; anal fin II,8; pectoral fin 14–14; pelvic fin I,5; principal caudal rays 9 + 8; simple pored lateral-line scales 24; transverse scale rows above lateral line 2; transverse scale rows below lateral line 5–6; median predorsal scales 2; circumpeduncular scale rows 12 (5+2+5). Total gillrakers 14–15 (14), well developed 9–10 (9), upper arch 2+1, lower arch 8–9+2–3 (8+3).

Villiform teeth in a wide band on the premaxilla and dentary; two rows on the palatine and vomer; none on ectopterygoid, endopterygoid or basihyal.

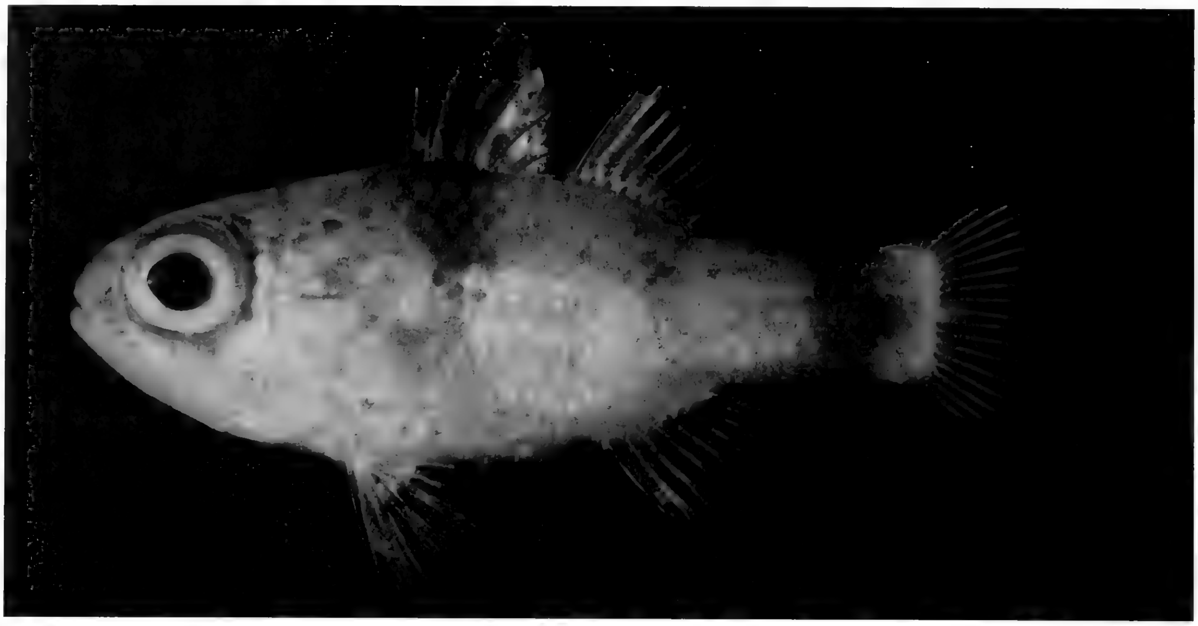

Fig. 4. *Apogon gardineri*, BPBM 24775, 42 mm SL, from Mauritius, off Flic en Flac by J. E. Randall.

Supramaxilla absent. Posttemporal smooth on posterior margin. Preopercle serrate on vertical and horizontal margins, smooth on ridge. Infraorbitals smooth, posterior ones with crenulations. Scales ctenoid. Caudal fin weakly emarginate.

Life colors.—Based on a Ektachrome transparency of the Mauritian specimen the color pattern is as follows: Iris yellow; head (without dark or pale spots, bars or stripes) and body with a light tannish background; a small brownish spot at the beginning of pored lateral-line scales; a darker brownish bar beginning at the base of first five dorsal spines and extending to about level of pectoral fin, as a chevron, angled posteriorly; a second fainter bar or blotch under last four or five soft rays of second dorsal fin reaching to or just below pored lateral line; a full dark brownish mark (spot or bar-like) on caudal peduncle; first dorsal fin with a dark brownish bar extending over first five spines and contiguous with bar on the body, membrane behind the fifth to seventh spines pale; second dorsal, anal and caudal fins pale without spots, bars or stripes; pelvic fin pale except for the last third of the first two soft rays.

Preserved color pattern.—In 70% ethyl alcohol: The holotype has no color remaining. Regan (1908) reported: "Faint traces of 3 dark vertical bars, the first below the spinous dorsal, the second below the soft dorsal, the third on the caudal peduncle. Spinous dorsal blackish except posteriorly; ventrals blackish at the tips". The Mauritian specimens have a pale intestine, with a few melanophores on the stomach, peritoneum pale; first dorsal fin dark, with a mark extending onto the body to about even with the pectoral fin; a second saddle extends downward from the posterior part of the second dorsal fin base; a diffuse blotch on the caudal peduncle; a faint cheek mark and a spot behind the eye.

Distribution.—Known only from the Mascarene Plateau.

Remarks.—Regan (1908) suggested that *A. gardineri* was related to *Apogon bandanensis* Bleeker, 1854a. *Apogon bandanensis* has more gill-raker (total gillrakers 25–29) and has black stomach and intestine. Smith (1961) synonymized *A. gardineri* with *Apogon nigripinnis* Cuvier *in* Cuvier & Valenciennes, 1828. The holotype of *A. nigripinnis* is a different species with 16 pectoral-fin rays, 16 total rudiments and gill rakers, 12 well-developed rakers (3+2 upper arch, 10+1 lower arch), two predorsal scales, a deeper body (depth 42.9% standard length), soft dorsal and anal fins blackish and a uniform brownish body without an obvious ocellated spot on the side of the body (faded?) or basicaudal spot (faded?). The holotype of *Apogon thurstoni* Day, 1888, shares all of the above-listed characters of *A. nigripinnis,* 16 pectoral-fin rays, 16 total rudiments and gill rakers, two predorsal scales, a body depth of 43.4% of standard length, but has 10 well developed gill rakers (2+2 upper arch, 8+4 lower arch) and an obvious ocellated spot on side about midline. All of the Southern African material specimens here as *A. nigripinnis* have an ocellus on the side, but otherwise have meristics and body depth similar to the type: 15–16 pectoral-fin rays, 16–18 total rudiments and gill rakers, 11–12 well-developed rakers (2–3+2 upper arch, 9–10+1–4 lower arch), two predorsal scales, a body depth of 42–48% of standard length.

Apogon taeniatus Cuvier *in* Cuvier & Valenciennes, 1828, appears closely related to *A. nigripinnis* and may also be confused with *A. gardineri.* However, *A. taeniatus* variably has an ocellated spot within the first dorsal saddle above the pectoral fin, a small basicaudal spot, faint stripes on body, 16–19 total rudiments plus gill rakers, 9–12 well-developed rakers (2–4+1–2 upper arch, 8–10+3–5 lower arch), 14–15 pectoral-fin rays, 3 predorsal scales and a greater body depth of 40–45% standard length. The holotype of *Apogon suezii* Sauvage, 1883, shares with *A. taeniatus* an ocellated spot above the pectoral fin, 17 total rudiments and gill rakers, 12 well-developed rakers (2+2 upper arch, 10+3 lower arch), 15 pectoral-fin rays, three predorsal scales and a body depth of 40.9% standard length, but it has a small basicaudal spot within a darkish bar.

The low gill-raker count, body shape and color pattern of *A. gardineri* may cause some confusion with *Apogon timorensis* Bleeker, 1854b and two of its synomyms *Apogon fraxineus* (Smith, 1961) and *Apogon striatus* Fourmanior & Crosnier, 1964, which differs in having a thin, dark cheek line from the eye onto the preopercle, a black stomach and intestine, 15–17, usually 16 pectoral rays and fewer developed (6–8) and more rudiments (4–7) on the lower arch. Fourmanoir and Crosnier's name is an unavailable name as a secondary homonym of *Apogon striatus* (Radcliffe *in* Smith & Radcliffe, 1912).

Apogon gardineri is found in deeper water. It does not appear to have been reported from any of the shallow-water collections from Mauritius, Cargados Carajos or the Seychelles in the past several decades. Many of the species in this complex appear to have continental distributions, for example, Gon (1986, map 1). *Apogon gardineri* represents an insular species endemic to the Mascarene Plateau.

Apogon regani Whitley, 1951

Figs. 2 & 5

Synonyms: *Apogon punctatus* Regan, 1908, preoccupied by *Apogon punctatus* Klunzinger, 1880.

*Material examined.–*Syntypes: *Apogon punctatus* BMNH 1908.3.23.86–89; 4(31.9–65.4); Cargados Carajos; 39–55 m. Other material: BPBM 35475; (45); Seychelles, N. of Aride I., 4°10′S, 55°44′E; R/V *Tyro,* Station 714, 2.4-m *Agassiz* trawl; J. van der Land et al.; 19 Dec 1992; 55 m, color photo; USNM 307706; (44); Indian Ocean, Saya de Malha Bank, 10°16′00″S, 61°09′00″E; Vityaz Cr. 17; Sta 2810; 8 Jan 1989; 50–70 m; x-ray.

Comparative material.—See *A. gardineri.*

Diagnosis.—A species of *Apogon* in the subgenus *Ostorhinchus* with 15–17 pectoral rays, 4–6 rows of small spots on the body, pale stomach, intestine and peritoneum and 14–16 total gill rakers.

Description.—For general body shape see Fig. 5. Range of proportions (as percentages of standard lengths, syntypes in parentheses): greatest body depth 44 (40.7–43.0); head length 37–42 (40.4–42.5); eye diameter 10–13 (10.8–12.5); snout length 10–11 (9.4–10.6); bony interorbital width 9.6–9.8 (8.7–9.7); upper-jaw length 23

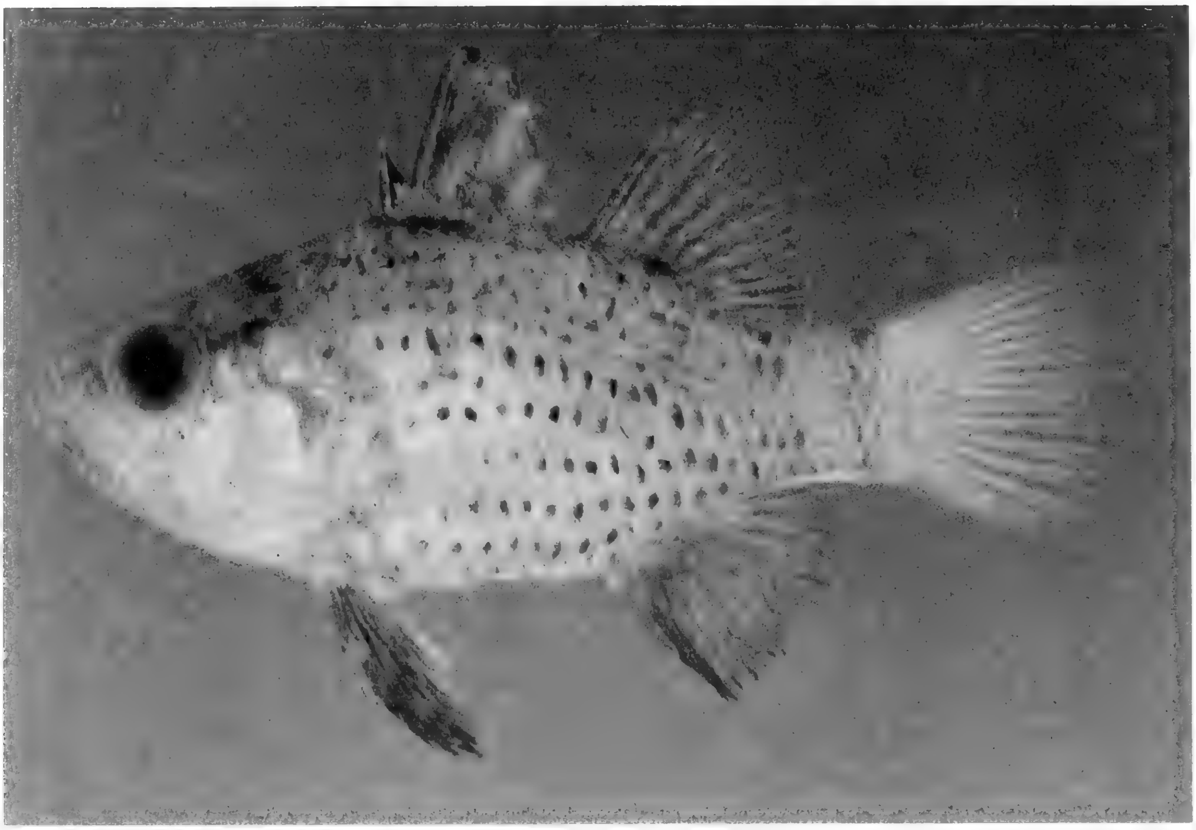

Fig. 5. *Apogon regani,* BPBM 35475, 45 mm SL, from the Seychelles, N. of Aride I. by J. E. Randall.

(20.8–22.6); caudal-peduncle depth 17–19 (15.9–17.0); caudal-peduncle length 20–22 (18.5–20.8); first dorsal-spine length 3.7–3.9 (3.0–4.1); second dorsal-spine length 10 (6.6–8.1); third dorsal-spine length 22–23 (18.5–21.6); fourth dorsal-spine length 20–22 (17.9–20.3); spine in second dorsal fin 16–18 (13.3–14.5); first anal-spine length 4.1–5.0 (3.0–4.1); second anal-spine length 15–16 (12.0–13.3); pectoral-fin length 21–23 (21.9); pelvic-fin length 29–33 (25.7–27.7).

Dorsal fin VII–I,9; anal fin II,8; pectoral fin 15–15, 15–16, 16–16, or 17–17; pelvic fin I,5; principal caudal rays 9 + 8; pored lateral-line scales 24–25; transverse scale rows above lateral line 2; transverse scale rows below lateral line 6–7; median predorsal scales 2–3; circumpeduncular scale rows 12(5+2+5). Total gillrakers 14–16, well-developed 10–11, upper arch 2+2 and lower arch 8–9+1–3.

Villiform teeth in a band on the premaxilla, the outer row slightly larger; several rows anteriorly, two rows on side of the dentary; one to two rows on the palatine, two rows on vomer; none on ectopterygoid, endopterygoid or basihyal.

Vertebrae 10 + 14. Five free hypurals, one pair of slender uroneurals, three epurals, a free parhypural. Three supraneurals, two supernumerary spines on first dorsal pterygiophore. Basisphenoid present. Supramaxilla absent. Posttemporal serrate on posterior margin. Preopercle serrate on vertical and horizontal margins, smooth on the ridge. Infraorbitals smooth, the second crenulate and third with a single spine. Scales ctenoid. Caudal fin truncate.

Life colors.—Based on an Ektachrome transparency of the Seychelles specimen the color pattern is as follows: Iris pale; head and body with a pale tannish background on the upper parts; a dark brown oblique line behind the eye; head silvery below eye level; body silvery below the pored lateral line on body to about the end of anal-fin base, faint brownish spots on some, but not all scales above the pored lateral line; larger brownish spots on each scale below the pored lateral line, forming about five lines of spots, reducing to two lines on the anterior portion of the caudal peduncle; a brownish area on the dorsum below the first four or five spines; another mark on dorsum below the fifth soft dorsal ray; caudal and pectoral fins pale; first dorsal dusky and whitish with a spot near the base of the fourth to sixth spines; second dorsal fin dusky; anal fin with a dark brownish edge to the second anal spine and first soft ray, the rest of fin dusky, pelvic fins dark brownish except the fifth soft ray pale.

Preserved color pattern.—In 70% ethyl alcohol: the syntypes with three to four rows of small spots below the lateral line on side of body. The pelvic fins and second dorsal fin blackish. Stomach, intestine and peritoneum pale. The other two specimens with six rows of small spots on side of body to caudal peduncle, one row above the lateral line; three marks behind eye, a narrow oblique cheek mark, a mark between the eye and preopercle just below the mid-line of the head, and an oblique mark past the top of the preopercle; all vertical fins darkish, caudal fin pale.

Distribution.—Known only from the Mascarene Plateau.

Remarks.—Whitley (1951) created the replacement name, *A. regani* for *A. punctatus* Regan, 1908, which is preoccupied by *Apogon punctatus* Klunzinger, 1880, a primary homonym. Klunzinger's species is presently placed in *Vincentia,* a mostly warm temperate species group from Australia and Tasmania. According to the International Commission on Zoological Nomenclature (1985: Art 59b) Regan's homonym is to be treated as permanently rejected.

Regan suggested a relationship with *A. nigripinnis.* Smith (1961) synonymized *A. punctatus* with *A. nigripinnis.* However, *A. regani* differs from all known species in the *A. nigripinnis* group by the presence of small spots, one per scale, on the body. *A. regani* represents an insular species in this group.

This species is found in deeper water. Randall & Egmond (1994) reported *A. regani* as *A. punctatus* from the Seychelles and provided a color photograph without description. It does not appear to have been reported from any of the shallow-water collections from Mauritius or Cargados Carajos in the past several decades. *Apogon regani* represents the second insular species endemic to the Mascarene Plateau in the *A. nigripinnis* complex.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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A new species of *Pogonophryne* (Pisces: Perciformes: Artedidraconidae) from East Antarctica

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Abstract.—A new species of notothenioid fish, *Pogonophryne squamibarbata,* is described from East Antarctica. This dorsally-spotted species belongs to the "*mentella*" group of the genus and is characterized by having a relatively short mental barbel (16% SL) with bluntly palmate, overlapping, scale-like processes on its terminal expansion, a wide interorbital region (6.9% SL), and a long opercular-subopercular distance (19.2% SL).

German research cruises of the R/V *Polarstern* in Antarctic waters have yielded several new species of the artedidraconid genus *Pogonophryne* (Eakin 1987, Balushkin & Eakin 1998, Eakin & Balushkin 1998). The "*mentella*" group is the most speciose of the genus, comprising at least 10 species, three of which have been recently described (Balushkin & Eakin 1998, Eakin & Balushkin 1998, Eakin & Eastman 1998). This paper continues our descriptions of new species of *Pogonophryne* in the Zoological Museum collections at Hamburg University.

Measurements and counts follow those of Balushkin & Eakin (1998) and Eakin & Eastman (1998). Opercular-subopercular distance is measured from the posterior edge (hook) of the opercular bone to the anterior edge of the subopercular bone. Measurements are presented as percentages of standard length unless otherwise indicated. ISH refers to the Zoological Museum collections (formerly Institut für Seefischerei) currently maintained at Hamburg University (ZMH).

Pogonophryne squamibarbata,
new species
Figs. 1–2

Holotype.—ISH 65-1991; male, 147 mm SL; R/V *Polarstern* station 211, East Antarctica (69°58.9′S, 05°8.4′E), 651–742 m; 10 Mar 1991.

Diagnosis.—This species of *Pogonophryne* belongs to the "*mentella*" group. The relatively short (16% SL) mental barbel has a terminal expansion composed of bluntly palmate, flattened processes arranged in an overlapping, scale-like pattern. This species also has a wide interorbital region (6.9% SL) and a long opercular-subopercular distance (19.2% SL).

Description.—Body robust anteriorly, tapering to low, narrow caudal peduncle. Head length 43.5; posttemporal ridges not well developed (upper limb of posttemporal bone not arched upward to form a prominent curved ridge), depth of head at this level 19.7; head width at preoperculars 37.4. Body depth at second dorsal fin origin 17.3; body depth at anal fin origin 13.6; body width at anal fin origin 10.5; caudal peduncle depth 6.5. Snout broadly rounded in dorsal view; internostril distance 9.2; snout length 8.6; eye filling orbit; diameter of orbit 9.9. Interorbital region wide, bony measurement 6.9. Opercular-subopercular distance long, 19.2. Postorbital length of head 23.7. Jaw width at posterior ends of maxillaries 25.5. Upper jaw length 19.3; posterior end of maxillary extending slightly beyond pupil of eye; lower jaw project-

Fig. 1. *Pogonophryne squamibarbata*, holotype, ISH 65-1991; male, 147 mm SL.

ing beyond upper a distance 7.8 of head length. Tongue long, extending anteriorly slightly in front of tip of upper jaw. Upper jaw with two rows of teeth (largest near symphysis) in a broad arc. Lower jaw teeth in two rows near symphysis, becoming uniserial posteriorly (nine large teeth on both sides) in a V-shaped pattern. Mental barbel (Fig. 2) rather short (16% SL) and with a terminal expansion composed of bluntly palmate, flattened processes arranged in an overlapping, scale-like pattern and continuing onto stalk; barbel length 16.0; terminal expansion 34.0 of barbel length and slightly wider than stalk. Anterior gillrakers on first arch 2 + 0 + 7 = 9; posterior gillrakers 0 + 1 + 7 = 8; total 17.

First antedorsal distance 37.4; second antedorsal distance 46.3; anteanal distance 64.6. Length of second dorsal fin base 52.4; length of anal fin base 33.0; length of caudal fin 25.3; length of pectoral fin 28.7; width of pectoral fin base 10.5; length of pelvic fin 20.4. Interdorsal distance 7.5. First dorsal fin with two spines of about equal length, 9.2. Second dorsal fin with 27 rays; length of longest (fifth) ray 15.3. Ratio of longest first dorsal fin spine to longest second dorsal fin ray 0.60. Anal rays 17. Pectoral rays 20. Upper lateral line with about 26 (left) and 27 (right) pores (tubular scales), ending under the twenty-first ray of the second dorsal fin. Middle lateral line with about 11 tubular scales (13 pores) on the left side and 11 tubular scales on the right side; tubular scales originate under the eighteenth ray of the second dorsal fin. Cephalic lateral-line pores typical for *Pogonophryne:* preoperculo-mandibular canal with nine pores; infraorbital canal with seven pores; supraorbital canals with two nasal pores, two interorbital pores, and one unpaired coronal pore; temporal canal with six pores; and supratemporal canal incomplete across occiput (one pore on each side). Vertebrae 16 + 21 = 37 (second preural vertebra appears double, being longer than the others and possessing two neural and two hemal spines, but is counted as one element).

Radiographic analysis of skeleton.—Number of vertebrae to first pterygiophore of first dorsal fin 2; to first pterygiophore of second dorsal fin 6; to first pterygiophore of anal fin 16. Free caudal vertebrae counting from last pterygiophore of second dorsal fin 6; counting from last pterygiophore of anal fin 6. Four pterygiophores anterior to first pterygiophore of second dorsal fin; the anterior two support spines of the first dorsal fin, while the posterior two are rayless pterygiophores. One pterygiophore anterior to first caudal vertebra under abdominal section of vertebral column. Four hypural plates attached to urostyle; parhypural (PH) + lower complex hypural (H1 + H2) + upper complex hypural (H3 + H4) + minimal hypural (H5). All hypural plates except H5 fused to urostyle. Caudal fin with 21 rays (4 upper procurrent + 13 principal + 4 lower procurrent). Distribution of principal caudal rays with reference to hypural plates: 1–6–4–2. Epurals 3, the anterior two of which resemble in shape the neural spine of the first preural vertebra. One pair of uroneurals.

Color in alcohol.—Head and body with brownish markings dorsally and laterally on yellowish background. Markings on head in the form of round spots and vermiculations; those on body larger and more irregular. A broad, dark horizontal marking extends along base of anal fin. Ventral surfaces of head and body dusky and unmarked. First dorsal fin light; second dorsal fin with dark oblique stripes. Anal fin light. Caudal fin with about six dark vertical stripes. Pectoral fins with about six dark vertical stripes. Pelvic fins light. Mental barbel light.

Etymology.—Named for the overlapping, scale-like processes on the mental barbel (Latin *squama*: a scale; *barb*: a beard).

Comparative notes.—The new species belongs to the "*mentella*" group of the genus which is generally characterized by having a well developed mental barbel (elongation, complex terminal expansion,

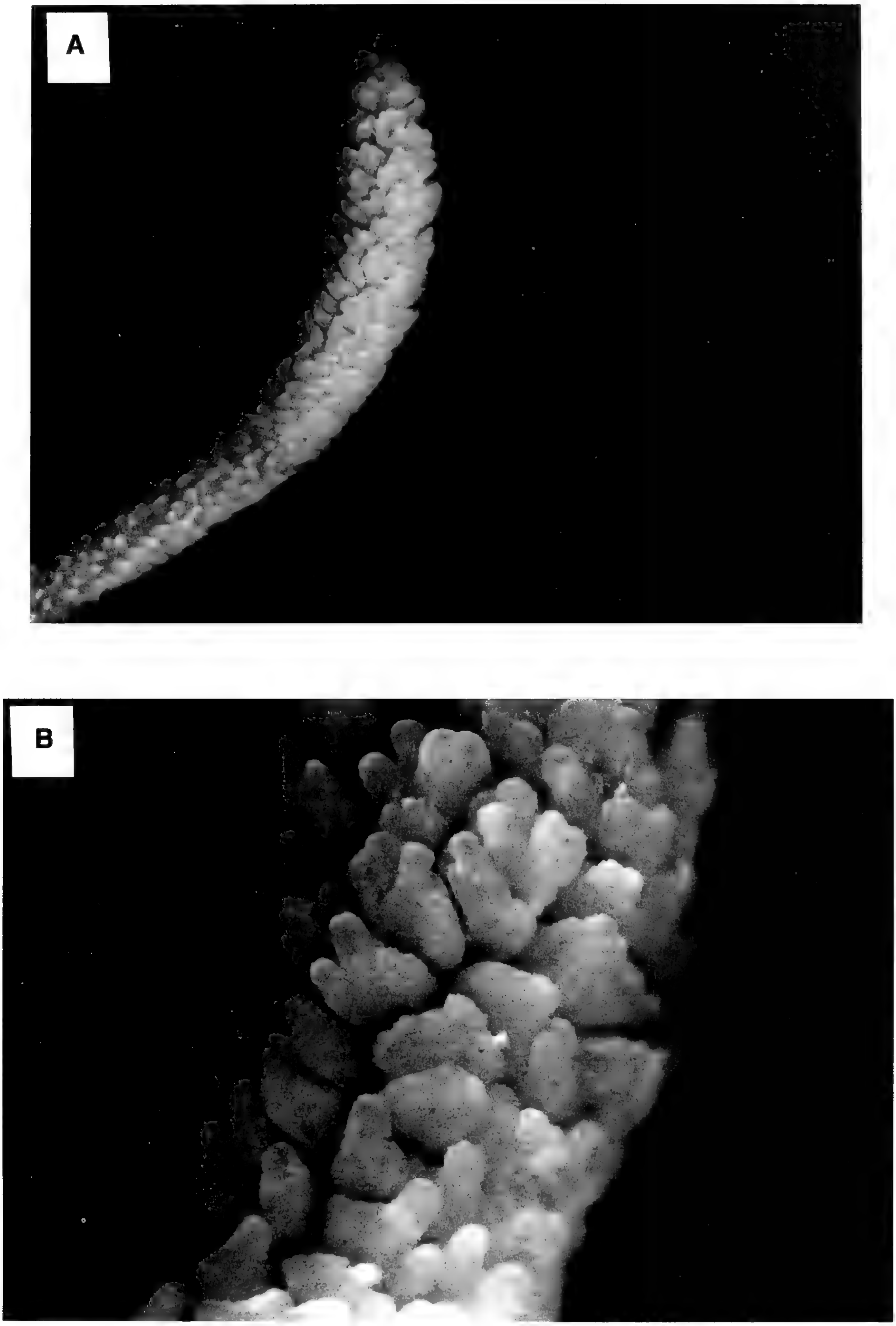

Fig. 2. Mental barbel of *Pogonophryne squamibarbata,* holotype; a, terminal expansion (×10); b, detail of terminal expansion showing overlapping, palmate processes (×40).

or both), relatively undeveloped posttemporal ridges (upper limb of posttemporal bone not arched upward to form a prominent curved ridge), and large, sparsely distributed, round spots and vermiculations on the dorsal and lateral surfaces of the head (Balushkin & Eakin 1998). The mental barbel somewhat resembles that of *P. mentella* in having a terminal expansion composed of bluntly palmate, flattened processes. However, the barbel of *P. squamibarbata* is much shorter (16% SL) than that of the holotype of *P. mentella* (27.1% SL; Andriashev 1967) and has a relatively longer terminal expansion (34% of barbel length compared to 26.4% of barbel length; measured from Andriashev 1967, Fig. 1). The scale-like pattern of densely packed, overlapping processes on the mental barbel of *P. squamibarbata* is unlike that of any other species of *Pogonophryne.* This species also has a wide interorbital region (6.9% SL) and a long opercular-subopercular distance (19.2% SL).

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A new genus and species of inseminating fish (Teleostei: Characidae: Cheirodontinae: Compsurini) from South America with uniquely derived caudal-fin dermal papillae

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Abstract.—*Kolpotocheirodon theloura,* a new genus and species of the cheirodontine tribe Compsurini, is described from the uppermost tributaries of the rio São Francisco and rio Paraná in central Brazil. Males of the new species bear a caudal-fin organ formed by fin-ray hooks and hypertrophied elongate dermal flaps along the fin rays, mostly in the ventral lobe of the caudal fin. The largest flap, attached dorsally to the nineteenth principal caudal-fin ray (ventral principal fin ray of the ventral caudal-fin lobe), is bordered with a series of tabs, and extends dorsally over most of the flaps extending from caudal-fin rays 17 and 18. There are also a series of fleshy papillae distributed along the border of the remaining ventral caudal-fin ray flaps or along the fin rays just dorsal to the flap-bearing fin rays. These tabs and papillae are unknown in both other inseminating and all externally fertilizing characids and therefore are considered derived. The new species is referred to the Compsurini of the Cheirodontinae on the basis of a cladistic diagnosis of these taxa. The relationships of *K. theloura* with other inseminating compsurins bearing modified caudal fins are discussed.

Resumo.—*Kolpotocheirodon theloura,* gênero e espécie novos da tribo Compsurini de Cheirodontinae, é descrito para os tributários superiores do rio São Francisco e rio Paraná no Planalto Central do Brasil. Machos da nova espécie possuem um órgão formado por ganchos nos raios da nadadeira caudal e por dobras de pele ("flaps") hipertrofiadas ao longo dos raios, principalmente no lobo ventral da nadadeira caudal. O maior "flap", conectado ao longo da face dorsal do 19° raio da nadadeira caudal (raio principal inferior do lobo ventral da nadadeira caudal), é marginado por uma série de tabiques, e se estende dorsalmente sobre as dobras de pele originadas nos 17° e 18° raios. Existe ainda uma série de papilas carnosas distribuídas ao longo das demais dobras de pele do lobo ventral da nadadeira caudal ou ao longo dos raios imediatamente superiores aos raios com dobras de pele. Estes tabiques e papilas são desconhecidos em outros caracídeos, tanto naqueles com inseminação como nos com fertilização externa, sendo considerados como caracteres derivados. A espécie nova é referida aos Compsurini em Cheirodontinae com base em uma diagnose cladística destes táxons. São discutidas as relações de K. theloura com outros compsuríneos de nadadeiras caudais modificadas.

The new genus and species herein described (see Figs. 1–3) is a cheirodontine with modified, possibly glandular tissues, and hooks on the caudal fin of males. It was discovered in the collections of the Museu de Zoologia, Universidade de São Paulo by one of us (L.R.M.) while reviewing cheirodontine characids of southeastern and eastern Brazil. The species was first hypothesized to belong to a cheirodontine clade diagnosed by specialized modified anal-fin hooks and derived scales, fin rays and/or hypertrophied soft tissues on the caudal fin. In the unpublished thesis of Malabarba (1994), this clade includes *Saccoderma* Schultz, *Compsura* Eigenmann, *Macropsobrycon* Eigenmann, *Acinocheirodon* Malabarba & Weitzman, and the Central American "*Odontostilbe*" *dialeptura* (Fink & Weitzman) and "*O.*" *mitoptera* (Fink & Weitzman). Later, the new taxon (listed as undescribed genus and species A in Burns et al. 1997) and all cheirodontine taxa listed above (see Burns et al. 1997) were found to be inseminating species. Subsequently, this putative clade was recognized as a cheirodontine tribe, the Compsurini (Malabarba, Weitzman, & Burns in Malabarba 1998), including the taxon described herein (therein referred as new genus and species A). The significance of these characters in resolving the phylogeny of compsurin cheirodontines, as well as its possible homology to similar characters found in glandulocaudine characids, were further discussed by Malabarba & Weitzman (1999).

Males of the new genus and species have hooks on the caudal fin (Fig. 4) and hypertrophied dermal flaps along the caudal-fin rays (Fig. 5). The largest flap attached dorsally to the 19th ventral lobe caudal-fin ray is bordered with a series of tabs, and extends dorsally over most of the flaps extending from caudal-fin rays 17 and 18. There is also a series of fleshy papillae distributed along the border of the remaining ventral caudal-fin ray flaps or along the fin rays just dorsal to the fin rays bearing flaps. These tabs and papillae are unknown in the remaining inseminating cheirodontines, as well as on other inseminating or externally fertilizing species of characids and are consequently hypothesized to be derived. This is the only species of the Compsurini known to have aquasperm (a nearly spherical or spherical sperm nucleus, similar to that found in externally fertilizing characids; see Burns et al. 1997:434, fig. 1A). All other species of the Compsurini so far investigated have elongate sperm cell bodies (see Burns et al. 1997:434, fig. 1B–H).

Methods

The systematic methods, counts and measurements used here are the same of those described and used by Malabarba & Weitzman (1999). The following acronyms are used for institutions and collections: MCP, Museu de Ciências e Tecnologia, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre; and MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo. The following abbreviations are used in the text or figures: SL = standard length; HL = head length; c&s = alizarin red s and alcian blue stained specimens cleared with trypsin; spm(s) = specimen(s). The comparative material is the same listed in Malabarba & Weitzman (1999).

Kolpotocheirodon, new genus

Type species.—*Kolpotocheirodon theloura,* new species.

Diagnosis.—The following apomorphies diagnose *Kolpotocheirodon*:

A specialized caudal organ (Fig. 5) is present at the proximal region of the ventral caudal-fin lobe of the males (=character number 36 in Malabarba 1998). This consists of hypertrophied elongate dermal flaps attached along the fin rays and a series of relatively flat tabs attached along the exposed border of the largest flap. The base of this flap is attached along the anterior approximately one-third of the nineteenth caudal-fin ray. Visually moving dorsally, the flaps decrease in length and width until those of the thirteenth or fourteenth fin rays are relatively short, narrow, and almost undetectable. Each flap, other than that of the nineteenth ray, bears papillae in a single series along its exposed border. The tabs of the nineteenth fin ray flap extend dorsally while the papillae of the fourteenth to at least the sixteenth or seventeenth flap are directed ventrally.

Hooks on the anal-fin rays of mature males (Fig. 6) occur along the posteriolateral border of the posterior unbranched and five anterior branched anal-fin rays (Character 30 in Malabarba 1998). Although the number of hook-bearing anal-fin rays in any species of the Characidae with hooks is variable according to the degree of maturation, it seems to be constant in fully mature specimens of some species. All fully mature males of *Kolpotocheirodon theloura* have fully developed hooks restricted to six of the anterior anal-fin rays. The remaining species of the Compsurini have hooks on a larger number of anal-fin rays, with the exception of the species of *Saccoderma,* which have anal-fin hooks only along the posterior ray of the anterior unbranched rays and the four most anterior branched anal-fin rays.

The twelfth and thirteenth caudal-fin rays are somewhat curved, being noticeably concave along their dorsal borders at about their basal half lengths (Fig. 4) and somewhat convex along their ventral borders where the segments are slightly expanded longitudinally (character 34, state 2 in Malabarba 1998). This feature separates *K. theloura* from other cheirodontines. *Acinocheirodon melanogramma* Malabarba & Weitzman (1999), another compsurin, also has the basal halves of the caudal-fin rays dorsally concave with ventrally expanded segments, but in this species they are thirteenth and fourteenth, rather than twelfth and thirteenth rays.

Etymology.—The first component of the name *Kolpotocheirodon* is from the Greek, *kolpotos* = formed into folds, and refers to the caudal organ formed by hypertrophied dermal folds along the caudal-fin rays. The second component refers to the characid genus *Cheirodon* Girard, in reference to our referral of this new genus to the Cheirodontinae.

Kolpotocheirodon theloura, new species
Figs. 1–3

All specimens from Brazil, Brasilia, Distrito Federal, except when noted.

Holotype.—MZUSP 55194, 1 male, 27.3 mm SL, small marsh at Curva da Morte, Goiás, 3 May 1978, E. K. Bastos.

Paratypes.—Rio Paraná tributaries: MCP 11161, 1 male, 25.9 mm SL, c&s, MZUSP 38840, 2 females, 27.9 and 29.7 mm SL, and MZUSP 38839, 1 male, 29.9 mm SL, ribeirão do Gama, just above the mouth of ribeirão Taquara, 1 Oct 1985, J. P. Viana Mendes. MZUSP 39014, 1 female, 24.0 mm SL and MCP 11160, 1 female, 22.2 mm SL, ribeirão Riacho Fundo, tributary of rio São Bartolomeu, 3 Jul 1985, M. Ribeiro. MZUSP 42802, 1 male, 27.8 mm SL, 1 female, 24.6 mm SL, collected with the holotype. Rio São Francisco tributaries: MCP 12204, 4 spms. (1 alcohol, 3 c&s), 14.0–16.0 mm SL, and MZUSP 35722, 12 spms, 14.7–19.5 mm SL, córrego Várgem de Trás, 1–2 Apr 1979, N. A. Menezes & E. K. Bastos. MZUSP 42801, 2 males, 22.9–23.8 mm SL and 1 female, 20.2 mm SL, lagoa Feia, 3 May 1978, E. K. Bastos.

Diagnosis.—The same as for the genus.

Distinguishing characters.—The presence of spherical sperm nuclei (aquasperm; see Burns et al. 1997:434, fig. 1A and tab. 1, "undescribed genus and species A") is plesiomorphic for the Compsurini, according to the parsimony analysis in Malabarba (1998). Its presence in *K. theloura* distinguishes this species from all other species of the Compsurini so far investigated, which have elongated sperm nuclei (see Burns et al. 1997:434, fig. 1B–H and tab. 1).

Kolpotocheirodon theloura also has an atypical color pattern for the Cheirodontinae of three to five very small vertical bars on the sides of the body, crossing the narrow lateral horizontal body stripe. These are

Fig. 1. *Kolpotocheirodon theloura,* new species, holotype, male, MZUSP 55194, SL 27.3 mm; small marsh at Curva da Morte, Goiás, Brazil.

located dorsal to the visceral cavity, and between the pseudotympanum and the area ventral to the dorsal fin (Figs. 1–3).

Kolpotocheirodon theloura can also be distinguished from other cheirodontines by a conspicuous dark brown band formed of a series of spots distributed along all of the hook-bearing portion of the anal-fin of the males. These pigment spots are placed at approximately the midlength of the posteriormost of the anterior unbranched anal-fin rays and the five anteriormost branched anal-fin rays. The most conspicuous and darkest spot is at the anterior surface of the first branched ray (Fig. 1; although also present in the paratypes, the dark brown spot cannot be seen in the black ground Figs. 2–3). A similar, but less conspicuous band of spots occurs in females along the midlength of the anal-fin rays. These are more strongly pigmented in the anterior portion of the fin.

Description.—Morphometric data summarized in Table 1.

Body moderately elongate and compressed, greatest depth at dorsal-fin origin. Predorsal profile convex, slightly concave in region of supraoccipital process. Profile of body from base of posterior dorsal-fin ray to origin of adipose fin straight or moderately convex. Ventral profile of body convex from tip of lower jaw to pelvic-fin origin and moderately concave from there to anal-fin origin. Body profile along anal-fin base of males moderately concave in anterior half and convex posteriorly. In female entire fin base relatively straight. Dorsal and ventral profile of caudal peduncle concave. Largest mature male examined with an expanded and rounded dorsal and ventral caudal-peduncle profiles. Caudal peduncle about as long as deep or somewhat shorter than deep.

Head small and snout short, rounded. Mouth terminal. Maxilla short, positioned at an angle of approximately 45 degrees relative to long axis of body. Posterior extremity of maxilla reaching vertical that passes through anterior border of eye.

Premaxilla with 4 (rarely 5) symmetrical teeth having 9–11 small evenly spaced cusps all about equal in size (Fig. 7). Cutting edge arched in most medial tooth and almost straight in most lateral tooth. Maxilla with 2 (rarely 3) teeth, similar in form to those of premaxilla, with 7–11 cusps. Cutting edge slightly arched to almost straight. Dentary with 4 large teeth with 5, 7, or 9 cusps; followed by 1 or 2 smaller teeth with 3, 5 or 7 cusps. Teeth following second tooth asymmetrical with most lateral cusp situated towards tooth base and most medial cusp more distally located. Cusps small and regular and approximately equal in size. Cutting edge slightly arched to almost straight.

Dorsal-fin rays, ii, 9, $n = 29$. First unbranched ray about half length of second.

Dorsal-fin origin approximately at mid-length of body. Proximal portion of dermal flaps along largest unbranched and first branched dorsal-fin rays bordered by series of papillae in both sexes. Adipose-fin origin at, or slightly anterior to, vertical through insertion of posteriormost anal-fin ray.

Anal-fin rays, iii, 18, (ii–iv, $\bar{X} = 3.3$, 17–21, $\bar{X} = 19.1$, $n = 22$). Anal-fin origin slightly posterior to vertical passing through base of posteriormost dorsal-fin ray. Anal fin of females with anterior 5–6 branched rays very long, forming prominent anterior lobe. Rays posterior to anterior lobe abruptly shorter and distal border of anal fin concave posterior to anterior lobe. Distal border of male anal fin decreasing in length gradually so that although anterior lobe larger than but not as abruptly distinct as in females. Anal-fin rays of males with slender, elongate retrorse hooks on longest unbranched ray, and anterior first 5 branched rays, usually with 4 to 5 segments bearing hooks on each ray (Fig. 6). Hooks inserted at posterolateral border of fin rays, bent over lateral surface of fin ray and anteriorly directed. Hooks located on posterior branches of rays only; never on proximal portions of main body of rays. One, rarely two, bilateral pair of bony hooks per ray segment.

Pectoral-fin rays, i, 9, (i, 8–11, $\bar{X} = 9.2$, $n = 28$). Distal ends of longest rays extend slightly beyond pelvic-fin origin. Pelvic-fin rays, i, 7, (i, 7–8, $\bar{X} = 7.1$, $n = 29$). Pelvic-fin origin anterior to vertical passing through dorsal-fin origin. Tip of fin reaching anal-fin origin in males but not in females. Male pelvic fins with unilateral, ventromedial retrorse bony hooks (Fig. 8); branched rays bearing one, rarely two slender hooks per segment along most of branched ray lengths, including both primary branches and often posterior secondary branches. Distal sections of unbranched part of each branched ray with one to occasionally few hooks. Number of hooks varies among different males, those males bearing more hooks appearing more mature

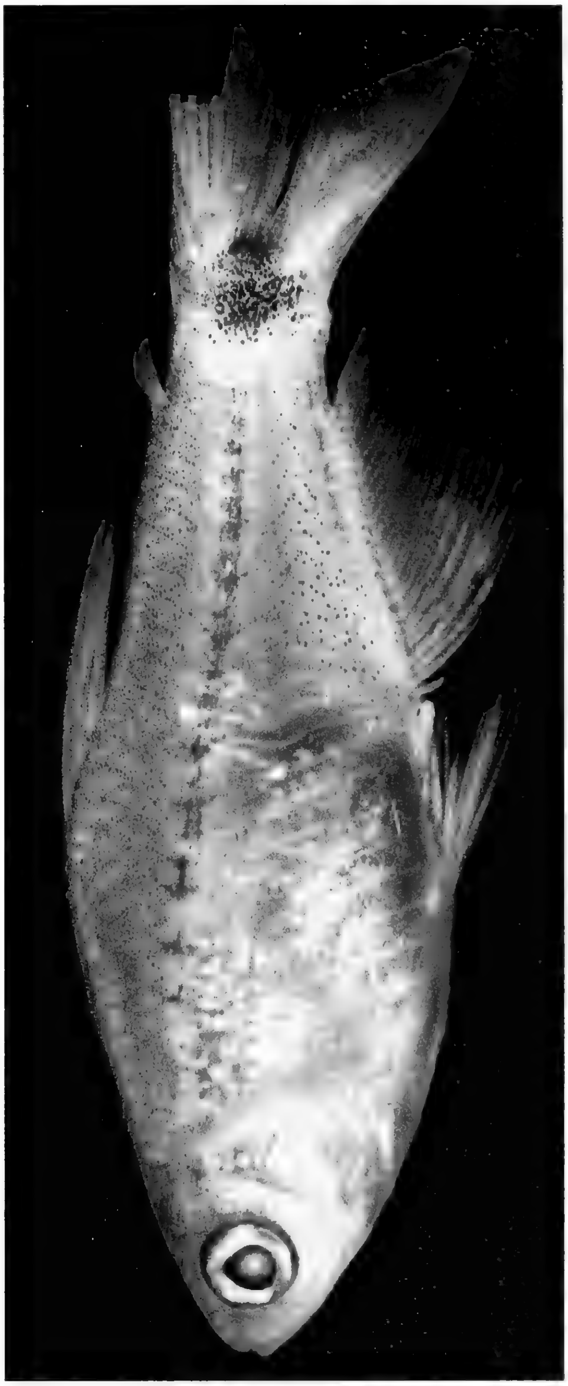

Fig. 2. *Kolpotocheirodon theloura*, new species, paratype, male, MZUSP 42802, SL 27.8 mm; small marsh at Curva da Morte, Goiás, Brazil.

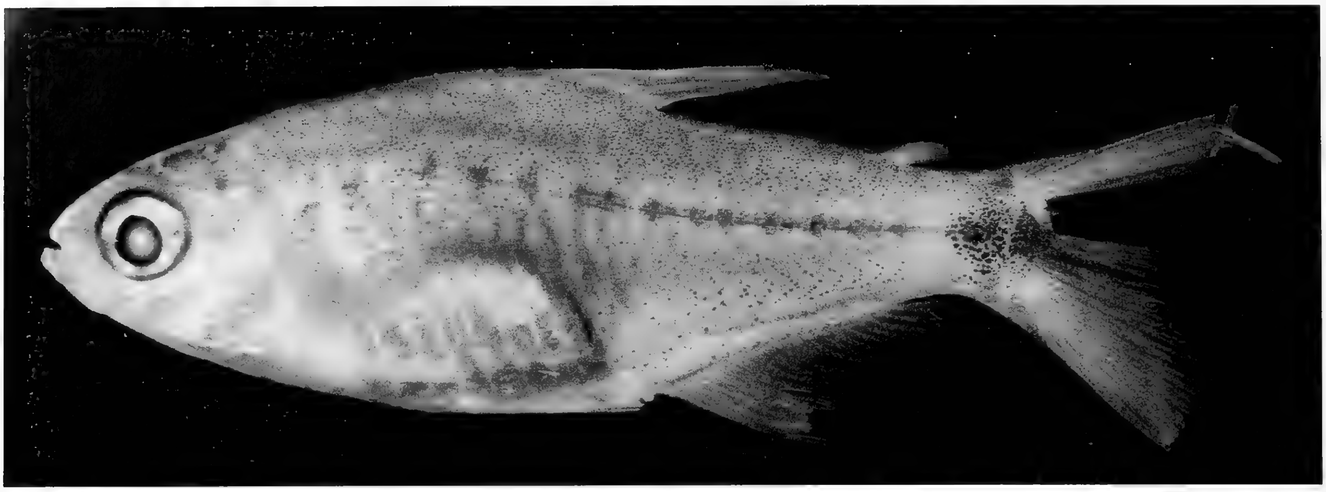

Fig. 3. *Kolpotocheirodon theloura,* new species, paratype, female, MZUSP 42802, SL 24.6 mm; small marsh at Curva da Morte, Goiás, Brazil.

when considering other secondary sexual characters such as caudal-fin papillae.

Principal caudal-fin rays 10/9, $n = 29$. Proximal portion of thirteenth or fourteenth through nineteenth caudal-fin rays in ventral caudal fin lobe with hypertrophied dermal flaps. Largest flap extending dorsally from nineteenth principal caudal-fin ray (Fig. 5). Each flap bordered by one series of external papillae, more numerous and more developed in males. Proximal portion of third caudal-fin ray in dorsal caudal-fin lobe with hypertrophied dermal flaps and external papillae only in males. Males with modified 12th to 14th or 15th principal caudal-fin rays; these rays bearing (on each side) row of 4–6 dorsoanteriorly directed hooks along dorsal divisions (Fig. 4). Dorsal and ventral procurrent rays equivalent in numbers and structure in both sexes, similar to those of most characids. Dorsal procurrent caudal-fin rays, 13 (9–13, $\bar{X} = 10.8$, n

Table 1.—Morphometrics of *Kolpotocheirodon theloura,* new species. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Range includes the holotype, MZUSP 55194, and following paratypes MZUSP 38839, MZUSP 42801, MZUSP 42802, MCP 11161, MZUSP 38840, MZUSP 39014, MCP 11160.

			Males				Females		
	Holotype	n	Low	High	$\bar{X}$	n	Low	High	$\bar{x}$
Standard length (mm)	27.3	6	22.9	29.9	26.3	5	22.2	29.7	25.7
Snout to anal-fin origin	62.3	6	60.1	63.9	61.8	5	62.2	66.3	65.2
Snout to dorsal-fin origin	49.5	6	48.9	51.5	50.0	5	48.3	53.0	51.1
Snout to pelvic-fin origin	45.4	5	41.7	46.5	44.9	5	44.1	45.5	44.6
Dorsal-fin base length	11.7	5	11.7	13.1	12.5	5	12.6	14.0	13.3
Anal-fin base length	29.3	5	26.4	29.4	28.6	5	26.2	28.5	27.4
Caudal peduncle length	9.9	5	9.9	12.4	11.0	5	11.0	12.2	11.6
Caudal peduncle depth	14.7	5	12.9	14.7	13.7	5	11.3	13.3	12.2
Depth at dorsal-fin origin	35.5	5	32.4	36.1	34.3	5	30.4	37.6	34.4
Dorsal-fin height	28.2	5	27.0	30.4	28.3	5	25.2	29.3	27.9
Pelvic-fin length	20.9	5	19.4	21.7	20.4	5	15.0	18.6	17.1
Pectoral-fin length	23.8	5	20.5	23.8	21.9	4	19.5	23.3	21.4
Bony head length	26.0	5	24.4	26.8	25.8	5	25.9	27.1	26.5
Snout length	18.3	5	18.3	24.1	22.2	5	21.5	24.7	22.9
Upper jaw length	25.4	4	25.4	29.2	27.3	2	29.7	32.2	31.0
Horizontal eye diameter	35.2	5	32.4	39.7	36.1	5	35.6	38.5	36.8
Least interorbital width	29.6	5	29.6	36.2	31.3	5	29.2	31.2	30.6

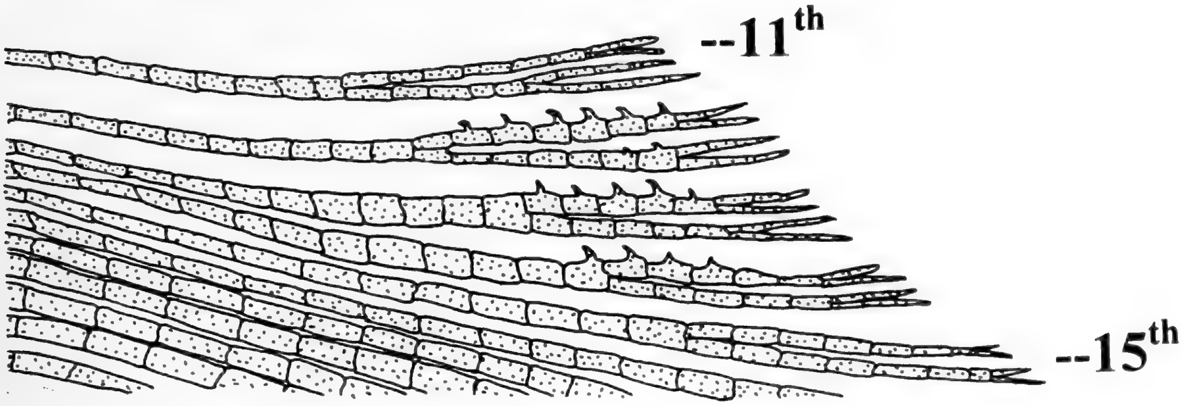

Fig. 4. *Kolpotocheirodon theloura*, new species, paratype, MCP 11161, c&s male, SL 25.9 mm. Caudal-fin rays eleven (11th) through fifteen (15th) of the ventral caudal-fin lobe, other lower caudal-fin rays only partially indicated. Figure illustrates the position and number of caudal-fin ray hooks along fin rays twelve to fourteen. Anterior is to left.

= 5). Ventral procurrent caudal-fin rays, 9 (n = 5).

Scales cycloid, moderately large. Lateral line poring incomplete, 8, (6–10, $\bar{X}$ = 7.6, n = 21) anterior perforated scales. Scales in lateral series 33, (31–34, $\bar{X}$ = 32.8, n = 19). Scale rows between dorsal-fin origin and lateral line 5, (5–6, $\bar{X}$ = 5.1, n = 22). Scale rows between lateral line and pelvic-fin origin 4, (3–4, $\bar{X}$ = 3.6, n = 22). Predorsal scales, when in regular series 11 (10–11, $\bar{X}$ = 10.8, n = 9). Scale rows around caudal peduncle 14 (n = 5). Scale sheath on anal-fin base consisting of 3–5 scales covering unbranched rays and anterior 4–5 branched rays.

Supraneurals, 5 (3–5, $\bar{X}$ = 4.3, n = 8). Precaudal vertebrae, 15 (15–16, $\bar{X}$ = 15.1, n = 12). Caudal vertebrae, 17 (17–18, $\bar{X}$ = 17.5, n = 12).

Color in alcohol.—Head and body pale brownish yellow. Black lateral body stripe very narrow, pale on caudal peduncle and anterior to dorsal-fin origin (Figs. 1–3). Lateral body stripe crossed by 3–5 very small vertical bars between pseudotympanum and area ventral to dorsal fin. Humeral spot absent. Caudal-fin base and posterior termination of caudal peduncle bear dark black, vertically-elongate, lozenge-shaped spot that reaches dorsal and ventral margins of caudal peduncle. Caudal spot extends just to most proximal portion of middle caudal-fin rays otherwise white or pale brownish yellow. All other fins hyaline except anal fin. Anal fin of males with conspicuous dark brown band distributed along all hook-bearing portions of fin (approximately middle length of last unbranched anal-fin ray and five anteriormost branched anal-fin rays). Pattern most conspicuous at anterior surface of first branched ray. Less conspicuous similar band of spots occurs in females, along midlength of most anterior branched anal-fin rays.

Sexual dimorphism.—The females lack hooks on the pelvic, anal, and caudal fins, while the males bear numerous small hooks on the pelvic and anal-fin rays. The male holotype and paratypes bear about 4–6 hooks on caudal-fin rays 12–14 with more of these hooks on ray 12 than on ray 14. Both sexes bear dermal tabs and papillae on the caudal fin, but the females lack these papillae in the dorsal caudal-fin lobe although they are present in males. The females have the distal border of the anal fin with a distinct anterior lobe that is abruptly curtailed at about branched rays 6–7. The male distal anal-fin profile is not lobate. Instead the fin rays gradually diminish in length from the anterior to posterior terminations of the fin. The pelvic fins are longer in the males (19.4–21.7% of SL) than in the females (15.0–18.6% of SL), reaching past the anal-fin origin in the males, but not

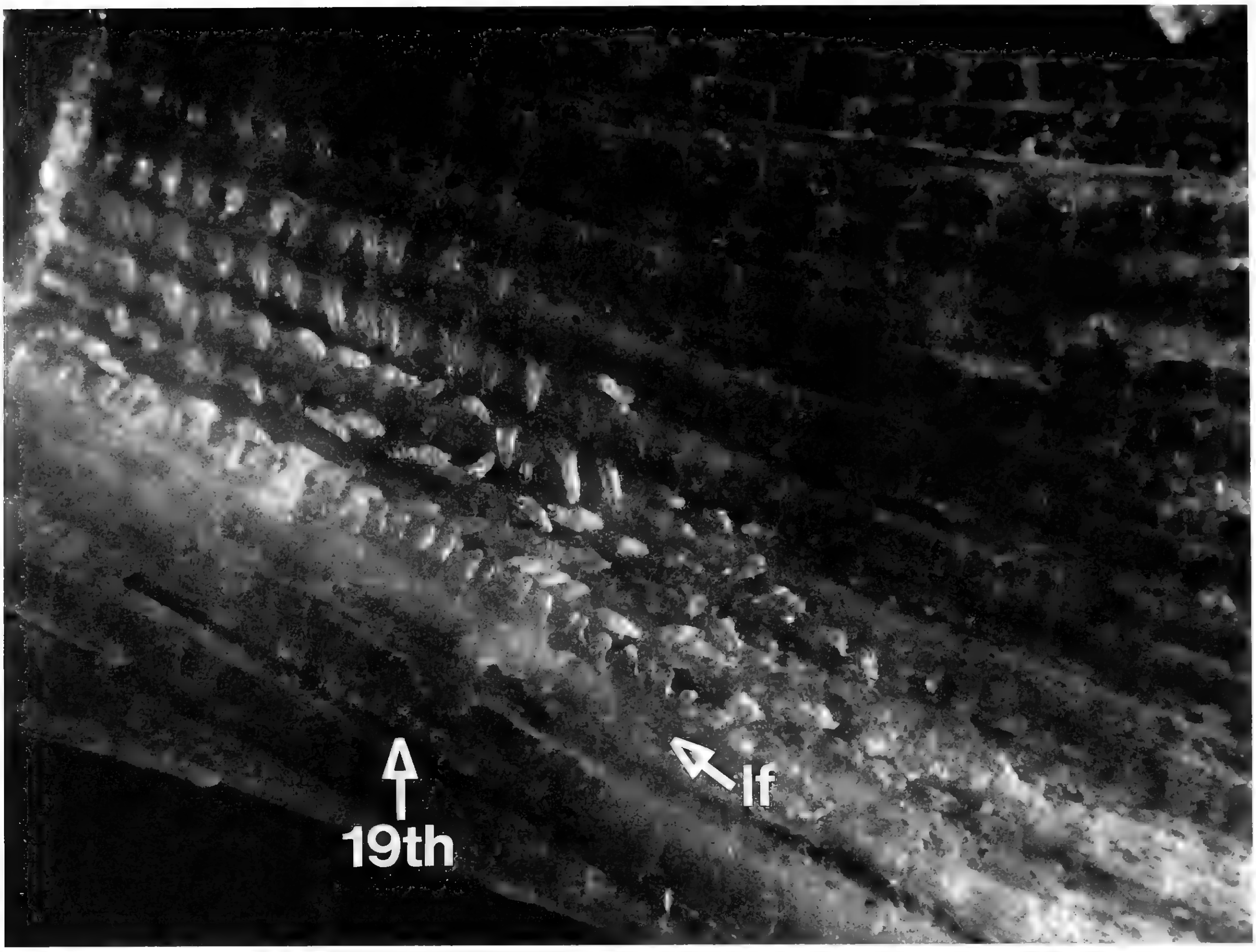

Fig. 5. *Kolpotocheirodon theloura,* new species, holotype, male, MZUSP 55194, SL 27.3 mm. Proximal portion of the ventral caudal-fin lobe. Figure illustrates the derived hypertrophied flaps bearing tabs and papillae along the caudal-fin rays. White arrow indicates largest flap (1f) extending dorsally from the nineteenth principal caudal-fin ray (19th), bordered by one series of flat tabs. All other flaps are bordered by one series of fleshy papillae.

females. The relative position of the anal fin also seems to be sexually dimorphic, with the snout to anal-fin origin distance in males (60.1–63.9% of SL) shorter than in females (62.2–66.3% of SL). However, our sample size is small and the examination of larger population samples is necessary to confirm this pattern of difference between males and females.

Distribution.—*Kolpotocheirodon theloura* has an interesting distribution, along the uppermost tributaries of both the rio São Francisco and the upper rio Paraná basins, near Brasília, in central Brazil. It is found close to an area called Águas Emendadas (joint waters), in allusion to the close proximity of the head waters of the upper tributaries of the rio São Francisco, alto rio Paraná and rio Tocantins. This may explain the distribution of this species in two of these major basins. So far, this species is unknown from the rio Tocantins tributaries, but samples from that area are too rare to assure its absence in that drainage.

Etymology.—The name *theloura* is from the Greek *thele* meaning nipple and *oura* meaning tail. The name refers to the presence of papillae on the ventral lobe of the caudal fin. The name is a noun in apposition.

Discussion.—The relationships of *Kolpotocheirodon theloura* to other cheirodontine characids is supported by the presence of all four synapomorphies diagnosing the Cheirodontinae (Malabarba, 1998). These are: The presence of a large, nearly triangular, hiatus among the muscles covering the anterior chamber of the swimbladder

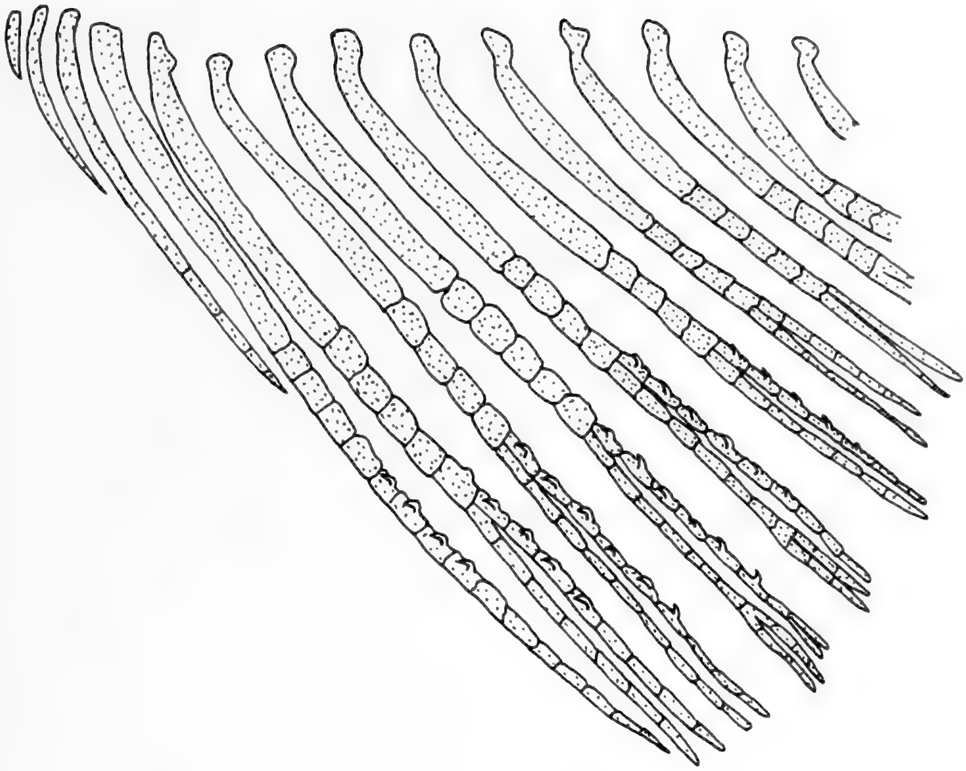

Fig. 6. *Kolpotocheirodon theloura,* new species, paratype, MCP 11161, c&s male, SL 25.9 mm. Anterior portion of anal fin bearing hooks. Figure shows anal-fin hooks positioned along posterolateral border of anal-fin rays, bent anteriorly over lateral surface of anal-fin ray to which it is attached, and distal tip pointing anteriorly.

between the first and second pleural ribs (pseudotympanum—Figs. 1–3). This hiatus is limited dorsally by the *lateralis superficialis* muscle, posteriorly by a naked anterior face of the second pleural rib, postero-ventrally by the *obliquus inferioris* muscle, and antero-ventrally by the *obliquus superioris* muscle. See also Malabarba (1998: 200–201, figs. 2B and 3A) and Weitzman & Malabarba (1999:7 and 16, figs. 5, 6, 16 and 17). The humeral spot is absent (Figs. 1–3). The teeth are pedunculated, largely expanded and compressed on their distal borders (Fig. 7). An unique regular, single tooth row is present on the premaxilla. The teeth of this row are perfectly aligned and similar in shape and cusp number (Fig. 7).

Kolpotocheirodon theloura is included among the members of the cheirodontine tribe Compsurini (Malabarba, Weitzman, & Burns *in* Malabarba, 1998) because it has the following synapomorphies of that tribe: The species is inseminating. The anal-fin hooks are positioned along the posterolateral border of the anal-fin rays, but are bent more or less anteriorly over the lateral surface of the anal-fin ray to which each is attached. The distal tip of each anal-fin hook is directed towards the anterior border of the anal-fin ray to which it is attached (Fig. 6), instead of pointing posteriorly or dorsally as in most other characids that have anal-fin hooks. Hooks are present on the dorsal surface of some of the caudal-fin rays and inclined towards the caudal-fin base (Fig. 4). Hooks are distributed along the distal lengths of the principal caudal-fin rays 11 to 14 (Fig. 4). The anal fin is more strongly pigmented along the distal portion of the branched rays (Fig. 1). *Kolpotocheirodon theloura* was placed as the most basal species (identified as Species A) of the Compsurini in the parsimony analysis of Malabarba (1998). We herein further discuss and describe the characters of *K. theloura* in order to better hypothesize its relationships to other compsurin species.

The presence of insemination, where

Fig. 7. *Kolpotocheirodon theloura,* new species, paratype, MCP 11161, c&s male, SL 25.9 mm. Right maxilla and premaxilla and teeth, internal view.

sperm are introduced into the ovary (noted above), is so far found in the species of the Glandulocaudinae (Burns et al. 1995), in the species of the tribe Compsurini of the Cheirodontinae (Burns et al. 1997; Malabarba, Weitzman, & Burns *in* Malabarba 1998), and species of uncertain relationships including *Monotocheirodon pearsoni* Eigenmann *in* Pearson (1924), *Brittanichthys axelrodi* Géry (1965), "*Cheirodon*" *ortegai* Vari & Géry (1980) and "*Bryconamericus*" *pectinatus* Vari & Siebert (1990), (Weitzman & Malabarba 1998, Burns et al. 1999). The absence of cheirodontine synapomorphies among the taxa just listed above and the hypothesis that the Compsurini is a derived branch arising from externally fertilizing cheirodontines (see cladogram, fig. 1 of Malabarba 1998) suggests a hypothesis that insemination in the compsurin cheirodontines arose from externally fertilizing ancestral cheirodontine stock, and that it probably arose independently of the Glandulocaudinae and of the other taxa listed above. At least all cheirodontines, including the compsurins, lack the following synapomorphy of the glandulocaudines used in part to diagnose that subfamily by Weitzman & Menezes (1998): presence of a sperm storage area in the tes-

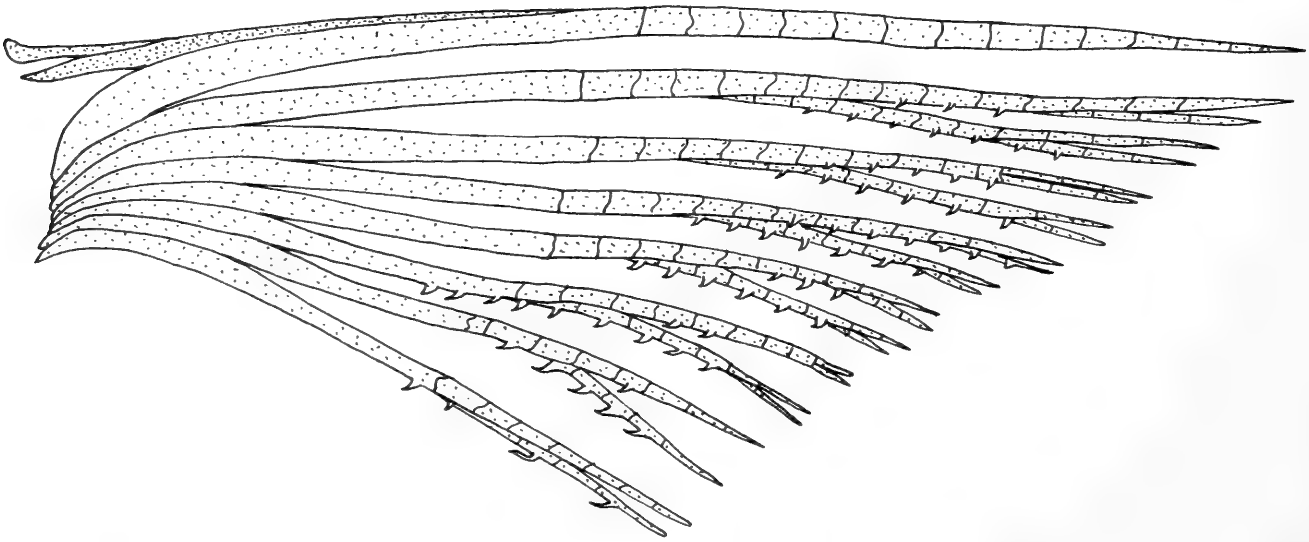

Fig. 8. *Kolpotocheirodon theloura,* new species, paratype, MCP 11161, c&s male, SL 25.9 mm. Figure illustrates the pelvic-fin rays and hooks in the left pelvic fin, anterior to left. Ventral view.

tes. Although rather tentative because not all glandulocaudine taxa have yet been sampled, the presence of an elongate cytoplasmic collar binding the flagellum to the nucleus at some stage of spermiogenesis or in mature sperm cells in glandulocaudines (see Burns et al. 1998) is absent in at least one compsurin species, *Macropsobrycon uruguayanae.*

The presence of elongate sperm nuclei was independently pointed out by Weitzman & Menezes (1998) as a synapomorphy for the Glandulocaudinae, and by Malabarba et al. *in* Malabarba (1998) as a synapomorphy for a subclade of the Compsurini (excluding *K. theloura*). This requires some explanation. Sperm with spherical or slightly oval nuclei are often referred to as "aquasperm" and considered to be the plesiomorphic sperm type for teleosts (Jamieson 1991). Elongation of sperm nuclei is a derived feature and seems to be related to, but not necessarily needed for, sperm transfer to and storage within ovaries (Jamieson 1987). Such a modification is found in the two inseminating characiform groups listed above and in several inseminating or internally fertilizing teleosts. Although the sperm cells in these groups have undergone changes in shape resulting in sperm cells different from the spherical or slightly oval nuclei of "aquasperm," these changes are not necessarily homologous. Although we still lack information on the ultrastructural morphology of the sperm cells of most compsurins and several glandulocaudines, the evidence so far noted in Burns et al. (1998) indicates the elongated sperm cells are derived in different ways in the compsurin *Macropsobrycon uruguayanae* and in the glandulocaudines *Diapoma speculiferum* Cope (1894), *Diapoma* sp., *Corynopoma riisei* Gill (1858), *Pseudocorynopoma doriae* Perugia (1891), *Mimagoniates barberi* Regan (1907), and *M. microlepis* (Steindachner, 1876). Thus, elongation of the sperm nuclei in glandulocaudines and elongation of the sperm nuclei in at least part of the compsurins appear to have been acquired in different ways and are non-homologous, and thus likely constitute different synapomorphies for each clade. However, much of the ultrastructural evidence from sperm cell morphology in the species of both clades remains to be discovered and described.

The anal-fin hook arrangement of the Compsurini, including *Kolpotocheirodon theloura,* is also hypothesized to constitute a synapomorphy. Compsurin cheirodontines, except for *Acinocheirodon melanogramma,* have hooks inserted along the posterolateral border of the anal-fin rays and bent anteriorly over the lateral surface of the anal-fin ray where each is attached (Fig. 6). Thus, instead of pointing posteriorly and dorsally as in most characids, the distal tip of the anal-fin hooks are directed anteriorly. Non-compsurin cheirodontines have retrorse hooks positioned along the posterolateral border of the anal-fin rays, and directed posteriorly and towards the anal-fin base. Some glandulocaudines such as the xenurobryconins have the anal-fin hooks recurved and pointing dorsoanteriorly, but in most cases these differ in shape from those of the compsurins, do not bend anteriorly over the lateral surface of the anal-fin ray, and do not pass across the point where it is attached (see Weitzman & Fink 1985:figs. 38–43; Weitzman et al. 1994:fig. 11; and Weitzman & Ortega, 1995:fig. 4). Among xenurobryconins, *Argopleura chocoensis* Eigenmann has modified large anal-fin hooks, anterodorsally and laterally directed, on rays 6–7 to 12–14, resembling those of the compsurins (see Weitzman & Fink 1985:fig. 38). However, these hooks in *A. chocoensis* are part of a complex pattern of hook development (see Weitzman & Fink 1985:29, apomorphy 7) absent in compsurin species. In any case, parsimony analysis also indicates that the condition in the Xenurobryconini and the Compsurini are non-homologous.

The presence of hooks on the dorsal surface of some of the caudal-fin rays (character 7) is also found among inseminating glandulocaudines (see Menezes & Weitzman 1990:fig. 5, *Mimagoniates microlepis* and fig. 24, *Mimagoniates rheocharis* Menezes & Weitzman (1990); Weitzman & Fink 1985:fig. 11, *Xenurobrycon macropus* Myers & Miranda-Ribeiro (1945), fig. 12, *Xenurobrycon heterodon* Weitzman & Fink (1985), fig. 16, *Corynopoma riisei,* fig. 17, *Gephyrocharax atricaudatus* (Meek & Hildebrand 1912), fig. 19, *Mimagoniates microlepis*; Weitzman et al., 1994:fig. 5, *Ptychocharax rhyacophila* Weitzman et al. (1994), in the incertae sedis species *Brittanichthys axelrodi* (see Malabarba & Weitzman 1999:figs. 9–10) and "*Cheirodon*" *ortegai.* The possible homology of the caudal fin modifications of the inseminating compsurin cheirodontine *Acinocheirodon melanogramma* with two *Mimagoniates* Regan (1907) species and with *B. axelrodi* were extensively discussed in Malabarba & Weitzman (1999) and rejected. Homology of the caudal-fin hooks in *K. theloura* with all non-compsurin taxa listed above is also rejected because these inseminating characids lack the synapomorphies diagnosing the Cheirodontinae.

The putative caudal gland of *Kolpotocheirodon theloura* does not have gross similarities to those of the inseminating glandulocaudines, except possibly *Landonia latidens* Eigenmann & Henn *in* Eigenmann et al. (1914) of the tribe Landonini that also has folds of tissue in the caudal-fin region. Although a detailed comparison of the histological nature of these species needs to be done, it is very unlikely the folds in the Compsurini and Landonini are homologous in a parsimony analysis. The caudal organ of *K. theloura* also does not resemble those found in *Compsura* and *Saccoderma.* Species of these genera have derived scales associated with their caudal organs. Instead the caudal organ of *K. theloura* is formed by derived dermal flaps found along the proximal length of the thirteenth or fourteenth to nineteenth caudal-fin rays. Although not sharing a tabular or papillose margin, the caudal glands of other inseminating compsurins are also partially formed by derived hypertrophied dermal flaps along the ventral lobe caudal-fin rays, as described by Malabarba & Weitzman (1999) along the thirteenth through fifteenth caudal-fin rays of *Acinocheirodon melanogramma,* and fifteenth or sixteenth to nineteenth caudal-fin rays in the *Saccoderma* species and *Compsura heterura* Eigenmann. The caudal glands of compsurin species, although formed in different ways, are always derived from modified dermal flaps along the ventral lobe caudal-fin rays. This seems to reinforce the monophyly of the group and the hypothesized homology or common origin of insemination among compsurin cheirodontines.

Males of *Kolpotocheirodon theloura* have modified twelfth to the fourteenth or fifteenth principal caudal-fin rays. These rays bear 4–6 retrorse hooks on each side in a row along their dorsal divisions (Fig. 4). Among the Compsurini, Malabarba & Weitzman (1999) listed and described the presence of hooks in *Acinocheirodon melanogramma* (caudal-fin rays 13–14, rarely on ray 15), *Saccoderma hastata* Eigenmann (1915) (caudal-fin rays 13–18), "*Odontostilbe*" *dialeptura* (caudal-fin rays 12–16), and in *Macropsobrycon uruguayanae* (caudal-fin rays 12–14, plus several spinelets along the proximal half of the caudal-fin rays 14 to 18). Although these hooks are present on the ventral lobe of the caudal fin in all these species, we noted (Malabarba & Weitzman 1999) that they do not all occur on the same caudal-fin rays in all species and are of different shapes. Additionally, not all compsurin species have caudal-fin hooks, as for example *Compsura heterura, Compsura gorgonae* Evermann & Goldsborough and "*Odontostilbe*" *mitoptera.* We also pointed out that the use of the presence of caudal-fin hooks in diagnosing a clade among the Compsurini species would be parsimoniously incongruent with other derived characters, as for example the presence of derived pouch scales in the ventral lobe of the caudal fin, found in some hook-bearing *Saccoderma* species and some non-hook-bearing species such as *Compsura heterura* and *C. gorgonae.* A parsimony analysis of character distribution indicates the presence of hooks as a synapomorphy for the compsurin cheirodontines, and its lack a secondary reversal in some of its species (Malabarba et al. *in* Malabarba 1998).

Kolpotocheirodon theloura was placed as the most basal species among the Compsurini, in the phylogeny proposed by Malabarba et al. (*in* Malabarba 1998). Among the characters that placed the new species as the most basal compsurin is the presence of aquasperm (see Burns et al. 1997:434, fig. 1A), as found in externally fertilizing cheirodontines. In other words, the presence of derived elongate sperm nuclei (see Burns et al. 1997:434, table I) in the remaining inseminating compsurins represents a synapomorphy for these derived fishes.

Another character that seems to corroborate a basal position for *Kolpotocheirodon theloura* is the lack of enlarged caudal-pouch scales as a possible pumping mechanism in the ventral lobe of the caudal fin associated with a caudal gland (see Weitzman & Fink 1985:96–99; Malabarba & Weitzman 1999). *Compsura heterura, C. gorgonae,* and *Saccoderma* species have the posterior ultimate scale of the scale row immediately ventral to the lateral-line scale row enlarged, connected dorsally to ligaments arising from the twelfth and thirteenth principal caudal-fin rays, and ventrally to a skin flap connected to the nineteenth principal caudal-fin ray, forming a pouch with a posterior opening that may serve as a pumping mechanism. *Acinocheirodon melanogramma* does not have any pumping mechanism involving caudal-fin scales. Instead it has two large skin flaps between the thirteenth and fifteenth principal caudal-fin rays (Malabarba & Weitzman 1999:fig. 6), that occur just ventral to and surrounding the hypertrophied soft tissue found around the hooks of the thirteenth and fourteenth fin rays. Malabarba & Weitzman (1999) suggested that these flaps might also be part of a mechanism for increasing the rate of pheromone dissemination in the surrounding water during courtship. We found no putative active pumping mechanism in *Kolpotocheirodon theloura* that might be related to an increase in pheromone dissemination in water during courtship. The papillose margins of the dermal flaps of *K. theloura* seem to be a passive strategy for increasing pheromone dissemination.

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Calls and calling behavior of the frog *Leptodactylus natalensis* (Amphibia: Anura: Leptodactylidae)

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Abstract.—*Leptodactylus natalensis* has a prolonged calling season, typically from May to September. Individuals occur in and call from the most forested patch of habitat on the campus of the Universidade Federal de Sergipe. Two kinds of calls were recorded and analyzed—advertisement and chirp calls. The function of the chirp call is unknown. The advertisement call has two carrier frequency bands, known to date for only two other species of *Leptodactylus*. The two carrier bands may correspond to different frequency tuning sensitivities in males and females, as females have slightly larger tympani than males, corresponding with their larger overall size.

Published natural history information for the frog *Leptodactylus natalensis* Lutz, 1930, consists of comments on calling and microhabitat made by Lutz (1930) in his original description of the species and a recent study of some reproductive aspects, including the first description of the tadpole for the species (Oliveira & Lírio Júnior 1999). Calls of *Leptodactylus natalensis* have not been analyzed previously (Heyer 1994). One of us (CMC) had the opportunity to observe calling behavior and recorded the calls of *L. natalensis.* The purpose of this paper is to report these observations and describe the calls.

Methods and Materials

Observational data and recordings of *Leptodactylus natalensis* were made by CMC on the campus of the Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil. Incidental information on calls at Santo Amaro das Brotas, Sergipe, was also obtained by CMC.

Recordings were made from two individuals. Five recordings (USNM tape 323, cut 1) were made from specimen MZUSP 89945 (MZUSP = Museu de Zoologia, Universidade de São Paulo collection), SVL (snout–vent length) 33.9 mm, on 22 June 1998, at an air temperature of 25°C, water temperature 24°C, the last recording completed at 1955 h. One recording (USNM tape 323, cut 2) was made from specimen MZUSP 89947, SVL 32.4 mm, also on 22 June 1998, air 25°C, water 24°C, the recording completed at 2030 h. It was not raining when these recordings were made, but a brief heavy rain occurred at 2100 h.

Calls were recorded with a Sony TM-5000 cassette recorder with a M 44 N(C) Beyer Dynamic Soundstar II microphone.

Terminology follows that of Heyer et al. (1990), with the following clarifications. Carrier frequency is the frequency broadcast by the calling frog to the environment. Often, the carrier frequency embraces a range of frequencies loud enough to be heard by the intended receiver (male or female). The dominant frequency as used here is the single frequency value (or very narrow range of frequencies) that has the most sound energy in the call.

Recordings were analyzed using "Canary 2.1" software (Charif et al. 1995). Call rates and durations were measured from wave form displays, beginning and ending carrier frequencies from audiospectrogram displays, and dominant frequencies from spectral displays. Although the initiation of calls is clear on the wave form displays, the ends of the calls are not very distinct, perhaps due to the level of background noise and possible microphone ringing.

Advertisement call rates were based on six calling sequences ranging from 7.8 to 15.2 sec from each of six recordings. Frequency data were taken from 10 consecutive calls from each of the six recordings; call duration and pulse data were taken on the same 10 calls for recordings 2 and 5 of MZUSP 89945 and for MZUSP 89947.

Chirp call data are from the six chirps loud enough to analyze in the second recording of MZUSP 89945.

Behavior and Calling Site

Leptodactylus natalensis has a prolonged calling season coinciding with the rainy season, typically from May to September (also see Oliveira & Lírio Junior 1999). Calling starts around 1600 h. Calling activity is most intense around 1900 and continues until 2300 or 2400 h. However, on rainy days, especially at the beginning of the rainy season, males can be heard calling at 0800 h, and continuing throughout the day and night. Males do not call during hot and sunny days during the rainy season.

The general site the frogs occupy on the campus is a small patch (100 × 400 m) of second growth (capoeira) on the right bank of the Rio Poxim, a seasonally partially flooded area (varzea) with many ponds. The site has 5–6 m high trees, many young palm trees, a thick grass ground cover, shallow litter, and white sand. The *Leptodactylus natalensis* were only heard calling from the capoeira—never from the left bank of the Rio Poxim, which has more artificial open areas and patches of mangrove swamps.

MZUSP 89945 was calling very close to the foot of a young palm tree surrounded by a pond with leaves in the water. The frog sat in the water, half submerged. A second male (MZUSP 89946) was about a half meter from the calling male. This second male was in a small burrow, with half the body exposed and uttered some "clicks" but no other calls. The "clicks" did not record adequately enough to analyze.

MZUSP 89947 was near the foot of a small tree, at the edge of a little channel of rain water, hidden in grass.

Leptodactylus natalensis infrequently jump when disturbed. Usually they take two or three steps backward and quietly hide under a leaf or other ground cover.

Advertisement Call

Calls (Fig. 1) consist of single notes given frequently when actively calling. Call rates vary from 3.4–4.1 per sec for MZUSP 89945 and at a rate of 3.0 per sec for MZUSP 89947. The call sequence with the least background noise is the fifth recording sequence for MZUSP 89945. In that sequence, each call (=a single note) has a duration of 0.06–0.07 (mode = 0.07) sec and consists of 5–7 pulses, modally 7. The call is partially pulsed (=incompletely amplitude modulated). In two other recordings with greater background noise, it appears that the terminal pulses are indistinguishable from the background noise in the wave forms. Three to five partial pulses (mode = 4) can be distinguished in calls from the second recording of MZUSP 89945, with an average duration of 0.04 sec. Two to three partial pulses (mode = 3) are distinguishable in the recording from MZUSP 89947, with an average duration of 0.02 sec. The calls are frequency modulated with extremely fast rise times (difficult to see because of time scale in Fig. 1, more visible in the two advertisement calls shown in Fig. 3). Beginning frequencies of the carrier (=fundamental) frequency range from averages of 550–600 Hz with the highest frequencies ranging from averages of 1370–

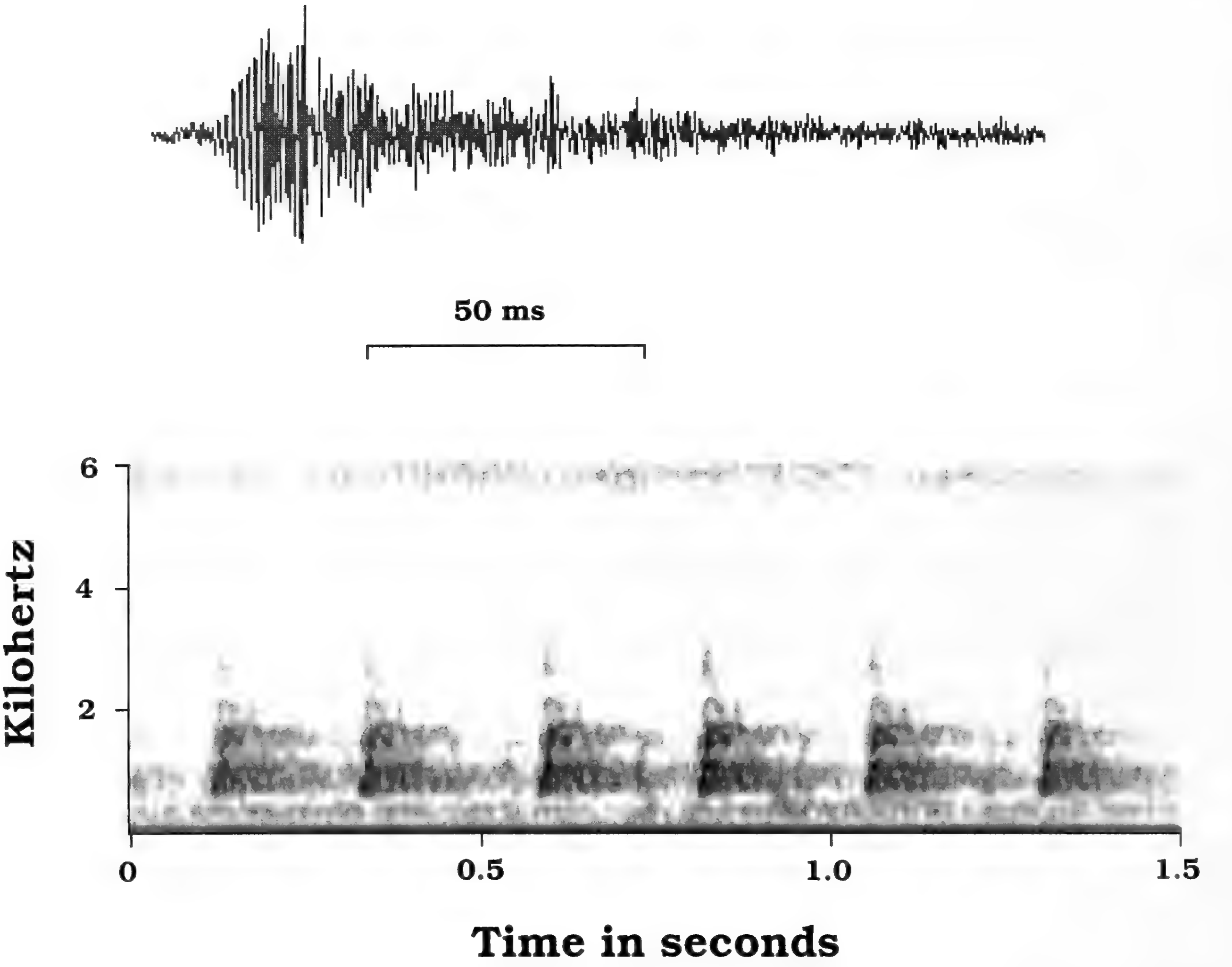

Fig. 1. Wave form (above) and audiospectrogram (below) of the advertisement call of *Leptodactylus natalensis,* USNM tape 323, cut 1, fifth recording. The wave form is of the first call shown in the audiospectrogram.

1830 Hz for MZUSP 89945. The average beginning dominant frequency for MZUSP 89947 is 650 Hz, with an average maximum of 1600 Hz. The dominant frequencies most often occur in two peaks in the calls of MZUSP 89945. For this frog, the first recording series usually has a dominant frequency of 760 Hz, with either a co-dominant or quieter frequency at 1050 Hz; the second recording has the dominant frequency at 770 Hz, with a secondary dominant at 1020 Hz; the third recording has the dominant frequency at 760 Hz, with a secondary dominant at 1040 Hz; the fourth recording has the most variation with either 780 and 1030 Hz being primary or secondary in loudness, 860 and 1030 Hz being primary or secondary in loudness, 1030 Hz loudest with a secondary dominant at 880 Hz, or a single dominant frequency at 1030 Hz; calls in the fifth recording have the dominant frequency at 1030–1040 Hz, with a secondary dominant at 760–770 Hz (Fig. 2). The calls of MZUSP 89947 have either a dominant frequency at 1030 Hz, or also with a secondary dominant at 875 Hz. The partial pulsing of the calls appears to be the cause of the sidebands weakly visible in the audiospectrograms (Fig. 1). Calls of MZUSP 89945 range from having no visible harmonics, a weak second harmonic, or intermediate strength second and third harmonics (Fig. 2). The calls of MZUSP 89947 have a weak second harmonic.

Chirp Call

Calls (Fig. 3) consist of either 1 or 2 notes. The loudest chirp calls are louder than the advertisement calls. In the two note

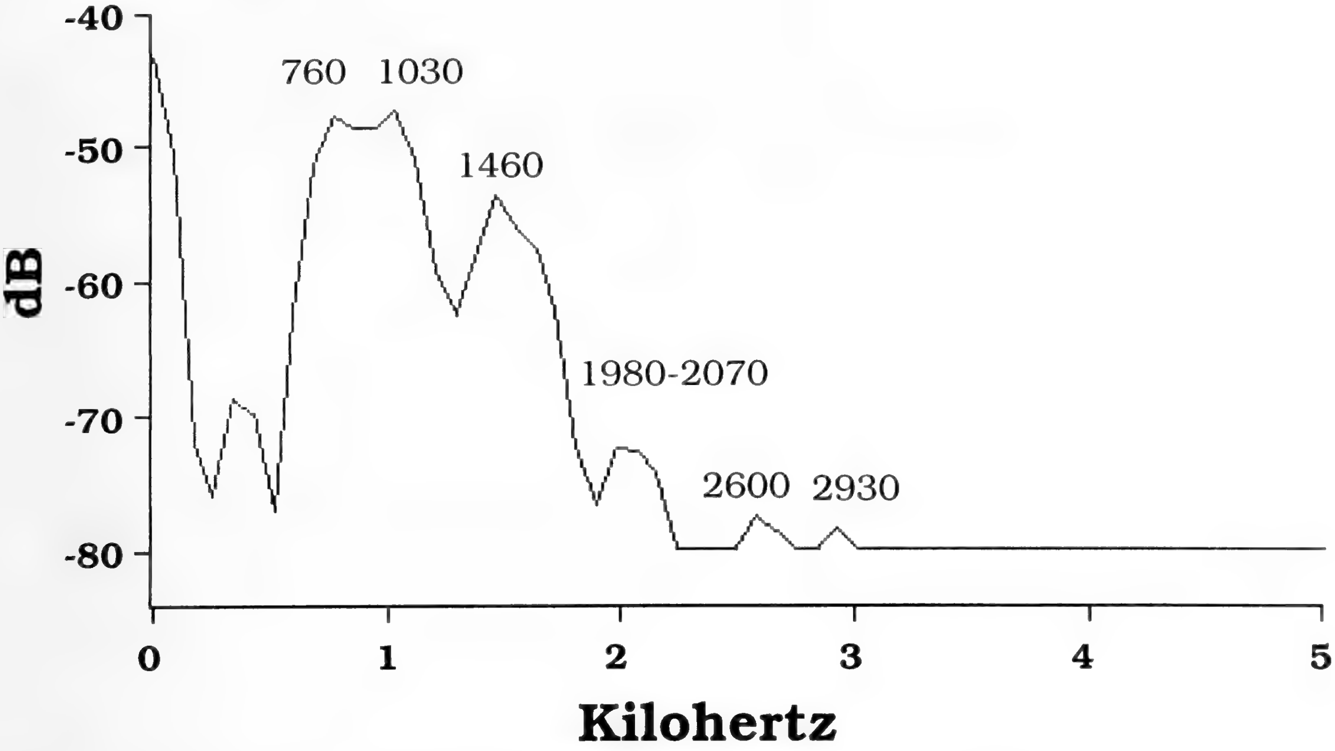

Fig. 2. Power spectrum of advertisement call of *Leptodactylus natalensis*, USNM recording 323, cut 1 (of second call in audiospectrogram of Fig. 1).

calls, the first note is shorter than the second (0.04 and 0.13 with an internote interval of 0.10 sec; 0.05 and 0.08 with an internote interval of 0.16 sec; 0.04 and 0.13 with an internote interval of 0.14 sec). The three single note chirp calls recorded range from 0.10–0.14 sec duration. From 3–10 partial pulses can be discerned in the wave forms. The calls are frequency modulated, at a noticeably slower rise time than the advertisement calls. The lowest carrier (=fundamental) frequency ranges from 530–650 Hz; the highest carrier frequency ranges from 990–1200 Hz. There is a suggestion of the carrier frequency briefly falling at the end of some calls, back to around 900–950 Hz. The dominant frequencies vary from 690–860 Hz. There are weak to strong second, second and third, or second, third, and fourth harmonics.

Discussion

The function of the chirp calls is unknown. Other members of the *L. melanonotus* group have these calls as well, which usually initiate calling bouts. In the case of the *L. natalensis* recording, the chirp calls were uttered after there was a slowing down in the rate of advertisement calls. The chirp calls are much more variable than the advertisement calls.

Many species of *Leptodactylus* have frequency modulated calls that result in broadcasting their calls over a range of frequencies. Most of these calls have a single (or narrow range) dominant frequency, however. *Leptodactylus natalensis* is unusual in that there are two peaks of loudness. Only *L. melanonotus* and *podicipinus* within the *L. melanonotus* group share this condition (of those for which the calls are known, Table 1). We hypothesize that these separate dominant frequencies correspond to different tuning curves in males and females, as demonstrated in *Eleutherodactylus coqui* (Narins & Capranica, 1976), although no experimental data are available for *L. natalensis*. Morphological data do not contradict this hypothesis. Other things being equal, a larger tympanum will be more sensitive to lower frequencies than a smaller tympanum and vice versa. Morphological

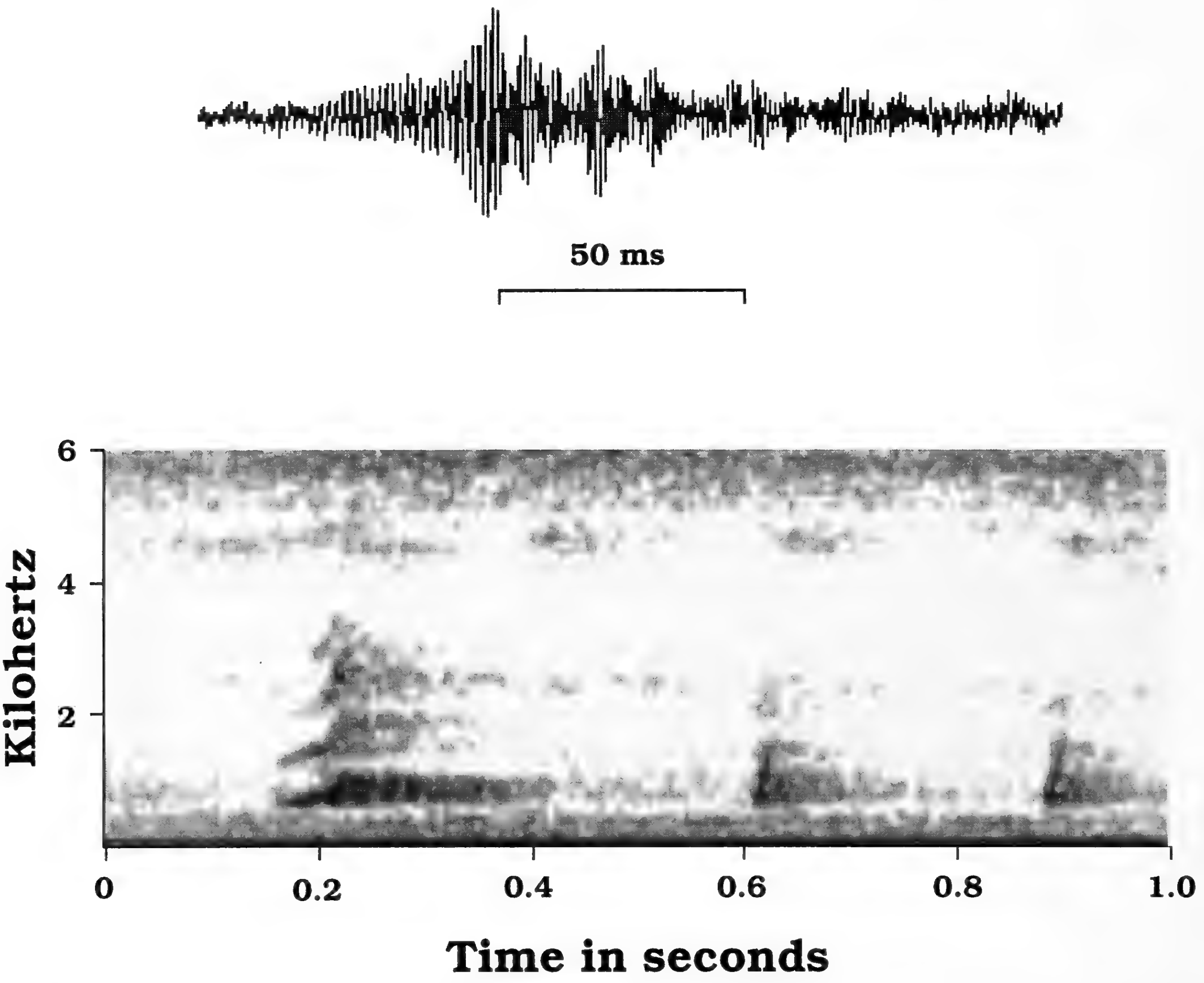

Fig. 3. Wave form (above) and audiospectrogram (below) of the chirp call of *Leptodactylus natalensis,* USNM tape 323, cut 1. In the audiospectrogram, a single-note chirp call is followed by two advertisement calls.

data are available from two localities represented by several males and females. The data indicate that the tympanum size does differ between males and females (Table 2). It would seem from the variability of calls in the fourth recording of MZUSP 89945 that an individual frog has control over whether more energy is broadcast in the lower or higher dominant frequency.

Sexual difference in tympanum size is the expected condition in most frogs, as most frog species are sexually dimorphic, with the females being larger. Broadcasting of higher and lower dominant frequencies, as seen in *L. natalensis,* is one solution to matching different receptor sensitivities to the advertisement call. The frequency modulation observed in other *Leptodactylus* species, such as *L. fuscus,* is another solution.

Our observations apparently conflict with those of Adolfo Lutz regarding the call of *L. natalensis.* In the original description of the species, Lutz observed (1930:27, English version of text): "This frog has a call with the strength of a whistle but sounding more like the voice of a cricket. It seems to have also another sound, heard during copulation, like a soft clucking, sometimes repeated by other males, so as to form a general concert. The specimens were caught near to the water but generally well hidden." CMC has not heard cricket-like calls from *L. natalensis* at either the campus at São Cristóvão or Santo Amaro das Brotas,

Table 1.—Advertisement call characteristics of members of the *Leptodactylus melanonotus* species group. Data taken from Heyer (1994), Heyer et al. (1996), and for *L. melanonotus*, from USNM tape 83, cut 1. Note that *Leptodactylus diedrus* is no longer considered a member of the *L. melanonotus* species group (Heyer, 1998). The duration and pulse data for *L. natalensis* are from the recording with the least background noise.

Species	Call duration in sec	Number partial pulses per call	Carrier frequency range	Dominant frequency range
L. griseigularis	0.01	1	1380–3060	2770
L. leptodactyloides	0.02–0.04	1 or 3–5	650–1600	1100–1300
L. melanonotus	0.07–0.08	4–6	820–2620	1320–1380 or 2330
L. natalensis	0.06–0.07	5–7	550–1830	760–880 or 1020–1040
L. nesiotus	0.03	4–5	1500–2000	1800–2000
L. pallidirostris	0.03–0.05	1 or 2–5	1500–3500	3000–3500
L. petersii A	0.04–0.05	3–4	700–1200	750–800
L. petersii B	0.03–0.05	1 or 2–4	800–1600 or 1800–2800	N.A.
L. podicipinus	0.02–0.04	3–7	1000–3500	1000–1200 or 3300–3500
L. sabanensis	0.04–0.06	very weak	900–2300	1400–1800
L. silvanimbus	0.15	about 20	420–1920	510
L. validus	0.03–0.06	1 or 2–6	1300–3500	2300–3500

but the call we describe as the advertisement call is a soft clucking call.

Advertisement calls in the *L. melanonotus* group are often not as species-specific as in other *Leptodactylus,* perhaps because the calls have a strong point-location orientation function overriding (or in addition to) a species-coding function (Table 1 and Heyer 1994:106–107). *Leptodactylus natalensis* has a disjunct geographic distribution relative to all other members of the *L. melanonotus* group. The species group member that most closely approaches the distribution of *L. natalensis* is *L. podicipinus* (compare Figs. 39 and 43 in Heyer 1994). Interestingly, as pointed out above, *L. podicipinus* is only one of two other known members of the *L. melanonotus* group beside *L. natalensis* to have two distinct loudest broadcast peaks in the dominant frequency band.

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Table 2.—Snout-vent length and tympanum diameter measurements for male and female *Leptodactylus natalensis* from two localities in the State of Sergipe, Brazil.

Locality	*n*	Sex	Snout–vent length			Tympanum diameter		
			Min.	Max.	Mean	Min.	Max.	Mean
Areia Branca	8	♂	28.7	36.5	33.1	2.2	3.2	2.8
Areia Branca	9	♀	33.9	42.6	38.8	2.7	3.4	3.0
Santo Amaro das Brotas	7	♂	30.6	34.6	32.5	2.4	2.7	2.6
Santo Amaro das Brotas	14	♀	33.1	37.0	35.1	2.5	2.9	2.7

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A new species of venomous coral snake (Serpentes: Elapidae) from high desert in Puebla, Mexico

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Abstract.—A new species of coral snake (*Micrurus pachecogili*) is described from southern Puebla, Mexico. Black body rings in this snake are monadal and the species is allopatric from all other coral snakes except perhaps *M. laticollaris,* a species in which black body rings are in triads. The new species is characterized by distinctive, well developed yellow rings, relatively short red rings, and a relatively large number of ventral scutes in comparison with *M. nebularis.*

Resumen.—Se describe una nueva especie de serpiente coral (*Micrurus pachecogili*) del sur de Puebla, México. En esta serpiente, los anillos corporales negros son monodales; la nueva especie es alopátrica de otras serpientes de coral, tal vez con excepción de *Micrurus laticollaris,* una especie en la que los anillos negros se disponen en triadas. La nueva especie se caracteriza por poseer anillos amarillos bien desarrollados, anillos rojos relativamente cortos y un número grande de escamas ventrales en comparación con *M. nebularis.*

Species of coral snakes are widespread, if not always conspicuous, components of New World herpetofaunal assemblages. They occur throughout most of the Neotropics and reach into both temperate North and South America. These snakes are often associated with mesic conditions and the majority of species occur in rainforest or cloudforest habitats. Coral snakes appear to be delicate and desiccate quickly when exposed to direct sunlight. Thus, most species are nocturnal or are active only during early morning or later afternoon, especially on rainy nights or overcast days. However, a fair number of coral snakes have become adapted to subhumid habitats, occurring in desert, thorn scrub, or tropical deciduous forest from the Sonoran Desert of the southwestern U.S.A. southward on the Pacific coast of Mexico and Central America and in various regions in South America. In Pacific Mexico, tropical deciduous forest is inhabited by *Micurus browni, M. distans, M. ephippifer, M. bogerti, M. laticollaris, M. proximans,* and *Micruroides euryxanthus,* with the latter species also extending into the Sonoran Desert (Campbell & Lamar 1989).

The arid lands of southern Puebla are situated in the northern part of the Mesa del Sur physiographic region and are just south of the Mesa Central (West 1964, fig. 3). Heretofore, this area was reported to harbor only a single species of coral snake, *M. laticollaris* (Campbell & Lamar 1989, Roze 1996), easily distinguishable from other Mexican coral snakes in being one of two species with black body rings in triads (the other triadal species being *M. elegans* of mesic forests on the eastern versant). Some years ago, I traversed on multiple occasions the countryside surrounding Zapotitlán Salinas in southern Puebla, during which time I assembled small collections of amphibians and reptiles. Among the material in these collections are two specimens of a species of coral snake that cannot be associated with any species known from Mexico.

Materials and Methods

Descriptions of characters and terminology of scales in the diagnosis and description of this new taxon follow Campbell & Lamar (1989) and Roze (1996). The sex of individuals was confirmed by checking for the presence of hemipenes by making a small midventral incision on the proximal section of the tail. Head measurements were taken to the nearest 0.1 mm using digital calipers held under a dissecting scope and the snout–vent and total length was taken to the nearest 1.0 mm using a meter stick.

Micrurus pachecogili, new species (Figs. 1–3)

Holotype.—An adult male (Figs. 1–2), UTA R-12546 (original number JAC 9752), from 5.6 km SSW Zapotitlán Salinas, 1494 m, Puebla, Mexico, collected in November 1983 by one of the children of E. Pacheco-Gil. This locality is in high tropical arid forest at 18°18′N, 97°31′W (Fig. 3).

Paratype.—A subadult male, UTA R-17145, from the type-locality, collected in December 1985.

Diagnosis.—*Micrurus pachecogili* differs most notably from other species of *Micurus* in central Mexico in being tricolored and having black body rings in monads (i.e., a body pattern of red-yellow-black-yellow-red), in having 220–223 ventrals in males, in possessing a wide pale parietal ring that includes all of the parietals and portions of adjacent scales, and in having non-melanized red body rings that are about equal to or shorter than black body rings. Indeed, these four characters, in combination, distinguish *M. pachecogili* from all other venomous Mexican coral snakes.

Micrurus bernadi differs in having mostly red and black body rings, although a yellow parietal ring and, rarely, narrow yellow edging may be present along black markings, black rings are usually reduced to dorsal spots or saddlelike bands, and males have 198–212 ventrals. *Micrurus browni* differs in having a black nuchal ring that covers the posterior portion of the parietals and adult males have supracloacal keels. In *M. b. browni* of Guerrero and Oaxaca, the subspecies that is geographically most proximate to Zapotitlán, males have 204–218 ventrals, the black head cap extends to the anterior part of the parietals and frontal, and the black nuchal ring covers the ultimate and penultimate supralabials (versus only the posterior edge of the ultimate supralabial). *Micrurus diastema* differs in that the red rings are either very long (>5 times wider than the black rings) or contain scales that are distinctly black-tipped, the black head cap includes the anterior portion of the parietals and/or the black nuchal ring includes the posterior portion of the parietals. *Micrurus distans* of western Mexico differs in having no more than 17 black body rings, males have ≤217 ventrals, and red body rings are usually at least three times longer than black rings. *Micrurus ephippifer* differs in having a black nuchal ring that covers the parietal tips, red rings have black-tipped scales, spots, or large saddlelike bands, and ≤219 ventrals in males. *Micrurus laticollaris* has black body rings arranged in triads (i.e., body pattern of red-black-yellow-black-yellow-black-red), has 1 + 2 temporals, and males possess ≤215 ventrals. *Micrurus limbatus* is bicolored with red and black rings and ≤192 ventrals. Overall, the color pattern of *M. pachecogili* is most similar to that of *M. nebularis*: similarities include red and black rings of relatively equal length, scales in red rings not black-tipped or distinctly spotted, well developed yellow body rings (1.0–1.5 dorsal scale lengths long in *M. nebularis* versus 2.0 in *M. pachecogili*), and tail with subequal black and yellow rings. *Micururus nebularis* differs by having a black nuchal ring that covers the posterior ends of the parietals, 203–208 ventrals in males, and seven black tail bands.

Description of holotype.—A single prenasal and postnasal on each side; nostril situated mostly in posterior part of prenasal; an elongate preocular on each side contacting postnasal; no loreal; anterior scales on head and snout, including mental and infralabials, with numerous tiny tubercles; postoculars 2/2; temporals 1 + 1 + 2; upper tertiary temporal large, about half size of parietal; supralabials 7/7; infralabials 7/7 (Fig. 1); ventrals 223; cloacal scute divided; subcaudals 47, all divided except proximal subcaudals 2–7; dorsal scale rows smooth, in 15 unreduced rows; no supracloacal keels.

Dimensions are as follows: head length 15.0 mm, head width 10.9 mm, total length 639, tail length 87 mm (comprising 13.6% of total).

The black head cap covers the rostral, first three supralabials, the upper and anterior edge of Supralabial 4, the anterior edge of the upper preocular, slightly more than three-fourths of the supraoculars, and about half of the frontal; there is no pale spot on snout. The yellow parietal ring extends from the black head cap to include all of the parietals, the primary and secondary temporals, and anterior part of the tertiary temporals, and all of the ultimate supralabial except for the posterior edge (Fig. 1). About half or slightly more of the lingual portion of the mental and the first three pairs of infralabials are black; the posterior gular area is immaculate yellow and continuous with the yellow parietal ring. The black nuchal ring does not reach the posterior tips of the parietals and involves less than half of the first dorsal scale situated partially between the parietals. The nuchal ring extends posteriorly along the middorsum ~1/2 + 5 + 1/2 dorsal scales; it is shortened ventrally to cover most of the first two ventrals and adjacent 1.5 preventrals. There are 24 black body rings, including the nuchal, with the posteriormost just anterior to the vent. Throughout most of the body black rings are about four dorsal scale lengths long, but the anterior three rings behind the nuchal ring are slightly longer, being about 4.5–5.5 scales in length (Fig. 2). On the belly, most black body rings are reduced to about three ventrals (one ring covers only two ventrals and several cover four), with an additional half ventral (divided along midventral line) associated with many rings. Black body rings tend to have vertical edges or, if shortened on the side of the body, they are reduced by no more than about 0.5 scale lengths. The yellow rings are immaculate and relatively wide throughout the body, being about two dorsal scales long. The cloacal scute is yellow. Most red rings are 3–4 scales in length with a few reduced to as short as one and one-half to two scale lengths on the posterior half of the body. Scales in the red rings are mostly immaculate but with slightly dusky free margins and there are a few irregular, inconspicuous black dots in a few of the red rings. There are five black tail rings that are one and one-half to three times the width of the yellow rings separating them; the tip of the tail is yellow.

Variation.—The paratype (UTA R-17145) is a subadult male, 327 mm in TL, with a tail length of 36, comprising 11.0% of the total. It agrees with the holotype in most respects of scutellation and pattern, but has 220 ventrals, 43 subcaudals (subcaudals 2–3 not divided); a black nuchal ring involving only the first ventral plus adjacent two and one-half preventrals; 27 black body rings, most of which are about four dorsal scales in length throughout the body; red body rings which are two to three dorsal scales in length throughout the body; and 6 black tail rings, exclusive of the black tail tip, which are 1.5–2 times longer than the yellow rings separating them.

Etymology.—The species name is a noun in the genitive case, formed in honor of Emiglio Pacheco Gil, a good friend and longtime resident of the Zapotitlán Valley. He, his wife, and about twelve children (I never knew the total number and am not sure he did either) always were gracious and hospitable hosts during my visits, most willing to share whatever meager provisions they had available. The country around Zapotitlán is harsh and Emiglio supplemented his income by working in the onyx mines which abound in the region. He was killed in a mining accident in 1982.

Remarks.—The morphology of coral

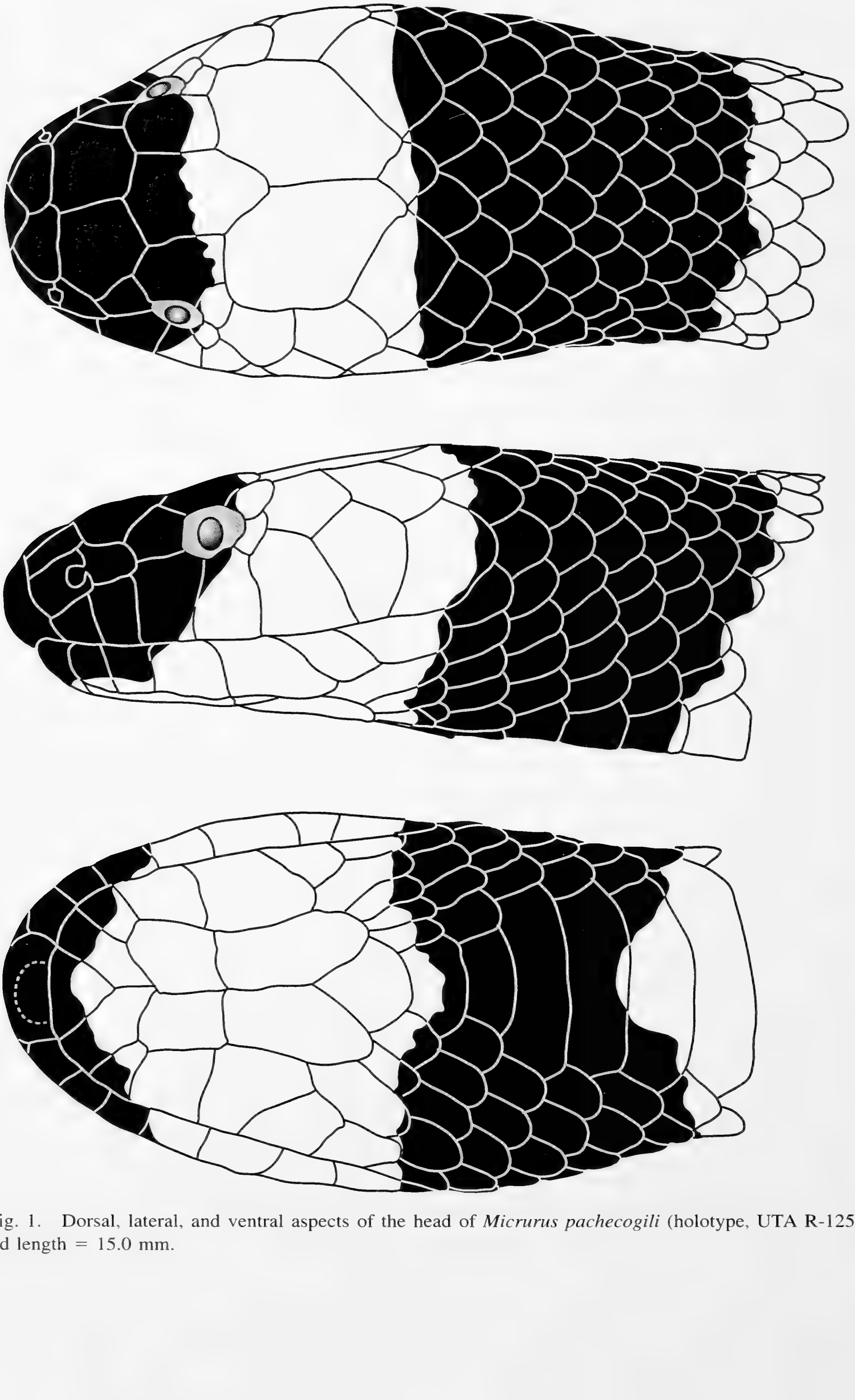

Fig. 1. Dorsal, lateral, and ventral aspects of the head of *Micrurus pachecogili* (holotype, UTA R-12546). Head length = 15.0 mm.

Fig. 2. Dorsal aspect of *Micrurus pachecogili* (holotype, UTA R-12546). Total length = 639 mm.

snakes is extremely conservative (Slowinski 1995) and the numbers and arrangement of most head scales, rows of dorsal scales, and even skull and dentition is remarkably consistent, with minor exceptions, throughout *Micrurus* (Campbell & Lamar 1989, Roze 1996). Perhaps, the most dramatic adaptation within the genus is the conspicuous elongation of the body apparent in certain coral snakes including the genus *Leptomicrurus* and various species of *Micrurus* in Lower Central America and northern South America. Many species of coral snakes are diagnosed primarily on the basis of color pattern and this has proven to be a generally reliable method for distinguishing most species, although a few species are notoriously variable (e.g., *Micrurus diastema*) which has resulted in a tangled taxonomic history for several species.

The habitats of coral snakes also may be useful for species identification, although many species occur over several ecological associations and may have elevational distributions of over 2000 m. Nevertheless it is worth noting that heretofore only a single species of coral snake has been reported from southern Puebla, namely *M. laticollaris,* a distinctive species and one of only two species in Mexico possessing black body rings arranged in triads. *Micrurus laticollaris* occurs on the west coast of Mexico in Jalisco, Colima, and Michoacán and through much of the Balsas Basin and associated tributaries into southern Puebla where it may be sympatric with *M. pachecogili.*

The distributions of a number of other species of *Micrurus,* all with monadal black body rings, approach the Zapotitlán Valley within about 150 km, but are characterized by markedly different habitats. The region around Zapotitlán is dry, being in a rainshadow valley. This region receives about 250–350 mm of precipitation annually, and the valley floor and surrounding slopes are covered by arid scrub forest dominated by many species of cactus. *Micrurus bernadi* occurs in northern Puebla in tropical ever-

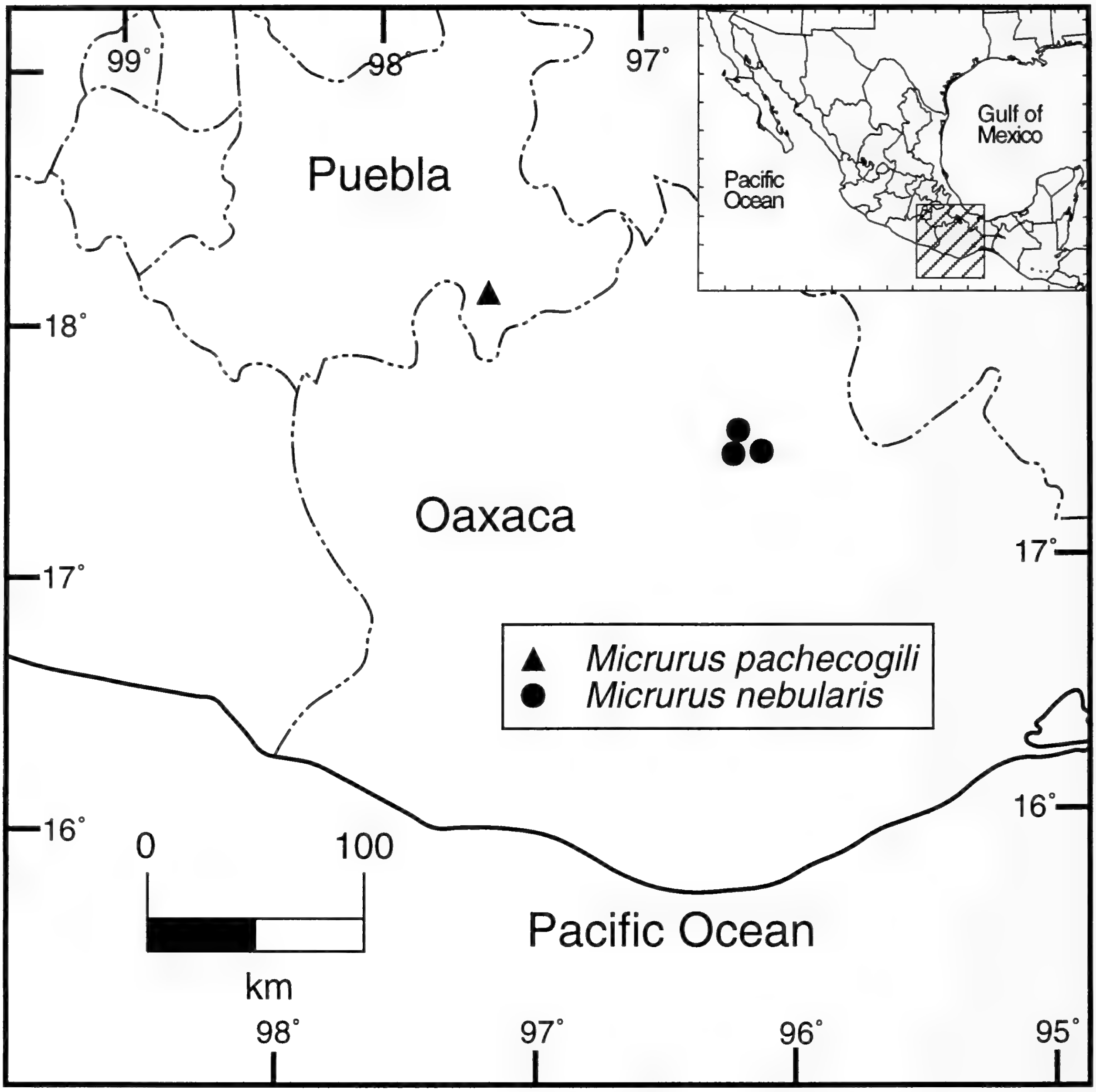

Fig. 3. Distributions of two species of coral snakes, genus *Micrurus*, from the highlands of southern Mexico.

green forest and cloudforest at elevations of 50 to about 2000 m. There is some evidence that this taxon is conspecific with *M. diastema* (Pérez-Higareda & Smith 1990), also known from the eastern versant of Mexico, but this allocation has not been universally accepted (Roze 1996). *Micrurus browni* is known from the subhumid coastal tropical forest, tropical deciduous forest, and dry pine-oak forest of southern Mexico from about sea level to over 2000 m. The extremely variable *M. diastema* inhabits tropical evergreen forest and cloudforest of eastern Puebla and adjacent Veracruz and Oaxaca, as well as in subhumid forests over most of the Yucatán Peninsula. It ranges from near sea level to about 1250 m. *Micrurus ephippifer zapotecus* occurs in highland pine-oak forest of central Oaxaca at elevations of 1700–2400 m; another apparently closely related population, *M. e. ephippifer,* occurs at lower elevations (100–1500 m) in tropical deciduous forest and in the ecotone of this forest with pine-oak forest. *Micrurus nebularis* occurs in pine-oak forest at elevations of 2100–2300 m on the southern slopes of the Sierra de Juárez in central Oaxaca; all known specimens have been collected in the vicinity of Ixtlán de Juárez (Fig. 3).

During the course of my investigations around Zapotitlán, I collected a series of distinctive *Lampropeltis triangulum* which subsequently became the type-series of a new subspecies (Quinn 1983). This snake closely resembles *M. pachecogili,* having relatively long yellow body rings and narrow red rings, thus serving as one more compelling example of mimicry.

Acknowledgments

I thank the Officials from the Dirección General de Flora y Fauna Silvestre for issuing collecting permits for Mexico. Howard Arnott kindly took the photograph in Fig. 2. For help at various times in the field, I appreciate the efforts of Barry Armstrong, William Lamar, and David Hillis.

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Fossil Red-shouldered Hawk in the Bahamas: *Calohierax quadratus* Wetmore synonymized with *Buteo lineatus* (Gmelin)

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Abstract.—A supposedly extinct genus and species of hawk, *Calohierax quadratus* Wetmore, was originally described from a fragmentary tarsometatarsus from Quaternary deposits in Little Exuma Island in the Bahamas. This and a referred tibiotarsus from New Providence, Island, were later assigned to the extant genus *Buteo,* but their specific identity remained uncertain. A previously unstudied humerus from a cave deposit on New Providence Island, Bahamas, is here identified with the extant Red-shouldered Hawk, *Buteo lineatus* Gmelin, a species widespread in eastern North America and common in peninsular Florida but unknown in the Bahamas. The other fossils are assigned to this species as well. *Calohierax quadratus* therefore becomes a synonym of *Buteo lineatus,* which species has retreated from the Bahamas in the late Quaternary for reasons that are unclear.

Among the several new species of birds that were described by Wetmore (1937) from Quaternary cave deposits on Little Exuma Island, Bahamas, was a new genus and species of hawk, *Calohierax quadratus,* based on the distal end of a tarsometatarsus. The site was not on Great Exuma as Wetmore originally reported (see Olson and Pregill 1982:3). Brodkorb (1959) later referred the distal end of a tibiotarsus from a cave deposit on New Providence Island, Bahamas, to the same species. Restudy of these specimens showed that the supposed characters of the genus *Calohierax* were founded entirely on artifacts of wear in the case of the holotype, or intrageneric variation in the case of the referred specimen (Olson & Hilgartner 1982). The specimens were otherwise considered to be too fragmentary for specific identification, falling within the range of size variation of the living Red-shouldered Hawk *Buteo lineatus* (Gmelin) or Gray Hawk *B. nitidus* (Latham).

Under present geographical and climatic conditions, the Red-shouldered Hawk, which occurs through most of eastern North America and is abundant in Florida, would be considered a more likely candidate for having occurred in the Bahamas. The Neotropical Gray Hawk now occurs only as far north and east as Arizona and Texas. Nevertheless, there is ample precedent for various Neotropical and western vertebrates having occurred in eastern North America, particularly Florida, in the Pleistocene (Emslie, 1998), so the possibility of *Buteo nitidus* possibly having once occurred in the Bahamas is not unthinkable.

The Bahaman fossil hawk was thus listed simply as "*Buteo* sp.", with the genus *Calohierax* Wetmore falling into the synonymy of *Buteo* Lacepede, 1799 (Olson & Hilgartner 1982). The idea that there was an extinct hawk in the Bahamas has lingered, however, and *Calohierax quadratus* has even appeared, in a reference that I can no longer recall, under the absurd name "Quadrate Hawk." Wetmore's specific name "*quadratus*", it should be noted, was derived from the squared appearance of one of the tarsometatarsal trochleae, a feature that turned out to be only an artifact of wear (Olson & Hilgartner 1982).

Because of the ambiguities surrounding the records of a medium-sized species of *Buteo* in the Bahamas, it is fortunate that an additional specimen bearing on its identity was located in the collections of the Florida Museum of Natural History. This is a nearly complete right humerus (UF 41801), lacking only a portion of the pectoral crest. It was collected by J. C. Dickinson and W. Auffenberg in the same "Banana Hole" on New Providence Island that yielded the fossils that formed the basis of Brodkorb's (1959) study and much of that of Olson & Hilgartner (1982). It was collected in 1958–1960, evidently after Brodkorb's study was completed, and since its collection has apparently been overlooked.

The fossil humerus is in all details and proportions identical with that in *Buteo lineatus* (Fig. 1) and in size falls squarely among males from Florida (Fig. 2), which belong to the southeastern subspecies *B. l. alleni* Ridgway, which is smaller than the nominate subspecies (Crocoll 1994). From the small sample of *Buteo nitidus* examined, it is clear not only that *B. nitidus* is a smaller species, with females in the range of males of *B. lineatus* in length of the humerus and the single male being much smaller (Fig. 2), but the humerus is also much more robust, the shaft especially being much thicker. Assuming that there was only one species of *Buteo* in the Bahamas in this size range, then the holotypical tarsometatarsus of *Calohierax quadratus* from Little Exuma would belong to the same species as the humerus from New Providence, both islands being on the Great Bahama Bank. Therefore the species *Calohierax quadratus* Wetmore, 1937, becomes a junior subjective synonym of *Falco lineatus* Gmelin, 1788.

The Red-shouldered Hawk is normally a bird of moist riparian woods or swamplands, hardly like the dry, scrubby habitats that predominate in the Bahamas today. Brown and Amadon (1968:578) remark that this species "seems to be incompatible with" the larger Red-tailed Hawk, *B. jamaicensis* (Gmelin), although this is as much a reflection of the preference of the latter for drier uplands rather than being due to competition or antipathy. In any case, it is the Red-tailed Hawk that occurs in the Bahamas today, although it is an uncommon resident only on some of the larger northern islands and may perhaps be a recent colonist, as it is absent in the fossil record.

Prior to the arrival of Europeans only a single terrestrial mammal lived in the Bahamas, the hutia *Geocapromys ingrahami* (Allen), which is now extinct on all but a single small islet. The adults of this species are too large to have served as prey for Red-shouldered Hawks, but because these hawks are very catholic in their choice of food, taking birds, reptiles, amphibians, large insects, and even crustaceans in addition to mammals (Crocoll 1994), and because all of these faunal elements are still present in the Bahamas, it would be difficult to correlate the extinction of *Buteo lineatus* there to lack of suitable prey.

Habitat in most places in the Bahamas is not now like that usually considered suitable for Red-shouldered Hawks, but is thought to have been even more xeric in the past (Pregill & Olson 1981, Olson & Hilgartner 1982). Thus, environmental and climatic changes are also difficult to invoke as an explanation for the disappearance of this species from the Bahamas in the late Quaternary.

The Bahaman fossil records constitute the only evidence of *Buteo lineatus* anywhere in the West Indies, although *B. ridgwayi* of Hispaniola is now usually considered to be a derivative of *B. lineatus* (e.g., Sibley & Monroe 1990), so the Bahamas may once have provided a stepping-stone for this colonization.

Acknowledgments

I am most grateful to the staff of the Florida Museum of Natural History (UF),

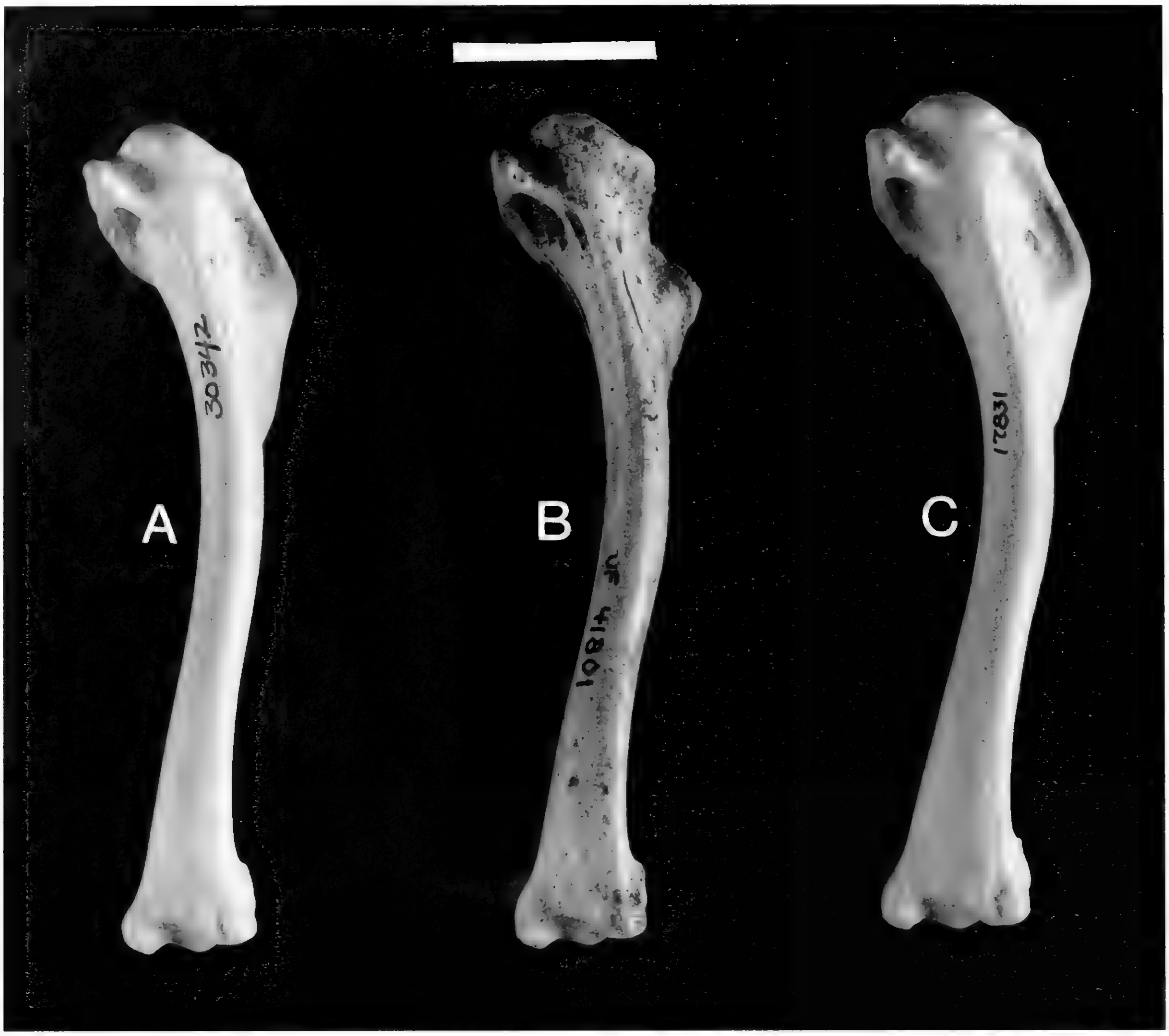

Fig. 1. Right humeri of *Buteo* in anconal aspect: A, male Red-shouldered Hawk, *B. lineatus,* (UF 23893); B, fossil referred to *B. lineatus* from New Providence Island, Bahamas (UF 41801); C, female Gray Hawk, *B. nitidus* (UF 33746). Scale bar = 2 cm.

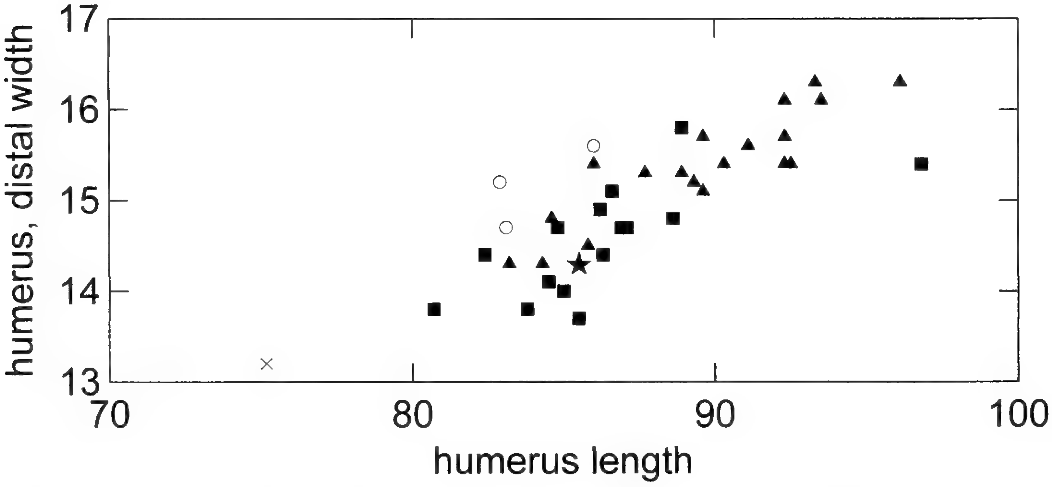

Fig. 2. Scatter diagram showing length of humerus vs. distal width of humerus in male *Buteo lineatus* (squares), female *B. lineatus* (triangles), the Bahaman fossil assigned to *B. lineatus* (star), female *B. nitidus* (circles), and male *B. nitidus* (×). Five obviously missexed specimens have been corrected. All specimens of *B. lineatus* are from Florida and are in the collections of the Florida Museum of Natural History.

Gainesville, for access to and loan of specimens that made this study possible: David W. Steadman and Tom Webber for modern birds, and Marc Frank for the fossils. The photograph is by John Steiner, Smithsonian Photographic Services, and Fig. 2 was prepared by Helen James.

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Revision of the extant taxa of the genus *Notiosorex* (Mammalia: Insectivora: Soricidae)

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Abstract.—We evaluated the taxonomic status of three specimens of gray shrews, *Notiosorex* (Insectivora: Soricidae), collected in isolated mountain valleys in Tamaulipas, Mexico, with specimens referable to the Recent taxa *N. crawfordi crawfordi* ($n = 229$) and *N. c. evotis* ($n = 34$). Statistical analyses of cranial morphometric data revealed that the specimens from Tamaulipas represented a heretofore unknown taxon which is described herein as a new species of *Notiosorex* (*N. villai*). Also, *N. c. evotis* was found to be equally distinct from *N. c. crawfordi,* thus was elevated to specific status.

Resúmen.—Se evaluó el estado taxonómico de tres especímenes de la musaraña gris *Notiosorex* (Insectivora: Soricidae), colectados en valles dentro de las motañas en Tamaulipas, México y referidos a los taxa recientes *N. crawfordi crawfordi* ($n = 229$) y *N. c. evotis* ($n = 34$). Análisis estadísticos morfométricos del cráneo indicaron que los especímenes de Tamaulipas representan un taxón desconocido, el cual se describe como una especie nueva de *Notiosorex* (*N. villai*). Asimismo, *N. c. evotis* se encontró distinto a *N. c. crawfordi,* por lo que se elevó al nivel específico.

Gray shrews of the genus *Notiosorex* (Insectivora: Soricidae) are widely distributed in the southwestern United States and northern and western Mexico (Fig. 1). They range from southern California, Nevada, Utah, Colorado, Oklahoma, and western Arkansas, southward to southern Baja California Sur, Michoacan, and southern Tamaulipas (Sealander 1952, Baker 1966, Armstrong & Jones 1972, Woloszyn & Woloszyn 1982, Carie et al. 1989). Insular records are known from Isla San Martín, Baja California Norte (Schulz et al. 1970), and Isla Palmito del Verde, Sinaloa, Mexico (Armstrong & Jones 1971). Gray shrews occur in a variety of habitats including desert shrub (characterized by mesquites, *Prosopis*; palo verde, *Cercidium*; *Acacia*; *Yucca*; *Agave*; and scattered *Juniperus*; Lange 1959), pine-oak forest (characterized by *Abies religiosa, Populus tremuloides, Juniperus flaccida,* four species of *Pinus,* and three of *Quercus*; Alvarez 1963), in grassland with oak chaparral (characterized by chamise, *Adenostomna fasciculatum*; scrub oak, *Quercus dumosa*; California live oak, *Q. agrifolia*; and mountain lilac, *Ceanothus*) and oak woodland habitats nearby (Cunningham 1956), coastal sage scrub (characterized by coastal sagebrush, *Artemesia californica*; black sage, *Salvia mellifera*; laurel sumac, *Rhus laurina*; and grasses), yellow pine forest (*Pinus australis*; Lange 1959), alkaline marsh (Stephens 1906), arid grasslands (containing scattered catclaw, juniper, and mesquite; Baker 1966), and sandy flats (characterized by *Artemisia tridentata, Ephedra viridis, Peucephyllum schottii,* and *Chrysothamnus viscidiflorus*; Fisher 1941). Elevations of occupied habitats range from 3 to 2618 m (Fisher 1941, Lange 1959, Baker 1966, Da-

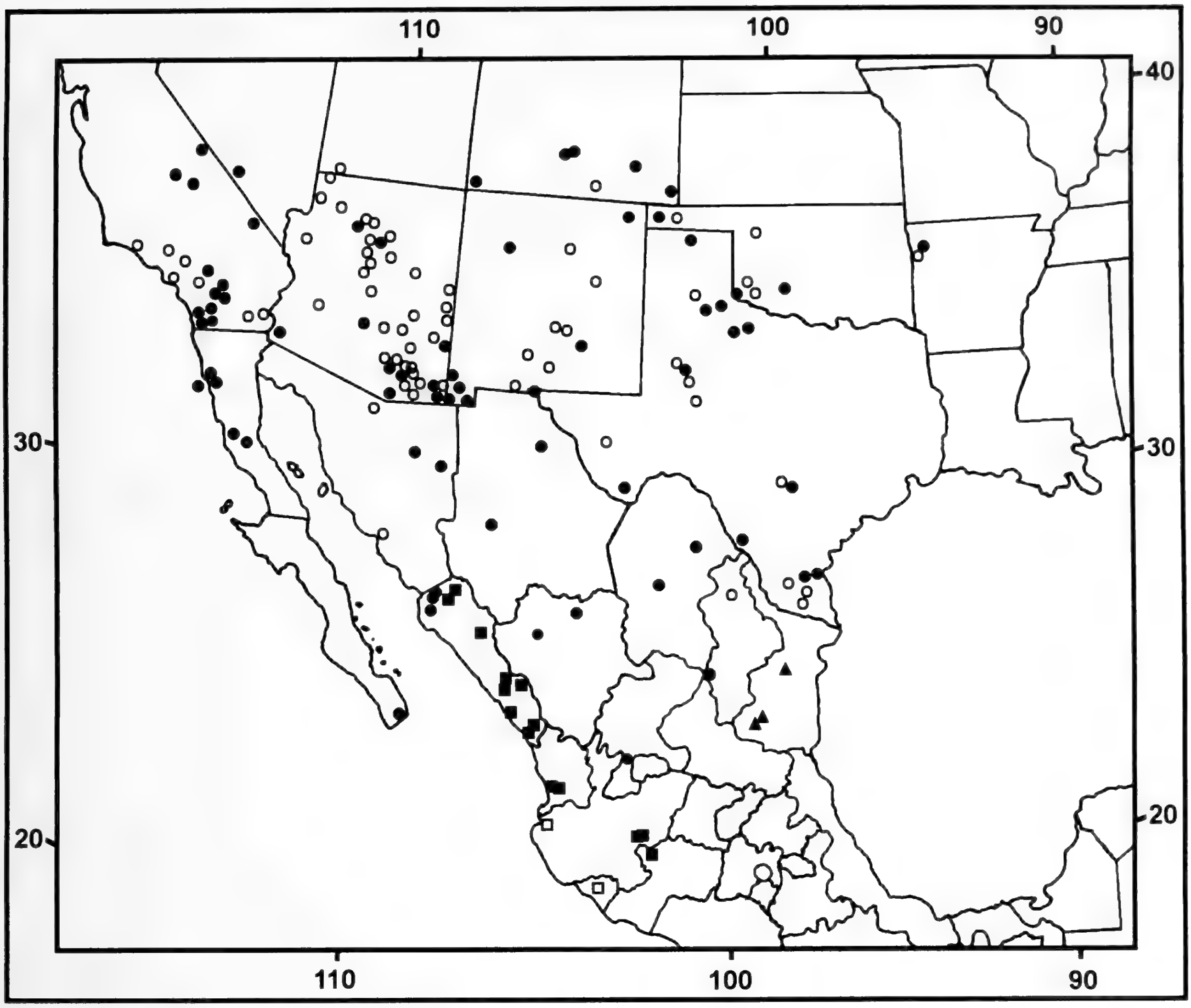

Fig. 1. Distribution of gray shrews (*Notiosorex*) based upon specimens examined herein: 1, *N. crawfordi crawfordi* (closed circles); 2, *N. c. evotis* (closed squares); and 3, *Notiosorex* unknowns from Tamaulipas (triangles). Open circles, *N. c. crawfordi,* and open squares, *N. c. evotis,* represent collection localities for which specimens were not examined (Bailey 1905; von Bloeker 1944; Cunningham 1956; Davis 1960; Baker 1966; Dalby & Baker 1967; Armstrong 1972; Armstrong & Jones 1972; Findley et al. 1975; Sealander 1979; Hoffmeister 1986; Caire et al. 1989; Rodríguez Vela 1999; Angeles Mendoza Duran, pers. comm.; Philip Myers, pers. comm.).

vis & Sidner 1989). Because of the wide range of habitats in which *Notiosorex* is know to occur, the commonly used vernacular name "desert shrew" (Hall 1981) is a misnomer. Herein, we recommend the use of gray shrew.

In 1953, Gerd H. Heinrich collected two specimens of *Notiosorex* and in 1976 George D. Baumgardner collected a third from western Tamaulipas. Findley (1955: 616) unequivocally categorized the former two specimens as *Notiosorex crawfordi crawfordi* "on geographic grounds," whereas Alvarez (1963:397) later referred them to *N. crawfordi* noting that "When more abundant material is available the *Notiosorex crawfordi* of northeastern México probably will be found to represent a new subspecies." Schmidly & Hendricks (1984: 23) examined all three specimens and referred them to *N. c. crawfordi* because it was "the name currently applied to desert shrews in Texas and northern México." As these Tamaulipian shrews are isolated geographically from the widespread *N. c. crawfordi* and are much larger and quantitatively different from that taxon, we evaluated their taxonomic status.

Materials and Methods

Specimens from throughout the distribution of *Notiosorex* (n = 266) were examined. Seven cranial and five mandibular characters were recorded for each of the 139 specimens measured (Fig. 2). Relative age of specimens was indexed by the lateral length of the right I1 (first upper incisor; Carraway et al. 1996). Quantitative characters were analyzed by age to determine if age caused a bias. Greatest length of skull, rostral breadth, least interorbital breadth, and cranial breadth were measured to 0.01 mm with Mitutoyo Digimatic electronic calipers. All other quantitative characters were measured by use of an ocular micrometer mounted in a Bausch and Lomb binocular microscope. Values were converted from number of ocular lines to millimeters for multivariate analyses and tabulation of reported values. The states of a qualitative character, roof of glenoid fossa extending laterally from side of cranium, also were recorded for each specimen.

Three a priori groups were formed of individuals of *Notiosorex crawfordi crawfordi, N. c. evotis,* and the three specimens from Tamaulipas; assignment of individuals to their a priori group was based on the geographic location of their collection site. Multivariate analyses of the three a priori groups were performed on the 12 quantitative cranial and mandibular characters by use of multigroup discriminant-function analysis in BIOΣTAT II (Pimentel 1995). A large sample of *N. c. crawfordi* (n = 54) from Huachuca Mts., Arizona, was examined for intraspecific geographic variation and a comparison with the remaining *N. c. crawfordi* was performed with multigroup discriminant-function analysis. Univariate and regression analyses were calculated by use of STATGRAPHICS Plus (Statistical Graphics Corporation 1995). For all analyses, $P < 0.05$ was accepted as statistically significant.

Standardized canonical vectors for the 12 quantitative variables were plotted on the same graph as the three a priori groups with the same canonical variate axes. The plot of the variable vectors, when placed at the origin of the canonical variates plot, provided an indication of the direction and magnitude of effect that each variable had in discriminating the three a priori groups (Jolicoeur, 1959).

Summary statistics ($\bar{X} \pm SE$, range, and CV) were calculated for all 12 quantitative variables for the three taxa of *Notiosorex* under consideration (Table 1). Color of hair in the pelage was determined by comparison with Munsell soil color charts (Munsell Color 1975).

Results

Multigroup discriminant function analysis of *Notiosorex crawfordi crawfordi, N. c. evotis,* and *Notiosorex* unknowns from Tamaulipas, resulted in 99% correct classification of individuals into their a priori groups (Fig. 3). The two significant canonical-variate axes (χ^2 = 153.61, d.f. = 24 and χ^2 = 37.73, d.f. = 11, respectively) acounted for 81.10 and 18.90% of the variation, respectively. Variance in the first axis (canonical variate I) was accounted for by greatest length of skull, 98.19%; cranial breadth, 99.03%; length of unicuspid toothrow, 98.35%; width across M2–M2, 92.69%; length of mandible, 99.39%; length of mandibular toothrow, 89.70%; height of coronoid process, 96.08%; and length of the coronoid process-ventral point of upper condylar facet, 97.64%. The second axis (canonical variate II) was affected by length of the coronoid process-ventral point of lower condylar facet (89.98%). Only one individual (KU 105409), from 5 mi WNW El Carrizo, Sinaloa, Mexico, was not placed into its a priori group, *N. c. evotis*; it was classified as a *N. c. crawfordi.* This individual also was classified as a *N. c. crawfordi* based on morphological comparisons by Jones et al. (1962). Herein, this individual is considered *N. c. crawfordi* for purposes of further analyses.

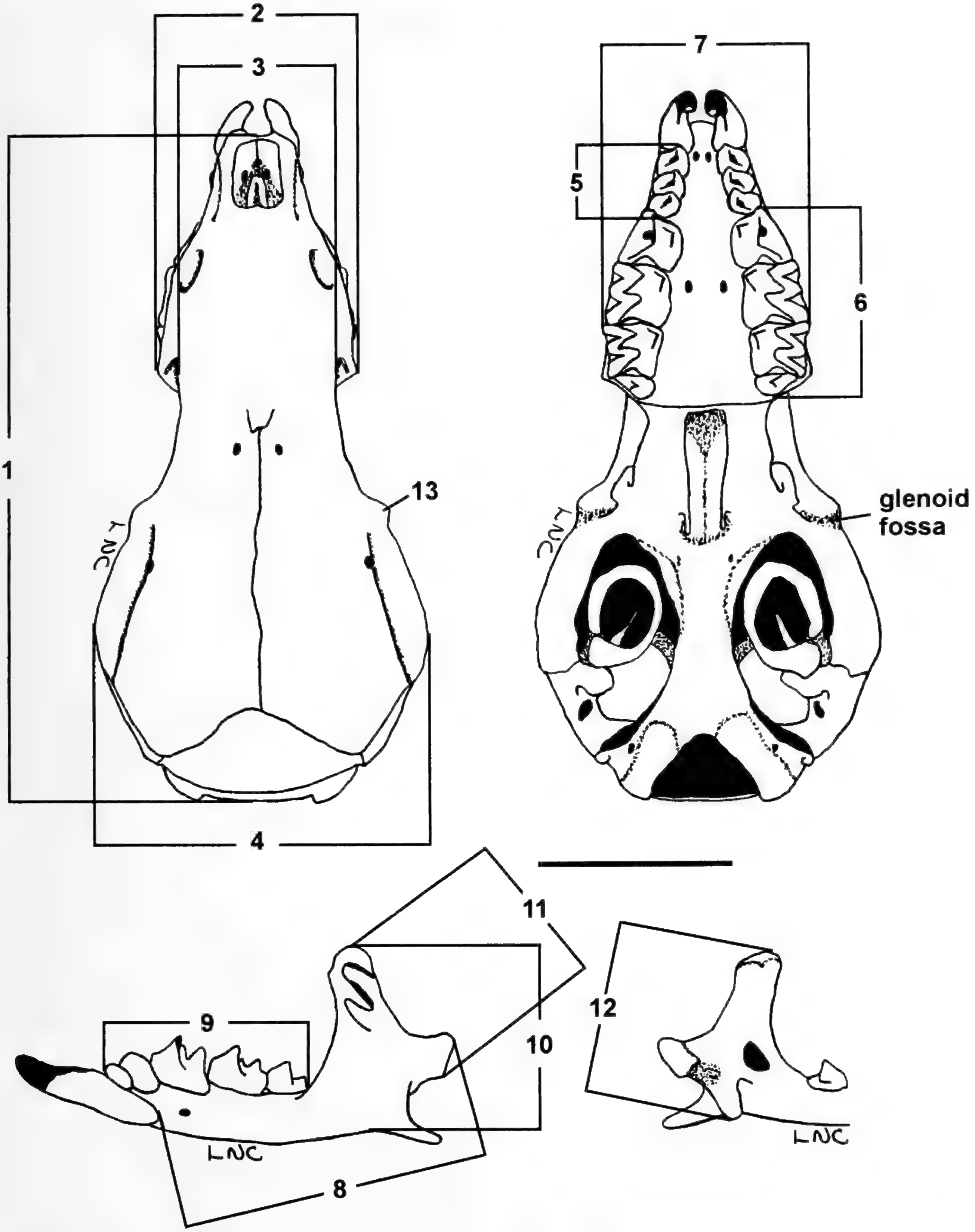

Fig. 2. Camera-lucida tracing of skull of a *Notiosorex* (KU 145262) illustrating skull dimensions measured: 1, greatest length of skull; 2, rostral breadth; 3, least interorbital breadth; 4, cranial breadth; 5, length of maxillary unicuspid toothrow; 6, length of maxillary complex toothrow; 7, width across M2–M2; 8, length of mandible; 9, length of mandibular toothrow; 10, height of coronoid process; 11, length of coronoid process-ventral point of upper condylar facet; and 12, length of coronoid process-ventral point of lower condylar facet. Qualitative character recorded is: 13, roof of glenoid fossa extending laterally from the side of the skull. Scale bar equals 5 mm.

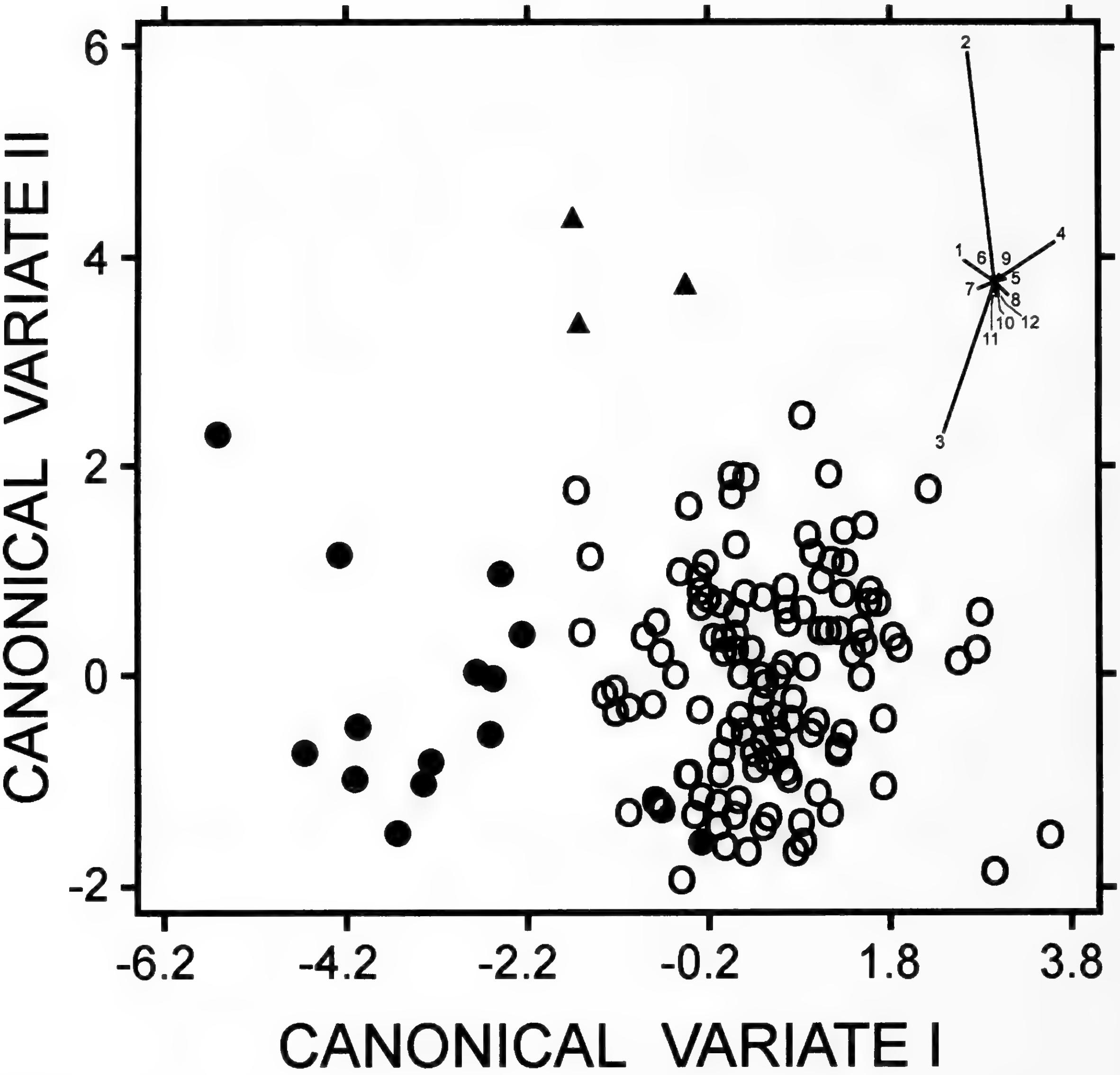

Fig. 3. Canonical-variates plot of *Notiosorex c. crawfordi* (open circles), *N. c. evotis* (closed circles), and *Notiosorex* new sp. (triangles) based on 12 measured variables. Canonical-variate axis I accounted for 81.10% and canonical-variate axis II 18.90% of the variation present among the three taxa. Differences in cranial morphology among the three taxa are characterized by the plot of the 12 variable vectors on the canonical-variates plot in the upper right corner. Numbers are as in Fig. 2. The relationship of the variables among the taxa are indicated by the length and orientation of the vector relative to the canonical-variate axes. From left to right, taxa have shorter skulls relative to cranial breadth and taller and narrower coronoid processes. From bottom to top, taxa have greater rostral breadth relative to length of maxillary complex toothrow.

Coefficients of variation for the *N. c. crawfordi* from Huachuca Mts., Arizona, ranged from 2.276% to 4.918% with one outlier at 6.46%. Whereas, the same values for the remaining *N. c. crawfordi* ranged from 3.028% to 8.098%. This indicates that among specimens of *Notiosorex* from the Huachuca Mts. the level of variation within and among the 12 quantitative characters examined is very low. The one discriminant function produced by a multigroup discriminant-function analysis of the two a priori groups of *N. c. crawfordi* was not significant at $P < 0.05$. Therefore, these two a priori groups are acting as a single unit.

Regression analyses indicated weak relationships between age and length of unicuspid toothrow for *crawfordi* ($r^2 = 0.24$) and *evotis* ($r^2 = 0.53$) and between age and least interorbital breadth ($r^2 = 0.04$) and length of mandible ($r^2 = 0.04$) for *crawfordi.* When the discriminant analysis was repeated without these three variables, 93.5%

of individuals still were classified correctly into their a priori groups.

For all *N. c. crawfordi* and *N. c. evotis* the roof of the glenoid fossa extends laterally from the cranium. However, among the *Notiosorex* from Tamaulipas the roof of the glenoid fossa does not extend laterally from the cranium.

Discussion

Morphometrically, the three specimens of *Notiosorex* from Tamaulipas are most similar to each other and are distinct from all specimens of *crawfordi* and *evotis* (Fig. 3) in terms of size and shape of their skulls. We had expected this outcome after making careful visual comparisons (with aid of a binocular microscope) of the three groups. The discovery that *evotis* was equally distinct from the two other groups (Fig. 3) necessitated a reevaluation of its taxonomic status. Previously, *N. c. evotis* was recognized as being larger than *N. c. crawfordi,* but we also found significant differences in the shape of skulls and mandibles between individuals of the two taxa.

Based on analyses reported herein we refer the three specimens from Tamaulipas to a new species and elevate *N. c. evotis* to species level.

Class Mammalia Linnaeus, 1758
Order Insectivora Bowdich, 1921
Family Soricidae Fischer von Waldheim, 1817
Subfamily Soricinae Fischer von Waldheim, 1817
Genus *Notiosorex* Coues, 1877
Notiosorex villai, new species
Villa's Gray Shrew
Fig. 4A

Notiosorex crawfordi.—Findley 1955:616, Ball & Kelson 1959:64 [part], Alvarez 1963:397, Hall 1981:65 [part], Schmidly & Hendricks 1984:22.

Holotype.—Adult, female, skin and skull; KU 54932, University of Kansas, Natural History Museum, Mammal Collection; from "Jaumave, Tamaulipas, Mexico, 2400 ft."; obtained 26 July 1953 by Gerd H. Heinrich, original number 7612. Alvarez (1963:386) recorded the latitude and longitude of Jaumave as 23°34′N, 99°23′W.

Distribution.—Known only from the Potosian Biotic Province (=Sierra Madre Oriental Biotic Province) of the central mountains of Tamaulipas, Mexico (Fig. 1).

Diagnosis.—As in all *Notiosorex,* specimens of *N. villai* (Fig. 4A) have a combination of a deeply emarginated area between the condylar processes, e.g., interarticular breadth about half the width of the superior condylar process; the alveolus of i1 extending posteriorly beneath at least part of paraconid of m1 (Carraway 1995); pigment present of some teeth; and three unicuspids.

Notiosorex villai can be distinguished from other *Notiosorex* by the roof of the glenoid fossa not extending laterally from the cranium when the skull is viewed from the dorsal aspect (Fig. 4A); and usually from *N. c. crawfordi* by greatest length of skull ≥16.97 mm and from *N. c. evotis* by length of maxillary unicuspid toothrow ≥2.0 mm, height of coronoid process ≤4.1 mm, length of coronoid process-ventral point of upper condylar facet ≤3.8 mm, and length of coronoid process-ventral point of lower condylar facet ≤3.4 mm. All specimens of *N. villai* can be separated from specimens of *N. c. crawfordi* and *N. c. evotis* by application of the following discriminant-function equation: discriminant score = 1.30722 (cranial breadth) − 0.34104 (height of coronoid process) − 0.01685 (length of maxillary complex toothrow) − 4.87675 (least interorbital breadth) − 0.10742 (length of coronoid process-central point of lower condylar facet) − 0.16575 (length of mandible) + 0.22460 (length of mandibular toothrow) + 0.88996 (greatest length of skull) + 0.22980 (length of maxillary unicuspid toothrow) − 0.03089 (length of coronoid process-ventral point of upper condylar facet) + 6.66117 (rostral breadth) − 0.23311 (width across M2–M2) − 11.0491. Those specimens with scores ≥ 3.359 are referrable to *villai* and those with scores ≤ 2.454 are referrable to *crawfordi* or *evotis.*

Description.—As in all soricids, *Notiosorex villai* has a double-faceted condylar process and a fissident I1 with a large hook-shaped anterior cusp and a posterior ventrally directed cusp. The skull is moderately large, smooth, and without prominent ridges and processes. The paroccipital processes are small and lie against the exoccipitals (Fig. 4A). The upper condylar facets are inflected; the corresponding areas in the superior portion of the glenoid fossas are depressed.

The pelage is composed of multibanded hairs. In summer, hairs of the dorsal pelage have a narrow band of silver gray (10YR 6/1) distally and a wide band of dark gray (7.5YR N4/0) proximally. Hairs of the venter are the same colors, except that the distal band of silver gray is wide and the proximal band of dark gray is narrow producing a silver wash. In winter, hairs of the dorsal pelage have a narrow band of very dark grayish-brown (10YR 3/2) distally, a narrow band of pinkish white (7.5YR 8/2) medially, and a wide band of very dark-gray (7.5YR N3/0) proximally. Hairs of the ventral pelage have a distal wide band of pinkish white (7.5YR 8/2) and a proximal narrow band of very dark-gray. The tail is very dark grayish-brown.

Measurements.—Individuals of *Notiosorex villai* are smaller than those of *N. c. evotis,* but larger than those of *N. c. crawfordi* (Table 1).

Ecology.—The three known specimens of *Notiosorex villai* were collected in different habitats within the Potasian Biotic Province (Alvarez 1963). The area of Jaumave is pine-oak forest, that of Palmillas is tropical forest, and the habitat of the collection site near Rancho Carricitos is riparian. The subprovince, within the Potosian Biotic Province, from which the three specimens were collected contains "low meseta-like folded mountains" characterized by "closely spaced ridges" (Ferrusquía-Villafranca 1993:33).

Mammal associates of the holotype were *Baiomys taylori, Onychomys arenicola, Oryzomys couesi, Peromyscus leucopus, Reithrodontomys fulvescens, Sigmodon hispidus, Liomys irroratus, Mephitis macroura,* and *Mustela frenata*; only *Peromyscus pectoralis* was collected in the vicinity of the specimen from Palmillas (G. H. Heindrich, in litt.). *Cryptotis parva, Mormoops megalophylla, Desmodus rotundus, Myotis californicus, Lasiurus borealis, L. cinereus, Antrozous pallidus, Tadarida brasiliensis, Sylvilagus floridanus, Sciurus aureogaster, S. alleni, Liomys irroratus, Peromyscus leucopus, P. pectoralis, P. boylii, Baiomys taylori, Mus musculus, Bassariscus astutus,* and *Mephitis mephitis* were collected in the vicinity of the specimen from SW of Rancho Carricitos (Schmidly & Hendricks 1984). One of the *C. parva* was collected in the same pitfall as the *Notiosorex.* The greater species richness noted for the latter locality is almost certainly the result of greater trapping effort and not necessarily an indication that the other mammal associations were depauperate.

Etymology.—The species epithet is a patronymic to honor Bernardo Villa-R., the "father" of Mexican mammalogy.

Remarks.—All three specimens of *Notiosorex villai* were collected in isolated mountain valleys. The extent of the distri-

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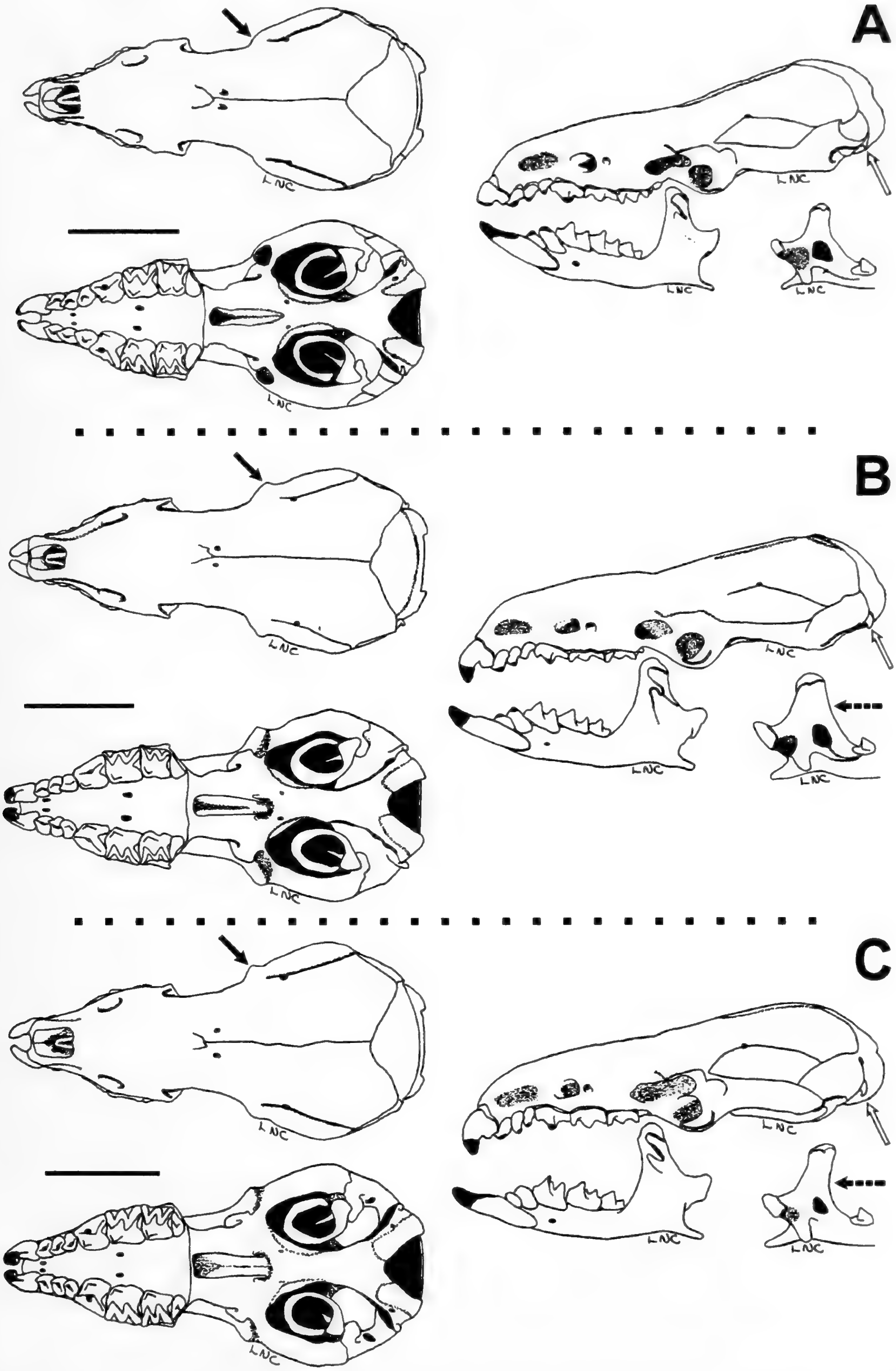
Fig. 4. Camera-lucida tracings of dorsal, lateral, and ventral views of the cranium, and lateral view of labial side of mandible and oblique view of posterior portion of lingual side of left mandible of taxa of *Notiosorex.* A, Holotype of *Notiosorex villai* (KU 54932, adult female). Note smooth lateral edge of cranium when viewed from dorsal aspect (solid arrow), absence of extension of roof of glenoid fossa, small paroccipital processes



lying against the exoccipitals (open arrow), and coronoid process slender relative to height. B, *N. evotis* (KU 89214, adult male). Specimen from 17 km SW Choix, Sinaloa. Note prominent ridge on lateral edge of cranium caused by extension of roof of glenoid fossa (solid arrow), low-set paroccipital processes extending at an oblique angle from skull (open arrow), and coronoid process broad relative to height (dashed arrow). C, *N. crawfordi* (KU 145262, adult male). Specimen from Peloncillo Mts., Guadalupe Canyon, Hidalgo Co., New Mexico. Note prominent ridge on lateral edge of cranium caused by extension of roof of glenoid fossa (solid arrow), small paroccipital processes lying against the exoccipitals (open arrow), and coronoid process slender relative to height (dashed arrow). Scale bar equals 5 mm.

bution of the species has yet to be determined. However, considering the three different habitat types represented, *N. villai* likely has a reasonably wide distribution in Tamaulipas.

Heinrich, both in his field catalog and on the specimen tag of one of the specimens included herein, clearly recorded the locality as Palmilla. However, on a map of Heinrich's collecting localities drawn on 1 September 1953 by Hildegarde Heinrich, his wife who accompanied him both in 1952 and 1953, the name is spelled Palmillas. The hand-drawn map used by Heinrich in 1953 is believed to be based on the copy of "Mapa de la Republica Mexicana—Estado de los Caminos Federales Estatales y Vecinales" (1944) on deposit in the Natural History Museum at the University of Kansas. Notations made by E. R. Hall on the latter map identify it as a gift to the museum. The name of the town on this map is spelled Palmillas; all subsequent authors who have published upon this specimen used the spelling Palmillas.

Specimens examined.—3, as follows.

Mexico: Tamaulipas: Jaumave, 2400 ft (KU 54932, ♀); Palmilla [sic], 4400 ft [23°18′N, 99°33′W; Alvarez 1963:386] (KU 54933, ♀); 0.3 mi SW Rancho Carricitos, San Carlos Mts., 1900 ft (TCWC 30492, ♂).

Notiosorex evotis (Coues)
Large-eared Gray Shrew
Fig. 4B

Sorex (Notiosorex) evotis Coues, 1877:652.
N[otiosorex]. evotis Coues, 1877:652.
Notiosorex crawfordi evotis Merriam, 1895: 34; Hall & Kelson 1959:64 [part], Jones et al. 1962:151, Hall 1981:65 [part].

Holotype.—Adult, no sex given, skin only; USNM 9066, National Museum of Natural History; from "area of Mazatlan, Sinaloa, Mexico"; obtained February 1868 by Ferinand Bischoff. The skull is mentioned by Coues (1877), but apparently was never cataloged into the National Museum collection. A sketch of the lateral view of the right-side rostral area of the cranium was included in Dobson (1890). However, by the time Merriam (1895) published his revision of the genus, the skull was missing.

Distribution.—Notiosorex evotis is known from the states of Colima, Jalisco, Michoacan, Nayarit, and Sinaloa, Mexico (Fig. 1).

Diagnosis.—Notiosorex evotis can be distinguished from *N. villai* by the roof of the glenoid fossa extending laterally beyond the curve of the cranium (Fig. 4B) and usually by length of maxillary unicuspid toothrow ≤2.1 mm, height of coronoid process ≥4.3 mm, length of coronoid process-ventral point of upper condylar facet ≥3.8 mm, and length of coronoid process-ventral point of lower condylar facet ≥4.0 mm; and usually from *N. crawfordi* by rostral breadth ≥5.2 mm, width across M2–M2 ≥5.1 mm, length of mandible ≥7.4 mm, height of coronoid process ≥4.3 mm, length of coronoid process-ventral point of upper condylar facet ≥4.0 mm, and length of coronoid process-ventral point of lower condylar facet ≥3.8 mm. *N. evotis* usually can be distinguished from *N. crawfordi* by use of a combination of height of coronoid process and cranial breadth (Fig. 5). Based on the results of the discriminant analysis, all specimens of *N. evotis* can be separated from specimens of *N. crawfordi* by application of the following discriminant-function equation: discriminant score = 1.73654 (cranial breadth) + 0.22159 (height of coronoid process) + 0.06177 (length of maxillary complex toothrow) − 0.65656 (least interorbital breadth) − 0.00471 (length of coronoid process-central point of lower condylar facet) + 0.27652 (length of mandible) + 0.08699 (length of mandibular toothrow) − 0.86213 (greatest length of skull) + 0.23251 (length of maxillary unicuspid toothrow) − 0.02611 (length of coronoid process-ventral point of upper condylar facet) − 0.92248 (rostral breadth) + 0.10899 (width across M2–M2) − 37.2423. Individuals with a score ≤−2.26 are referrable to *evotis* and those with a score ≥−1.65 are referrable to *crawfordi.*

Description.—Within extant members of the genus *Notiosorex, evotis* has the largest skull with prominent ridges (the roof of the glenoid fossa) on the lateral sides of the cranium and the paroccipital processes are set low on the mastoid and extend at an oblique angle from the skull (Fig. 4B). The coronoid processes are broad relative to their height (Fig. 4B; Choate 1969:473, fig. 3b) resulting in different placement of the condyloid processes relative to each other (Choate 1969:473, figs. 3b–c) for *N. evotis* and *N. crawfordi.*

The pelage is composed of multibanded hairs. In summer, hairs of the dorsal pelage have a narrow band of very dark grayish-brown (10YR 3/2) distally, a narrow band of pinkish white (7.5YR 8/2) medially, and a wide band of dark gray (7.5YR N4/0) proximally. The hairs of the venter have a wide distal band of pinkish white and a narrow proximal band of very dark-gray (7.5YR N3/0). The winter pelage consists of hairs of the dorsum with a wide distal band of very dark grayish-brown (10YR 3/2) and a proximal band of very dark-gray (7.5YR N3/0). The hairs on the venter have a wide distal band of light yellowish-brown (10YR 6/4) and a narrow proximal band of dark gray (7.5YR N4/0). The hairs on the tail are very dark grayish-brown.

Measurements.—Individuals of *Notiosorex evotis* are the largest members of extant *Notiosorex* (Table 1).

Ecology.—*Notiosorex evotis* is known to occur from 3-m elevation along the Pacific Coast to 550 m in the Sierra Madre Occidental, Sinaloa, and to 2317 m in the Sierra Moroni, Zacatecas. It is know to occur in habitats characterized by scattered cacti and dense thornbush, and abandoned agricultural fields bordered by an area of scattered cacti, thornbush, and mesquite (scientific names not given—Armstrong & Jones 1971); communities that "consisted mostly of dry, dense weeds and short, thorny shrub with a few trees" and "in low weeds near thorn bush" (Jones et al. 1962:148–149); "in damp spots under rocky ledges" (Fisher & Bogan 1977:826); and in "semi-desert habitat" (Schlitter 1973:423).

Reported small-mammal associates are *Liomys pictus, Chaetodipus pernix, Sigmodon hispidus,* and *Mus musculus* (Baker 1962, Jones et al. 1962).

Etymology.—The species epithet is derived from the Greek *ev,* meaning good, and *otus,* meaning ear, possibly in reference to its "extremely large" ears (Coues 1877:652).

Remarks.—A discussion of the taxonomic history of *Notiosorex evotis* is presented in Jones et al. (1962).

Specimens examined.—34, as follows.

Mexico: Jalisco: 13 mi S, 15 mi W Guadalajara (KU 33318); 21 mi SW Guadalajara (KU 42583–42585). Michoacan: 2 mi E La Palma, SE side of Lago de Chapala (KU 42586–42588). Nayarit: El Refilion (USNM 508358); Tepic (USNM 314064). Sinaloa: 20 km N, 5 km E Badiraguato (KU 96419); 16 km NNE Choix, 1700 ft (KU 89210–89213); 1 mi S El Cajón, 1800 ft (KU 100319); 15 mi SE Escuinapa (MSUM 5691); Isla Palmito del Verde, 6 mi NNW Teacapan (KU 98880); Laguna, 17 km SW Choix, 500 ft (KU 89214–89216); Mazatlán (KU 85533–85536; USNM 9066); 1 mi N Mazatlan, 10 ft (MSUM 8149); 1 mi N Mazatlan, 25 ft (MSUM 5690); Rosario, 500 ft (KU 90581); 10 km S, 38 km E Sinaloa (KU 125476–125479); 44 km ENE Sinaloa, 600 ft (KU 89998); HWY 15, 0.25 mi S Sonora state line (UMMZ 109403).

Notiosorex crawfordi (Coues)
Crawford's Gray Shrew
Fig. 4C

Sorex (*Notiosorex*) *crawfordi* Coues, 1877:651.

Notiosorex crawfordi Coues, 1877:652, True 1884:606, Merriam 1895:32, Hall & Kelson 1959:64 [part], Hall 1981:65 [part].

Holotype.—Adult, no sex recorded, skin

Table 1.—Means (±*SE*), ranges (in parentheses), and *CV*s of measurements (in mm) of skull characters of *Notiosorex crawfordi crawfordi* ($n = 122$), *N. evotis* ($n = 14$), and *N. villai* ($n = 3$).

Character	*Notiosorex*		
	crawfordi	*evotis*	*villai*
Greatest length of skull	16.08 ± 0.04[a] (14.95–17.25) 0.03	17.26 ± 0.13[b] (16.49–18.41) 0.03	17.17 (16.97–17.27)[c]
Rostral breadth	4.83 ± 0.02 (3.70–5.23) 0.04	5.33 ± 0.04[c] (5.0–5.63) 0.03	5.19 (5.01–5.30)
Least interorbital breadth	3.76 ± 0.01 (3.42–4.14) 0.04	3.98 ± 0.04[c] (3.65–4.16) 0.04	3.83 (3.57–4.01)
Cranial breadth	7.96 ± 0.02[a] (7.05–8.52) 0.03	8.56 ± 0.07[b] (8.02–8.99) 0.03	8.30 (8.07–8.53)[c]
Length of maxillary unicuspid toothrow	1.9 ± 0.01 (1.5–2.2) 0.05	2.0 ± 0.03 (1.80–2.3) 0.05	2.2 (2.0–2.3)
Length of maxillary complex toothrow	4.3 ± 0.01 (3.9–4.6) 0.02	4.6 ± 0.03[c] (4.5–5.0) 0.02	4.6 (4.4–4.7)
Width across M2–M2	4.8 ± 0.01 (3.7–5.3) 0.02	5.3 ± 0.03[c] (4.9–5.4) 0.02	5.0 (4.9–5.1)
Length of mandible	7.0 ± 0.02[c] (6.4–7.7) 0.03	7.7 ± 0.04 (7.4–8.2) 0.03	7.4 (7.3–7.5)[c]
Length of mandibular toothrow	4.7 ± 0.01[d] (4.4–5.1) 0.02	5.0 ± 0.03 (4.9–5.3) 0.02	5.1 (5.0–5.1)[c]
Height of coronoid process	4.0 ± 0.02 (3.4–4.9) 0.02	4.7 ± 0.05 (4.3–5.0) 0.04	4.1 (4.0–4.1)[c]
Length of coronoid process–ventral point of upper condylar facet	3.3 ± 0.02[c] (2.7–3.9) 0.06	3.9 ± 0.04 (3.8–4.2) 0.03	3.8 (3.7–3.8)[c]
Length of coronoid process–ventral point of lower condylar facet	3.7 ± 0.02 (3.2–4.3) 0.05	4.3 ± 0.05 (4.0–4.7) 0.05	3.4 (3.3–3.4)[c]

[a] Sample size reduced by 6.
[b] Sample size reduced by 2.
[c] Sample size reduced by 1.
[d] Sample size reduced by 3.

and skull; USNM 2653/4437, National Museum of Natural History; from "near Fort Bliss, about 2 miles above El Paso, El Paso County, Tex."; obtained September 1861 by S. W. Crawford.

Distribution.—From southern California, Nevada, Utah, Colorado, Oklahoma, and western Arkansas, United States, southward to southern Baja California Sur, and eastward to northern Sinaloa, and southern Zacatecas and Nuevo León, Mexico (Fig. 1).

Diagnosis.—*Notiosorex crawfordi* can be distinguished from *N. villai* by the roof of the glenoid fossa extending laterally beyond the curve of the cranium (Fig. 4C) and by the greatest length of skull usually ≤16.98 mm. It usually can be distinguished from *N. evotis* by rostral breadth ≤5.14

mm, width across M2–M2 ≤5.1 mm, length of mandible ≤7.5 mm, height of coronoid process ≤4.4 mm, length of coronoid process-ventral point of upper condylar facet ≤3.9 mm, and length of coronoid process-ventral point of lower condylar facet ≤4.1 mm. *N. crawfordi* usually can be distinguished from *N. evotis* by use of a combination of height of coronoid process and cranial breadth (Fig. 5). Specimens of *N. crawfordi* can be separated from 100% of specimens of *N. villai* and *N. evotis* by application of the discriminant-function equations presented in the Diagnoses sections of those species accounts.

Description.—The skull of *Notiosorex crawfordi* is much like that of *N. evotis*, except that it is much smaller, the coronoid processes are slender compared to their height, and the paroccipital processes are small and lie against the exoccipitals (Fig. 4C). The latter two characters are similar in form to *N. villai.* Although significant genetic differences (M. B. O'Neill, C. Porter, and R. J. Baker, pers. comm.) occur between populations of *N. crawfordi* in Baja California and Texas, we found no identifiable morphological differences.

The pelage is composed of multibanded hairs. In summer, hairs of the dorsal pelage have a narrow band of very dark grayish-brown (10YR 3/2) distally and a wide band of dark gray (7.5YR N4/0) proximally. The hairs of the venter have equal-width bands of pinkish white (7.5YR 8/2) distally and very dark-gray (7.5YR N3/0) proximally. The winter pelage consists of hairs of the dorsum with a narrow band of very dark grayish-brown distally, a narrow band of pinkish white medially, and a wide band of dark gray (7.5YR N4/0) proximally. The hairs of the venter have a wide band of white (7.5YR N8/0) distally and a very narrow band of gray (7.5YR N5/0) proximally creating a silvery wash effect over the venter. The hairs of the tail are dark grayish-brown (10YR 4/2).

Measurements.—Individuals of *Notiosorex crawfordi* are the smallest extant members of the genus (Table 1).

Ecology.—*Notiosorex crawfordi* is known to occur in habitats as diverse as desert shrub and yellow pine forest (Lange 1959), pine-oak forest (Alvarez 1963), in grassland with oak chaparral and oak woodland habitats nearby (Cunningham 1956), alkaline marsh (Stephens 1906), sandy flats (Fisher 1941, Yensen & Clark 1986), "arid grasslands with scattered catclaw, juniper and mesquite" (Baker 1966:345), and near "a mesquite tree on a moist mud flat" (Armstrong & Jones 1971:751). It is known to occur at elevations at least as great as 2618 m (Davis & Sidner 1989).

From throughout the range of Crawford's gray shrew, known mammal associates are members of the genera *Cryptotis, Sorex, Scapanus, Sylvilagus, Lepus, Tamias, Sciurus, Spermophilus, Thomomys, Cratogeomys, Liomys, Dipodomys, Perognathus, Chaetodipus, Baiomys, Neotoma, Peromyscus, Onychomys, Reithrodontomys, Sigmodon, Microtus, Mus, Rattus,* and *Odocoileus,* plus 14 species of bats (Chiroptera; Cunningham 1956, Anderson & Long 1961, Coulombe & Banta 1964, Baker 1966, Dalby & Baker 1967, Davis & Sidner 1989). Also, Crawford's gray shrew is well known for its association with woodrat (*Neotoma*) nests throughout its distribution (Armstrong & Jones 1972).

Etymology.—The species epithet is a patronymic to honor the collector of the type specimen, S. W. Crawford.

Remarks.—Although trapping success for specimens of *Notiosorex crawfordi* is limited, remains thereof commonly occur in pellets regurgitated by barn owls (*Tyto alba*) and great horned owls (*Bubo virginianus*) throughout its distribution in the United States and Mexico (Twente & Baker 1951, Baker 1953, Baker & Alcorn 1953, Cunningham 1956, Anderson & Ogilvie 1957, Lange & Mikita 1959, Bradshaw & Hayward 1960, Anderson & Long 1961, Glass & Halloran 1961, Schaldach 1966, Anderson 1972).

Jones et al. (1962:150–151), in a review of *Notiosorex* from Sinaloa, treated *evotis* and *crawfordi* as full species, stating that "*evotis* has a longer body and hind foot than *crawfordi* but a relatively (sometimes actually) shorter tail and ear, and a distinctly larger, heavier skull . . . . *Notiosorex evotis* differs cranially from *Notiosorex crawfordi* as follows: larger . . . ; mesopterygoid fossa squared rather than broadly U-shaped anteriorly; rounded process on maxillary at posterior border of infraorbital canal well developed . . . ; occipital condyles smaller and, in lateral view, elevated above basal plane of skull; upper molars slightly more crowded in occlusal view." Armstrong & Jones (1971:750), in their update on Sinaloan mammals, treated the two forms as subspecies stating that "the population in northern Sinaloa is intermediate between *crawfordi* and *evotis*" and that some of the cranial differences noted earlier now appear to be inconsistent. After examination of the 263 specimens referrable to *N. crawfordi* and *N. evotis* included in this study, we found that most of the characters presented in Jones et al. (1962) are either inconsistent or strongly age-related, thus are of limited use in distinguishing *crawfordi* and *evotis.*

A discussion of the natural history, fossil record, and reproduction of *N. crawfordi* can be found in Armstrong & Jones (1972) and Coulombe & Banta (1964).

Specimens examined.—229, as follows.

Mexico: Baja California: 9 mi N Catavina on Mexico HWY 1 (MVZ 159725); 10 mi SE El Rosario (MVZ 159726); San Martín Island, 300 yds. inland from Hassler's Cave (MVZ 136207); San Quintin (CAS 52); San Quintin, San Simon River (USNM 139592–139593); San Tomas (USNM 137142); Santa Anita (USNM 74550, 79088–79092, 146693, 146933–146934, 146936, 147352, 147421). Chihuahua: 3.5 mi ESE Los Lamentos (KU 76488); 2 mi W Minaca (KU 109475). Coahuila: 3 mi NW Cuatrociénegas (KU 51571–51572); Sabinas (USNM 277621). Durango: 2 km SE Atotonilco, 6680 ft (MSUM 13887–13888); 4.8 km SE Atotonilco, 6680 ft (MSUM 13889–13890); 7 mi NNE Boquilla, 6400 ft (MSUM 10260). Nuevo Leon: 3 mi SW Galeana, 5100 ft (MSUM 11238). Sinaloa: On HWY 15, 0.25 mi S Sonora line (UMMZ 109403); 5 mi WNW El Carrizo (KU 105409); El Fuerte (KU 75184). Sonora: 14.6 mi E [by road] Mazocahui (MVZ 148830); 4.1 mi NW [by road] Nacori Chico (MVZ 148831). Zacatecas: Plateado (USNM 90845).

United States: Arkansas: Crawford Co.: Natural Dam (USNM 286549). Arizona: Apache Co.: 1 mi N Spigerville (UMMZ 80236); Cochise Co.: 9.1 mi S Chiricahua (USNM 552386); Huachuca Mts. (MSB 62141–62144, 62146–62148, 62150, 62154–62155, 62158–62159, 62161–62166, 62168, 62171–62173, 62175–62177, 62179, 62183–62184, 62188–62189, 62210–62215, 62218–62219; 62223–62238); 20 mi E Pearce, Pinery Canyon, 6500 ft (UMMZ 64102); Coconino Co.: 10 mi SW Black Falls (USNM 244129); Grand Canyon (USNM 250676); Greenlee Co.: Blue River (USNM 144533); Maricopa Co.: Phoenix South Mt. (CAS 13928); Pima Co.: 36 mi S Tucson (USNM 272515–272516); 40 mi S Tucson (USNM 272844); Santa Cruz Co.: locality unknown (USNM 289955); Yuma Co.: Yuma (USNM 120357). California: San Bernardino Co.: San Bernardino (USNM 187011); Inyo Co.: Panamint Range Cottonwood Canyon (CAS 23228–23230); Saline Valley (CAS 21270); Saline Valley, Grapevine Canyon, 4036–5750 ft (CAS 23231–23232, 21249–21269); Silver Canyon Rd., 4.3 mi E [by road] jct. with California HWY 6 (MVZ 158116); Riverside Co.: Millard Canyon (CAS 23240); San Bernardino Co.: Cottonwood (CAS 23242); Deep Canyon (CAS 23238); Kingston Range (CAS 21518); San Gorgonia, Cottonwood (CAS 23233–23237, 23241); San Diego Co.: locality unknown (USNM 62619); Lakeside, head of Wildcat Canyon, 2100 ft (KU 92627); Escondido (MVZ 33582); 9 mi S Escondido (MVZ 33388); Santer Mts.

(USNM 62919). Colorado: Baca Co.: 14 mi N, 4 mi E Springfield (KU 116960); Fremont Co.: Phantom Canyon, Eightmile Creek (KU 125348–125367); Wet Mt. (KU 125368–125379); Montezuma Co.: Mesa Verde National Park (KU 105109); Otero Co.: 3 mi NW Higbee (KU 51673). New Mexico: Cibola Co.: Juan Tofoya (USNM 147966); Hidalgo Co.: locality unknown (KU 145266, MSB 46468); 7.5 mi W Animas, Antelope Pass (KU 145258–145259); Cienega Ranch ruins (KU 144031); 30 mi E Douglas, Guadalupe Canyon, Peloncillo Mts. (KU 145260–145265); San Luis Spring, Mexican Boundary (USNM 38250); Lincoln Co.: Capitan Mts. (USNM 127229); Shafer Ranch (UMMZ 114784); Otero Co.: 3 mi N Tularosa (UMMZ 81380); Union Co.: Tollgate Canyon, 10 mi N Folson (MWSU 15900). Nevada: Nye Co.: 1 mi N, 5 mi E Grapevine, Peak Mt., 5500 ft (MVZ 92391). Oklahoma: Cimarron Co.: 2 mi N Kenton (MWSU 15867–15868, 15895); 3 mi N Kenton (MWSU 15902); 4 mi N Kenton (MWSU 15779); Comanche Co.: Wichita Mts. National Wildlife Refuge (USNM 271959); Harmon Co.: 4 mi S Hollis (OSU 5823). Texas: Archer Co.: intersection US 82 and 277, 22 mi SW Holliday (UMMZ 167208–167209); 14 mi WNW Archer City (MWSU 8584, 8586); Lake Kickapoo (MWSU 5614), NW side Lake Kickapoo (MWSU 7016, 11106); Bexar Co.: San Antonio (USNM 125708); Brewster Co.: Burro Mesa, 3500 ft (MVZ 80281); Briscoe Co.: Tule Canyon (UMMZ 67277); Cottle Co.: 8 mi ESE Paducah (KU 64560); Dickens Co.: 1 mi E Dickens (MWSU 2543); El Paso Co.: near Fort Bliss, about 2 miles above El Paso (USNM 2653/4437); Garza Co.: locality unknown (MMNH 12502–12503); 1 mi SE Post (PSM 13878); Hansford Co.: 10 mi S, 3 mi W Gruver (KU 119395); Howard Co.: Big Spring (UMMZ 80248); Jim Wells Co.: near Alice (TCWC 53283); Knox Co.: 4 mi E Benjamin (MWSU 16023); Nueces Co.: Corpus Christi (USNM 120087). Locality unknown: (USNM 4437).

Conclusions

As presently understood, the geographic distributions of these three taxa do not overlap, although those of *Notiosorex crawfordi* and *N. evotis* are parapatric in northern Sinaloa. We believe the lack of overlap in geographic ranges is the result of these taxa being low in abundance wherever they occur, use of trapping techniques inappropriate for collecting shrews during surveys of small mammals, and lack of collecting effort for soricids over large segments of the distribution of *Notiosorex* in Mexico.

In multivariate space, not only can 100% of *N. villai, N. crawfordi,* and *N. evotis* be separated (Fig. 3), but *N. villai* can be distinguished from *N. crawfordi* and *N. evotis* by the qualitative character of the roof of the glenoid fossa not extending laterally from the cranium (Fig. 4). Also, *N. crawfordi* and *N. evotis* can be distinguished by the qualitative character of the relative shape of the coronoid processes (Figs. 4B–C; Choate 1969:473, figs. 3b–c) and the quantitative relationship of height of coronoid process and cranial breadth (Fig. 5).

With recognition herein of three species in the genus *Notiosorex,* the Mexican mammalian fauna now includes 28 species in the family Soricidae (Ramírez-Pulido et al. 1996, Woodman & Timm 1999). In Mexico, the greatest diversity of shrews is in the Trans-Mexican Volcanic Belt and the Sierra Madre del Sur provinces. Our discovery of the distinctive new species *Notiosorex villai* in Tamaulipas, part of the Sierra Madre Oriental Province, an area not especially known for endemism (Fa & Morales 1993), and that all three species of *Notiosorex* occur in Mexico, highlights the need for continued collection of specimens and study of available museum specimens to better understand the mammalian fauna of Mexico.

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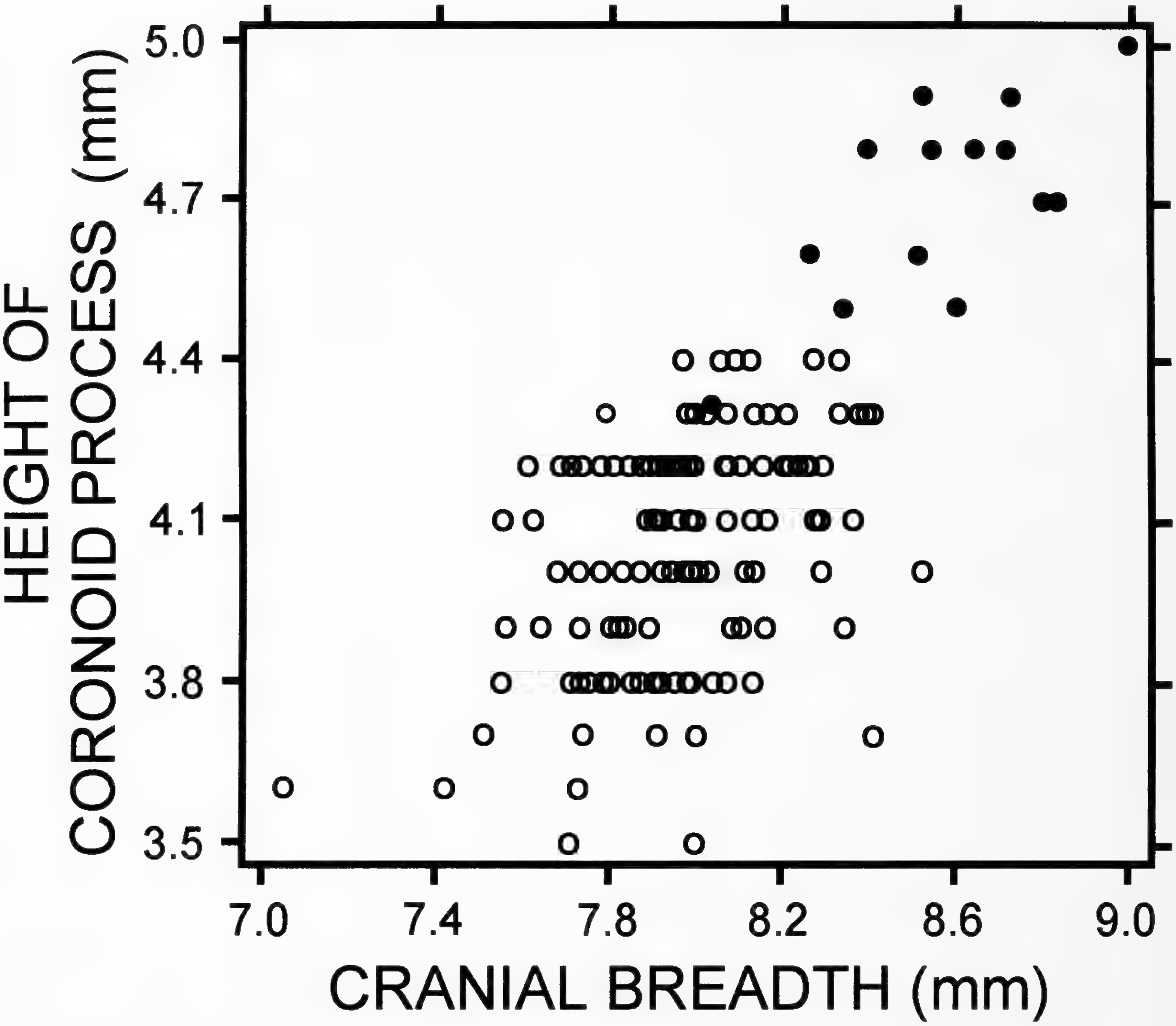

Fig. 5. Bivariate plot of height of coronoid process and cranial breadth illustrating almost complete separation of *Notiosorex evotis* (closed circles) and *N. crawfordi* (open circles).

es (CAS); Michigan State University Museum (MSUM); Midwestern University, Wichita Falls, Texas (MWSU); Mammal Division, National Museum of Natural History (USNM); Collection of Vertebrates, Oklahoma State University (OSU); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); Museum of Vertebrate Zoology, University of California at Berkeley (MVZ); Museum of Zoology, University of Michigan (UMMZ); James Ford Bell Museum of Natural History, University of Minnesota (MMNH); the Museum of Southwestern Biology, University of New Mexico (MSB); and James R. Slater Museum of Natural History, University of Puget Sound (PSM). We thank T. Holmes for preparation of problematic specimens, V. Sánchez-Cordero for translation of our Abstract into Spanish, and N. A. Slade for statistical advice. F. Cervantes, R. S. Hoffmann, V. Sánchez-Cordero, and B. J. Verts read earlier drafts of this manuscript.

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Status of the name *Odocoileus hemionus crooki* (Mammalia: Cervidae)

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Abstract.—The present name of the desert mule deer (*Odocoileus hemionus crooki*) is based on a specimen collected in southwestern New Mexico near the Mexican border. This specimen was originally described as a new species (*Dorcelaphus crooki*) of black-tailed deer, not as a mule deer, because many of its characteristics are intermediate between mule deer and white-tailed deer. In the same publication, *Dorcelaphus hemionus eremicus* is described from western Sonora, Mexico, as a new subspecies of desert mule deer. A number of mammalogists believed the type specimen of *crooki* to be a hybrid between desert mule deer and Coues white-tailed deer (*O. virginianus couesi*), while others hypothesized it represented extremes of normal variation in mule deer. I have reassessed the type specimen of *Dorcelaphus crooki* and reaffirm that it is a hybrid, invalidating the use of the *crooki* subspecies name. Consequently, the oldest available name for the desert mule deer is *O. h. eremicus*.

Resumen.—El nombre actual del venado bura del desierto (*Odocoileus hemionus crooki*) se basa en un ejemplar colectado en el suroeste de Nuevo Mexico cerca de la frontera con México. E. A. Mearns describió este ejemplar como una nueva especie (*Dorcelaphus crooki*) de venado cola negra, no como un venado bura, debido a que muchos de sus caracteres son intermedios entre los del venado cola blanca y los del venado bura. En la misma publicación, Mearns describió también a *Dorcelaphus hemionus eremicus* del occidente de Sonora, México, como una nueva subespecie de venado bura del desierto. Un gran número de mastozoólogos ha considerado que el ejemplar tipo de *crooki* es un híbrido entre el venado bura del desierto y el venado cola blanca de Coues (*O. virginianus couesi*), mientras que otros han hipotetizado que representaba extremos de la variación normal del venado bura. Después de reevaluar el ejemplar tipo de *Dorcelaphus crooki* concluyo que es en realidad un híbrido. Por lo tanto, el nombre válido más antiguo para el venado bura del desierto es *O. h. eremicus*.

Desert mule deer (presently known as *Odocoileus hemionus crooki* Mearns, 1897) inhabit the southwestern United States from West Texas through southern New Mexico and southern Arizona, and southward into Sonora, Chihuahua, Coahuila, Zacatecas, and Durango, Mexico (Leopold 1959, Cowan 1961, Wallmo 1981). In addition, a small herd has been translocated to Nuevo León, Mexico (Morrison et al. 1992; Fig. 1). Since its original description, the subspecific name of this taxon has been contentious due to uncertainties regarding the hybrid status of the type specimen.

Historical Review

Mearns (1897) described *Dorcelaphus crooki* as a new species of black-tailed deer because of its similarity to the Columbian black-tailed deer (*O. h. columbianus*). The type specimen (National Museum of Natu-

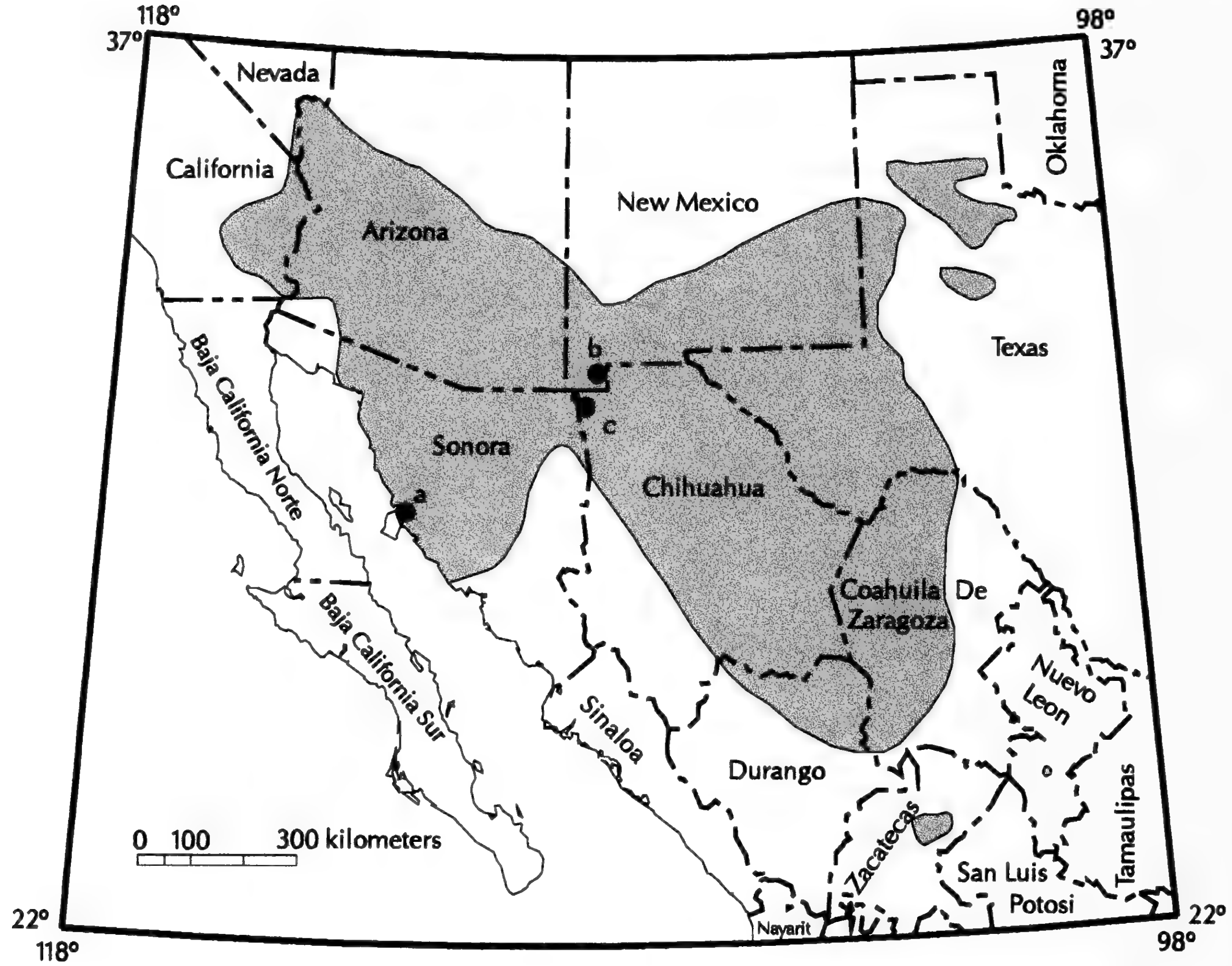

Fig. 1. Current distribution of desert mule deer in the southwestern United States and northern Mexico. Type localities identified for a) *Dorcelaphus hemionus eremicus* Mearns, 1897; b) *Dorcelphus crooki* Mearns, 1897; and c) *Odocoileus hemionus canus* Merriam, 1901.

ral History [USNM] 20572/35752) was collected in 1892 by E. A. Mearns on the summit of the Dog Mountains, Hidalgo County (formerly part of Grant Co.), New Mexico during the survey of the boundary between Mexico and the United States. No other deer with similar characteristics were collected at or near that locality.

In the same publication Mearns (1897) described the "Burro deer or desert mule deer," *Dorcelaphus hemionus eremicus* based on a male (USNM 63403, the type) collected in 1895 by W. J. McGee in the Sierra Seri, Sonora, Mexico. McGee did not keep the skull, but processed the hide as a deer skin rug. Mearns (1897) described the subspecies as pale gray in color with short pelage, a dark dorsal stripe, paler forehead markings, and wide, heavy antlers. This description was based on the skin of the male and two sets of antlers, each from different deer; one of which came from the Sonoyta Valley, Sonora (USNM 59910), the other from Black Butte, Baja California (USNM 60855). Pieces of skin trimmed from the hide as it was made into a rug comprised the only material representing the type specimen in the National Museum until 1902 when the rug was acquired from Anita McGee (Poole & Schantz 1942).

In 1901, Merriam described *Odocoileus hemionus canus* based on a male (USNM 99361) from Sierra en Medio, Chihuahua, Mexico. Merriam (1901) distinguished *O. h. canus* from the western subspecies *O. h. eremicus* solely on the basis of antler conformation. The Sierra en Medio lies only 40 km southwest of the type locality for *Dorcelaphus crooki* in New Mexico.

In his list of big game of North America, and replacing *Dorcelaphus* with the correct senior synonym *Odocoileus,* Seton (1898: 286) included *O. h. eremicus* as a subspecies of mule deer, but maintained the "Crook black-tailed deer" as *O. crooki.* Lydekker (1915) also listed this animal as a black-tailed deer, *O. columbianus crooki.* Following Merriam's (1901) description, *O. h. canus* was used for the desert mule deer in West Texas, Arizona, New Mexico, and northcentral Mexico (Seton 1909, Lantz 1910, Lydekker 1915, Bailey 1931, Cowan 1936, Cahalane 1939, Dalquest 1953).

Several mammalogists believed that *crooki* was based on a hybrid between Coues white-tailed deer (*O. virginianus couesi*) and a desert mule deer but lacked known hybrids for comparison (Lydekker 1898, Seton 1929, Bailey 1931, O'Conner 1939). Goldman & Kellogg (1939) examined the holotype of *O. h. canus* and other specimens from the Sierra en Medio, Chihuahua, along with the holotype of *Dorcelaphus crooki,* and concluded that the type of *crooki* was an unusual specimen of mule deer and not a hybrid. Because the name *crooki* antedates *canus,* they adopted *O. h. crooki* as the correct name for desert mule deer in the north-central states of Mexico and adjacent Arizona, New Mexico, and Texas. Hoffmeister (1962) also re-examined the type of *crooki* and compared it with specimens of *O. virginianus* and *O. hemionus.* He interpreted the specimen as simply a mule deer with some features that were intermediate with or shared by white-tailed deer.

Based on the type specimen from Sierra Seri, the range of *O. h. eremicus* was designated somewhat arbitrarily as western Sonora, southwestern Arizona, and extreme southeastern California (Mearns 1907:210). Hoffmeister (1962) listed *O. h. eremicus* as a synonym of *O. h. crooki* because he did not consider western Sonoran mule deer (burro deer) distinguishable from other populations of desert mule deer. Only Cowan (1936, 1961) and Longhurst & Chattin (1941) attempted to quantify differences between deer within the ranges of *eremicus* and *crooki.* Cowan's (1936) interspecific cranial distinctions were based on only four *eremicus* skulls; of the two additional *eremicus* specimens from Mexico that he used to differentiate external characteristics, one was from Tiburon Island, Sonora, which Cowan (1961) later considered to be a different subspecies (*O. h. sheldoni*). Cowan (1961) based his differentiation of *eremicus* on measurements of only one male and one female specimen, which may have been previously described (Cowan 1936, Longhurst & Chattin 1941). Longhurst & Chattin (1941) added descriptions of pelage variations to differentiate *eremicus,* but they had only one *crooki* skin and three skulls for comparison. Cowan's (1936:236) measurements of *eremicus* from southwestern Arizona and California are within the normal variation of *crooki* reported by Hoffmeister (1986). Hall (1981) continued to treat western Sonoran mule deer as a separate subspecies (*O. h. eremicus*), but provided no supporting information. Hoffmeister (1962) found mule deer from southern Arizona and northern Sonora within 80 km of the type locality of *O. h. eremicus* (Sierra Seri, Sonora) to be sufficiently similar to warrant treating *eremicus* as a synonym of *crooki.* Hoffmeister (1986), while remarking that he could not confirm that *O. h. eremicus* was a synonym of *O. h. crooki,* still implied that western Sonoran mule deer were not distinguishable from those farther east. The purpose of this study is to confirm hybrid status of the type specimen for *O. h. crooki* and clarify subspecific nomenclature for desert mule deer.

Material and Methods

I re-examine the type specimen of *O. h. crooki* to compare and contrast its qualitative and quantitative characters with corresponding features of mule deer, white-tailed deer, and their hybrids from southern Arizona, southern New Mexico, and adjacent Mexico. Published data from previous comparisons are supplemented by measurements (in millimeters) from female *O. h. crooki* (*n* = 12), female *O. v. couesi* (*n* = 17), the type specimen of *Dorcelaphus crooki,* and a known *O. h. crooki* × *O. v. couesi* F_1 hybrid. The type is an adult female, thus I included only adult females (≥2 years old), as determined from tooth wear and replacement (Robinette et al. 1957, Severinghaus 1949), for comparison. Cranial measurements (Table 1) include the six used by Hoffmeister (1962, 1986) in addition to depth of lacrimal fossa (determined as either shallow, deep, or "no decision" by Hoffmeister 1962). All cranial measurements were taken with a metric dial caliper and recorded to the nearest 0.1 mm. Values for paired measurements (e.g., length of right and left nasals) are averages. Elsewhere in this report, I use the term hybrid to refer to only verified *O. h. crooki* × *O. v. couesi* F_1 hybrids, unless otherwise noted.

Review of Characters

Hoffmeister (1962) reviewed characteristics useful for distinguishing *O. virginianus* and *O. hemionus* in Arizona in his evaluation of the type of *crooki.* These included cranial and external measurements (including size of metatarsal gland) along with qualitative descriptions of the type of antler, lacrimal pit, color pattern of the tail, and color and position of the metatarsal gland. He relied heavily on size because desert mule deer are larger than Coues white-tailed deer. Nevertheless, Hoffmeister did not have adults of known hybrids available to evaluate their size characteristics when deciding on the taxonomic status of the type of *crooki.* Although acknowledging Nichol's (1938) success in producing hybrids in captivity, Hoffmeister (1962:52) tended to discount the occurrence of hybrids in the wild. Today, however, data on dimensions and other characteristics are available for mule deer × white-tailed deer hybrids, including both captive produced and genetically confirmed, wild-taken animals. Characteristics of known hybrids produced in captivity provide a morphological basis for assessing suspected hybrids between mule and white-tailed deer encountered in the wild. The primary features used to distinguish between desert mule deer and Coues white-tailed deer concern the length and color pattern of the tail; size, position, and color of hair tuft of the metatarsal gland, depth of the lacrimal pit, and dimensions of the body and cranium (Table 1). My evaluation of the holotype of *crooki* based on these features follows.

Metatarsal glands.—Metatarsal glands of desert mule deer are positioned high on the metatarsus, exceed 75 mm in length, and are circumscribed with brown hair (Caton 1877, Hoffmeister 1986). Those of Coues white-tailed deer are positioned below the midpoint of the metatarsus, measure 25 mm or less in length, and are rimmed by white hairs (Quay 1971, Hoffmeister 1986). Unlike either parent, all known F_1 hybrids have metatarsal glands that are intermediate in length, location, and appearance (Table 2). As affirmed by Mearns (1907) and Bailey (1931), the position of the metatarsal gland in the holotype of *crooki* is intermediate in comparison to its location in white-tailed and mule deer (Fig. 2). It is nearly identical in location, length, and appearance to metatarsal glands of F_1 hybrids produced in captivity (Day 1980) and to wild mule × white-tailed deer hybrids whose status was confirmed genetically (Wishart 1980).

The metatarsal glands of the type of *crooki* (right = 34 mm, left = 42 mm) are longer than those of white-tailed deer (25 mm or less) and well below the range for desert mule deer (75–150 mm; Table 1). Day's (1980) measurements of the metatarsal glands of two adult hybrids born in captivity were 50 mm for a female and 73 mm for a male. Wishart (1980) reported lengths of glands from two wild-taken mule × white-tailed deer hybrids (status confirmed by electrophoresis) as 50 mm for a female and 62 mm for a male. Halloran & Kennedy (1949) and Lang (1957:14) gave lengths of metatarsal glands of adult female desert mule deer from southern New Mexico that averaged 2 to 3 times the length of the gland in the holotype of *crooki.*

Anderson et al. (1964) included the corona of hair (circumglandular hair tuft) in their measurements of the metatarsal glands of 431 adult female mule deer from the Sacramento and Guadalupe mountains of southern New Mexico. Metatarsal gland lengths of females from the Sacramento Mountains (identified as *O. h. hemionus*) averaged 138 mm (range, 100–190); those of the Guadalupe Mountains (identified as *O. h. crooki*), 131 mm (range, 90–190). The shortest (90 mm) is considerably longer than the longest circumglandular hair-tuft measurement (70 mm) on the type of *crooki.*

Mearns (1897, 1907) described the hairs surrounding the metatarsal gland of the type of *crooki* as "sooty at the base and white apically." On examination, these hairs are "sooty at the base;" however, while pale, they are not white apically (Fig. 2c). Instead they are nearly the same pale color as the remainder of the leg, which Mearns (1897, 1907) described as "cream-buff, except where new clay colored hair is coming in on the anterior border." Metatarsal glands of hybrids produced in captivity are either circumscribed with white hairs (G. I. Day, in litt.) or the hairs match the brown coloration of their mule deer parent (J. C. Haigh, in litt.).

Tail.—Mearns (1897:2) described the tail of *crooki* as "colored much as in *D. columbianus,* but has a longer terminal switch; upper side and extremity of tail all black, lower side white medially, and naked towards the base" (Fig. 3c). He gave its vertebral length as 195 mm, which is longer than that of a female hybrid (184 mm; G. I. Day, in litt.) and in the range of *O. v. couesi,* but at or exceeding the upper limit for desert mule deer (Table 1). The color pattern of the tail of the type of *crooki* resembles the tails of captive-born hybrids, which Day (1980) described as "dark reddish-brown or reddish-black above with white beneath and along the borders" (Fig. 3d). Tails of some subspecies of mule deer (e.g., *O. h. fuliginatus*) commonly have a dark dorsal surface; however, this pattern is rare in southern Arizonan and New Mexican populations. Of 349 desert mule deer observed in southeastern Arizona during January 1998, no adults had dark tails resembling the type of *crooki.* However, in areas of sympatry with white-tailed deer, two fawns seen in the company of female mule deer each had a wide, dark tail stripe. I do not know if these were hybrids or pure mule deer fawns; yet hybrid fawns are typically seen in the company of mule deer (Wishart 1980, Kay & Boe 1992), implying that the usual hybrid cross is between an aggressive white-tailed buck and a mule deer doe.

Length of hind foot.—Hoffmeister (1962, 1986) allowed that the length of hind foot (400 mm) of the *crooki* type is more characteristic of white-tailed deer. Based on the data at hand (Table 1), 400 mm is at the upper extreme of length of hind foot for Coues white-tailed deer and at the lower extreme for desert mule deer. G. I. Day's (in litt.) measurement of the length of hind foot in a captive-born hybrid is 405 mm.

Total length.—The total length of the type of *crooki* (1440 mm; Mearns 1897) and that of a female hybrid (1549 mm; G. I. Day, in litt.) is within the range for desert mule deer, but longer than normal for Coues white-tailed deer (Table 1). The ratio of tail length to total length for the type of *crooki* is 7.4× which is at the upper extreme for Coues white-tailed deer; however, the ratio in Day's female hybrid is 8.4× and within the normal range for desert mule deer (Table 1). The range of ratios of tail length to total length in Coues white-tailed deer is 5.6×–7.5×, whereas the normal range of

Table 1.—Comparison of Coues white-tailed deer (*Odocoileus virginianus couesi*), desert mule deer (*O. hemionus crooki*), and an *O. virginianus couesi* × *O. hemionus crooki* F_1 hybrid, and the type specimen of *Dorcelaphus crooki.* All measurements (in millimeters) are from adult females two years of age or older. Characteristics of the type of *Dorcelaphus crooki* from Mearns (1907); cranial measurements from A. L. Gardner (in litt.). Measurements of known hybrid (UA 22358) supplemented by morphological information from G. I. Day (in litt.). Sample sizes in parentheses.

Character	*O. v. couesi*	F_1 hybrid	Type of *crooki*	*O. h. crooki*	Interpretation of *crooki* type
Metatarsal gland:					
Location	Below midpoint of shank[a]	Intermediate	Intermediate	At or above midpoint of shank[a]	Hybrid
Length	Usually <25[a] 14–23 (4)[b] 18 (1)[d]	50	34R, 42L[m]	75–150[a] 102–121 (4)[c] $\bar{X}$ = 132[e]	Hybrid
Length hair tuft			70	90–190 (431)[f]	Hybrid
Color hair tuft	White[a,g]	Brown or white	Pale brown	Buff or Brown; never white[a,g]	Hybrid
Tail:					
Length	215–260 (3)[h] >188[a] 170–230 (9)[d]	184	195	170–228 (5)[h] 145–180 (8)[a] 152–191 (5)[c] 165–229 (8)[i] 127–185 (8)[j]	Mule deer or Hybrid
Dorsal color	White border, dull cinnamon[h] Gray, reddish-brown, grayish brown or almost black[a]	Dark reddish-black[d] Like white-tailed deer[k]	Black	White with black terminal brush[h] No white border, usually without midband[a]	Hybrid
Length of hindfoot	387–390 (3)[h] <404[a] $\bar{X}$ = 409[e] 332–405 (18)[d]	405	400	430–464 (5)[h] 380–490 (448)[f] 406–445 (5)[c] 406–475 (8)[a]	Hybrid
Total length	1410–1450 (3)[h] 1230–1420 (18)[d]	1549	1440	1370–1570 (5)[h] 1346–1549 (5)[c] 1397–1702 (8)[l] 1430–1582 (8)[j]	Mule deer or Hybrid
Ratio of tail to total length	5.6 ×–6.6× (3)[h] 5.9 ×–7.5 × (9)[d] 6.4 ×–7.3 ×[m] $\bar{X}$ = 5.7 ×[e]	8.4 ×	7.4 ×	6.0 ×–8.9 × (5)[h] 8.2 ×–10.5 ×[m] 8.1 ×–10.2 × (5)[c] $\bar{X}$ = 8.0 × (8)[i] $\bar{X}$ = 10.1 ×[e]	Hybrid
Depth of lacrimal fossa	3.0–5.7 (4)[n] Shallow[a,h]	5.3	5.9R, 6.3L	6.4–11.2 (11)[n] Deep[a,h]	Hybrid
Length of ear	<172[m] 145–170 (18)[d]	188	190	190–193 (2)[h] 184.2–203.2 (5)[c] 175–220 (8)[a] 194.7–209.6 (8)[l]	Mule deer
Basilar length	205–216 (4)[n] 190.9–216.2 (13)[o]	222	229[o]	239–265 (7)[n] 230–246 (12)[a]	Hybrid
Length of nasals	71.3–79.8 (5)[n] 60.4–76.7 (13)[o] 56.4–61.0 (3)[a]	72.0	80.7[o]	79.1–95.6 (8)[n] 79–95 (4)[h] 62.5–81.7 (12)[a]	Mule deer
Orbital width	55.3–59.7 (5)[n] 54.5–56.0 (4)[a]	63	64.2[o]	65.7–79.8 (10)[n] 68.0–81.0 (12)[a]	Hybrid

Table 1.—Continued.

Character	*O. v. couesi*	F_1 hybrid	Type of *crooki*	*O. h. crooki*	Interpretation of *crooki* type
	51.5–62.2 (13)[o]				
	51.4–60.8 (2)[p]				
Zygomatic width	87.8–97.7 (6)[n]	96.3		99.1–113.7 (9)[n]	Mule deer
	90–97 (4)[a]		102.1[o]	100–110 (13)[a]	
	89.4–100.4 (11)[o]				
	96.6–100.7 (2)[p]				
Length of upper P-M toothrow	63.5–67.2 (5)[n]	70.5		72.1–82.6 (11)[n]	Mule deer
	61.1–69.6 (13)[o]		76.4[o]	80–89 (4)[h]	
	63.4–66.8 (4)[a]			70.1–85.5 (12)[a]	
Length of lower P-M toothrow	72.5–76.2 (3)[n]	80.7		80.9–100.5 (10)[n]	Mule deer
	66.1–77.6 (11)[o]		87.2[o]	87–97 (4)[h]	
	72.1–74.4 (2)[a]			82.4–97.4 (12)[a]	
Usual topographic elevation (m)	1231–2154[q]		above 1800	<1400[r]	White-tailed deer

[a] Hoffmeister 1986.
[b] Quay 1971.
[c] Halloran & Kennedy 1949.
[d] G. I. Day, in litt.
[e] Lang 1959.
[f] Anderson et al. 1964.
[g] Caton 1877.
[h] Mearns 1907.
[i] Cowan 1961.
[j] J. C. Truett, in litt.
[k] Nichols 1938.
[l] Bailey 1931.
[m] Hoffmeister 1962.
[n] This study.
[o] A. L. Gardner, in litt.
[p] Krausman et al. 1978.
[q] Anthony & Smith 1977.
[r] Krausman 1978.

ratios in desert mule deer is 7.7×–10.5× (Mearns 1907, Hoffmeister 1962, G. I. Day, in litt.). An exception is a desert mule deer from west of El Paso, Texas (Mearns 1907), with an unusually long tail (228 mm) and short total length (1307 mm) yielding a ratio of 6.0×.

Length of ear.—Total length of ear for the type specimen of *O. h. crooki* (190 mm) is within the normal range for desert mule deer and is longer than that of a white-tailed deer (Table 1). The length of ear for two adult F_1 hybrids (*O. h. crooki* × *O. v. couesi*) was 188 mm (female), and 209 mm (male), also within the normal range for mule deer (G. I. Day, in litt.).

Lacrimal fossa.—Depth of the lacrimal fossa is diagnostic; it is deeper (6.4–11.2 mm) and larger in desert mule deer than in Coues white-tailed deer (3.0–5.7 mm). Hoffmeister's (1962:49) "no decision" on the depth of the fossa in the type specimen of *crooki* was because both fossae are fenestrate. However, the floor of each fossa is clearly evident and the depth of the right fossa measures 5.9 and the left fossa, 6.3. These measurements are intermediate between the ranges of lacrimal-fossa depths of the two species and confirms Wishart's (1980) observation for known mule × white-tailed deer hybrids. Depth of lacrimal fossa in another hybrid doe measures 5.3 (Table 1), which is near the upper range of that for white-tailed deer.

Table 2.—Comparison of length of metatarsal gland reported for the type specimen of *Dorcelaphus crooki*, several subspecies of mule deer (*Odocoileus hemionus*), and for known mule deer × white-tailed deer hybrids. Measurements (in millimeters) from adult females two years of age or older, unless otherwise noted.

Common name of subspecies	Scientific name	*n*	$\bar{X}$ length of metatarsal gland (range in parentheses)	Source
White-tailed × mule deer F_1 hybrid	*O. virginianus* × *O. hemionus*	2	50 (♀♀), 62 (♂♂)	Wishart 1980
Coues white-tailed × desert mule deer F_1 hybrid	*O. v. couesi* × *O. h. crooki*	2	50 (♀♀), 73 (♂♂)	Day 1980
Crook's blacktail	Type of *crooki*	1	34R, 42L	Hoffmeister 1962
Desert	*O. h. crooki*		132	Lang 1957
			(75–150)	Hoffmeister 1962
		4	110 (102–121)	Halloran & Kennedy 1949
Rocky Mountain	*O. h. hemionus*	1	110	Longhurst & Chattin 1941
		7	114	Cowan 1961
		2	108 (101–116)	Cowan 1936
Burro	*O. h eremicus*	1	162	Longhurst & Chattin 1941
Peninsula	*O. h. peninsulae*	3	95 (90–100)	Cowan 1936
California	*O. h. californicus*	2	90 (89–91)	Cowan 1936
Southern	*O. h. fuliginatus*	3	78 (65–93)	Cowan 1936
Columbian black-tailed deer	*O. h. columbianus*	14	51 (35–84)	Cowan 1936
Sitka black-tailed deer	*O. h. sitkensis*	3	44 (41–51)	Cowan 1936

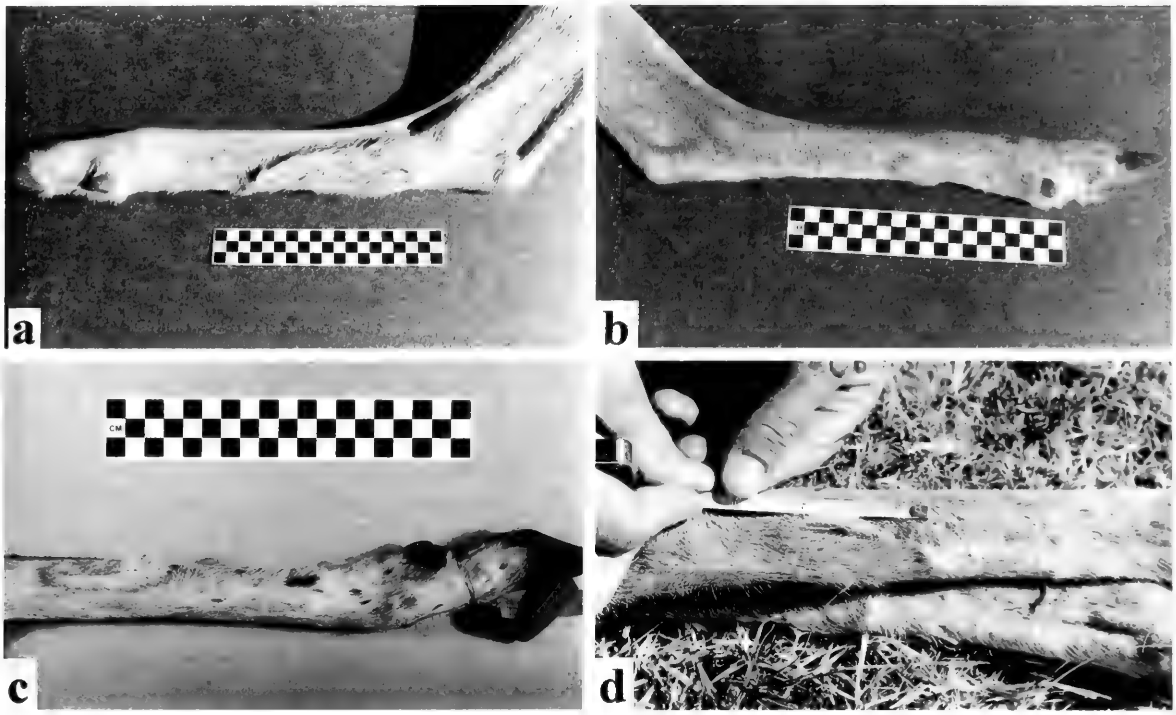

Fig. 2. Metatarsal glands of: a) desert mule deer (*Odocoileus hemionus crooki* [=*eremicus*]); b) Coues white-tailed deer (*O. virginianus couesi*); c) holotype of (*Dorcelaphus crooki*, USNM 20572/35752); d) known F_1 hybrid (*O. h. crooki* × *O. v. couesi*). Photographs by J. R. Heffelfinger (a & b), L. M. Snyder (c), and G. I. Day (d).

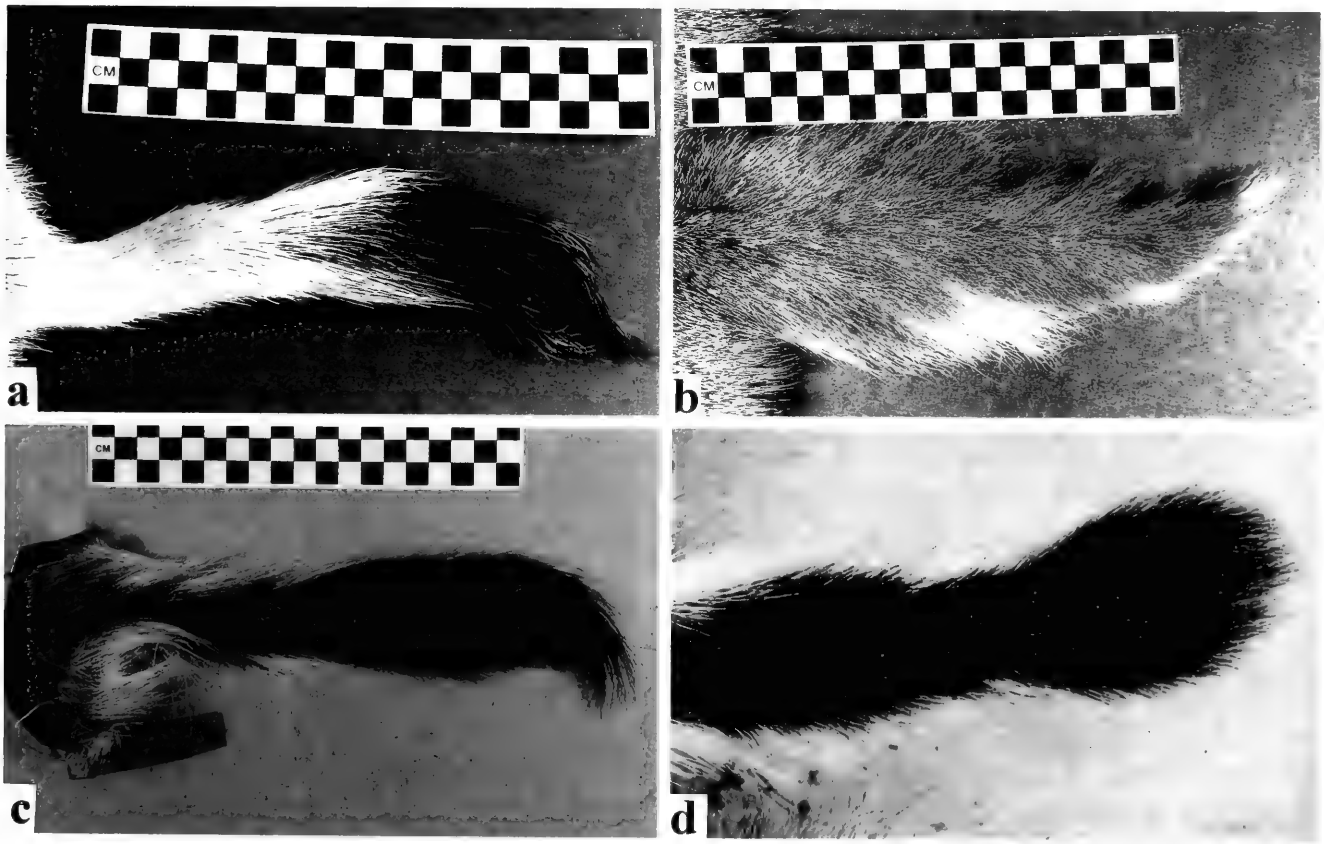

Fig. 3. Tails of: a) desert mule deer (*Odocoileus hemionus crooki* [=*eremicus*]); b) Coues white-tailed deer (*O. virginianus couesi*); c) holotype of (*Dorcelaphus crooki*, USNM 20572/35752); d) known F_1 hybrid (*O. h. crooki* × *O. v. couesi*). Photographs by J. R. Heffelfinger (a & b), L. M. Snyder (c), and G. I. Day (d).

Cranial measurements.—Hoffmeister's (1962, 1986) decision that the type of *crooki* was a mule deer pivoted on the use of skull measurements. Adult desert mule deer in the region of the type locality of *crooki* are much larger and may weigh twice as much as Coues white-tailed deer resulting in some cranial dimensions being interspecifically diagnostic. Hoffmeister (1962:48) provided generalized interspecific limits, but not actual ranges of the six measurements (basilar length of Hensel, length of nasals, orbital width, zygomatic breadth, and length of both upper and lower molariform toothrows) he used in separating female mule and white-tailed deer. He said all six measurements of the type specimen for *crooki* were within the lower range of these measurements for desert mule deer. However, I found that orbital width and basilar length were below the corresponding ranges for this measurement for mule deer; the remaining four measurements were within the normal range. The discrepancy between Hoffmeister's (1962) measurement of the nasals of the type of *crooki* and the longer measurement in Table 1 credited to A. L. Gardner results from Hoffmeister's measurement equaling the shortest distance from the frontal-nasal suture to the proximal margin of its anterior border between medial and lateral anterior projections. Gardner's measurement is the average of the greatest distance between anterior and posterior points of right and left nasals; the right nasal measures 80.0 mm and the left, 81.5 mm. Hoffmeister's (1986) principal components analysis using 11 cranial measurements grouped measurements of the type of *crooki* with those of mule deer. Cranial measurements of an adult captive-born hybrid doe are either intermediate or within the normal range for mule deer (Table 1).

Cowan (1962) reported four cranial dimensions (width of nasals, interorbital width, palatal width, and postpalatal width) used to differentiate mule deer and white-tailed deer in Alberta, Canada. Three of these four measurements from a male mule × white-tailed deer hybrid (as determined from metatarsal gland characteristics) were within the normal range for mule deer. Wishart (1980) used five cranial measurements in an analysis of a male and a female wild-taken hybrid (both confirmed by electrophoresis) in Alberta. All measurements fell within the normal range for mule deer with the exception of post-palatal width of the female, which was within the range for white-tailed deer.

Type locality.—Mearns (1897, 1907:190) collected the type of *Dorcelaphus crooki* on 9 June 1892, on the summit of "Emory Peak of the Dog Mountains, where I noted its range as from 1500 to 1868 meters." Mearns (1907:87) was camped at "Dog Spring . . . [which] is about 2 kilometers . . . north of [Boundary] Monument No. 55 . . . near the south extremity of the Dog Mountains, a rugged range of which Emory Peak, having an altitude of 1868 meters (6129 feet), is the highest." Dog Spring (31°21′N, 108°19′W) appears on several old maps as "Ojo del Perro." The Dog Mountains are known today as the Alamo Hueco Mountains. Apparently, the name Emory Peak does not appear on any topographic map of the area produced from 1881 through 1983 (C. Kollen, pers. comm.). A Department of the Interior, General Land Office map dated 1903 shows an "Emory Sp." northwest of Ojo del Perro, in the general vicinity of Pierce Peak (31°27′N, 108°20′W). As Pierce Peak is drained to the north by Emory Canyon and 11 km northwest of Dog Spring, it is most likely the same peak identified by Mearns as Emory Peak. The elevation of Pierce Peak is given today as 1877 m; however, a map of the area dated 1942 has the elevation as 6149 ft (1874 m). Mearns' (1907) elevation of 1868 m for Emory Peak is nearly equivalent; furthermore, Pierce Peak is covered with alligator juniper (*Juniperus deppeana*), which matches his description of the area.

The elevation at which the type of *crooki* was collected, presumed to be above 1800 m, is above the normal upper elevational limit for desert mule deer (1400; Krausman 1978, McCulloch 1972). Coues white-tailed deer, however, often occur in highest densities between 1230 and 2150 m elevation (Anthony & Smith 1977). Both species are present in the Alamo Hueco Mountains, but white-tailed deer are less common today than they were earlier in this century (Bailey 1931; Raught 1967; A. Hurt, pers. comm.).

Discussion

In the original description of *Dorcelaphus crooki,* Mearns (1897:3) said "The skull has very nearly the same conformation as that of *D. columbianus* [black-tailed deer], the lacrimal fossa being deeper than in the Virginia deer, but shallower than in the mule deer. The same intermediate condition obtains with respect to the vomer, in the relationships of the nasal and premaxillary bones, in the form and size of the teeth; and, in short, the whole animal appears to be a compromise between the characteristics of the white-tailed and mule deer."

In 1907, Mearns referred to this taxon as *Odocoileus crooki* and explained naming the deer for General George Crook. Mearns also received a specimen of a 2-year-old buck shot in the vicinity of Bill Williams Mountain, Arizona, in 1884 by a member of General Crook's hunting party. Mearns believed this specimen also represented his new species of black-tailed deer. I have not examined the male to verify its hybrid status because its identity has no bearing on the status of the name *crooki* because it is not the type. Mearns (1907:187) reported the length of metatarsal gland on this specimen as 13 mm, which is typical of a white-tailed deer (Table 1).

For several decades following Mearns' (1897) description of *Dorcelaphus crooki,* several authorities suggested that the type was a hybrid (Lydekker 1898, Seton 1929, Bailey 1931, O'Conner 1939) and Merriam's name *O. h. canus* was used for the desert mule deer. Goldman & Kellogg (1939), having noted that a mule deer (*O. h. peninsulae*) from lower Baja California, Mexico, had a tail color pattern similar to that of the type of *crooki* and reasoning that their animal could not be a hybrid because white-tailed deer were not in Baja California, concluded that the type of *crooki* was an abnormal specimen of mule deer. Hoffmeister (1962, 1986) acknowledged that the type of *crooki* was intermediate in some features, but believed the preponderance of evidence, particularly of size, supported his assessment that the animal was simply an abnormal mule deer. He also said that the metatarsal gland may be small or indistinct in some populations of mule deer elsewhere, citing Hershkovitz's (1958:538) observation that two mule deer from lower Baja California, Mexico, had poorly-developed glandular tissue underlying well-defined metatarsal hair tufts. Nevertheless, the type specimen of *crooki* has shortened metatarsal glands and circumglandular tufts unlike those of any known mule deer, but consistent in size, form, and position with those of known hybrids (Tables 1 & 2). Hoffmeister (1962:52), in his statement "The few 'hybrids' that I have been able to track down either prove to be clearly *O. hemionus* or *O. virginianus,*" implied that hybridization between these species probably did not occur in the wild.

White-tailed deer × mule deer hybrids are known to have been produced in captivity as early as 1865 (Gray 1972). Other examples of hybridization have been documented at captive facilities in Arizona (Nichol 1938, Day 1980), Colorado (Spraker et al. 1997), Illinois (Caton 1877), Texas (Derr 1990), Wyoming (Guiroy et al. 1991, E. S. Williams, in litt.), and Alberta, Canada (Lingle 1992, W. D. Wishart, in litt.). Whitehead (1972) reported white-tailed × black-tailed deer hybrids produced in captivity in Tennessee.

Hybridization between white-tailed deer and mule deer has been documented genetically or on the basis of metatarsal gland morphology in the wild in Arizona (Day 1964, P. A. Dratch, in litt., J. A. Holcomb, in litt.), Montana (Cronin 1991), Texas (Carr et al. 1986, Stubblefield et al. 1986, Derr 1990, Ballinger et al. 1992), Washington (Gavin & May 1988), Wyoming (Kay & Boe 1992), and in Alberta (Wishart 1980) and British Columbia (Cowan 1962), Canada. White-tailed deer and mule deer are sympatric in the vicinity of the type locality of *crooki* (Hoffmeister 1962; A. Hurt, pers. comm.), and hybrids are documented from adjacent areas in Arizona and Texas.

The only genetic tests that will differentiate white-tailed deer and mule deer are electrophoresis of albumin (Scribner et al. 1984) and erythrocyte acid phosphatase (P. A. Dratch, in litt.), and isoelectric focusing of muscle esterase (Oates et al. 1979). All of these analyses require fresh or frozen samples. No molecular markers are currently known that will differentiate these species from skin samples from museum specimens (P. A. Dratch, in litt.).

Known hybrids are large and some body (length of ear and total length) and cranial measurements (zygomatic breadth, length of nasals, and upper and lower molariform toothrows) are within the normal range for desert mule deer (G. I. Day, in litt.). The phenomenon of heterosis (hybrid vigor) in F_1 hybrids is well known in cervids (Krzywinski 1993, Tate et al. 1997). The deer farming industry has capitalized on heterosis by crossing the phenotypically diverse, but presumed conspecific, red deer and wapiti (*Cervus elaphus*). F_1 hybrids show higher and faster weight gains making them more profitable than either purebred parental stock (Pearse 1993). Variability in overall size of F_1 phenotypes means that most cranial and body measurements are poor choices for evaluating hybrid status in deer (Cowan 1962; Day 1980, in litt.; Wishart 1980).

Any mule deer may have an abnormal tail, metatarsal gland, lacrimal fossa, cranial measurements, or length of hind foot. However, many characteristics from the type specimen for *crooki* fall outside the normal range of variation for mule deer, and are consistent with those of known white-tailed × mule deer hybrids. The overwhelming concordance of morphologic evidence in this comprehensive analysis reveals the holotype of *Dorcelaphus crooki* as a hybrid between Coues white-tailed deer and desert mule deer. This, then, has serious repercussions for the current scientific name for desert mule deer. A scientific name based on a type specimen later found to be a hybrid is invalid and can not be used for either of the parental species even if it has priority over all other available names (ICZN 1985: Art. 23[h]). This reanalysis clarifies the long-standing confusion regarding the status of this contentious type specimen and therefore the correct scientific name for this taxon. The oldest available name for desert mule deer (formerly known as *O. h. crooki* and *O. h. canus*) is *Odocoileus hemionus eremicus* Mearns, 1897; an abbreviated synonymy follows:

Odocoileus hemionus eremicus (Mearns)

Dorcelaphus crooki Mearns, 1897:2; unavailable name because it is based on a hybrid.

Dorcelaphus hemionus eremicus Mearns, 1897:4; type locality "Sierra Seri, near the Gulf of California, in the most arid portion of Sonora, Mexico."

Odocoileus hemionus canus Merriam, 1901:560; type locality "Sierra en Media, Chihuahua, Mexico."

Odocoileus hemionus crooki: Goldman & Kellogg, 1939:507; name combination.

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Appendix I
Specimens Examined

With the exception of the two type specimens of mule deer (both males) listed below, specimens used in this analysis, including the type of *Dorcelaphus crooki*, are all adult females ($\geq$2 years), and deposited in the following institutions: Arizona State University (ASU); Arizona Game and Fish Department, Tucson (AGFD); University of Arizona (UA); National Museum of Natural History (USNM). A. L. Gardner measured the USNM specimens; I measured all others.

Odocoileus hemionus crooki [=*eremicus*] (14).—United States. Arizona: Yavapai Co., 8 km NE Horseshoe Dam (ASU 643); Maricopa Co., 3 km E Horseshoe Dam (ASU 637); Pinal Co., N side of Canyon Lake (ASU 643), Picacho Mountains (UA 24418–24420, 24429, 24430, 24436, 24478, 25299, 25308). Mexico. Chihuahua: Sierra en Medio (USNM 99361, type of *O. h. canus*). Sonora: Sierra Seri (USNM 63403, type of *O. h. eremicus*).

Odocoileus virginianus couesi (17).—United States. Arizona: Cochise Co., Chiricahua Mountains (UA 20340, 20346); Graham Co., Blue River (USNM 32115); Pima Co., Santa Rita Mountains (AGFD 10, UA 23304), Baboquivari Mountains (AGFD 53201); Santa Cruz Co., Santa Rita Mountains (USNM 202931). New Mexico: Catron Co., Mogollon Mountains (USNM 148574); Grant Co., 32 km W Silver City (USNM 286685), head of Mimbres River (USNM 147476); Hidalgo Co., near Cloverdale (USNM 35748). Mexico. Chihuahua: Colonia Garcia (USNM 99347, 99350); Sonora: San Luis Mountains (USNM 36320); E side of San Luis Mountains (USNM 35751, 37085); Pozo de Luis (USNM 59229).

Odocoileus hemionus crooki [=*eremicus*] × *O. virginianus couesi* hybrids (2).—Arizona: Pima Co., University of Arizona Captive Facilities (UA 22358). New Mexico: Hidalgo Co., Summit of the Dog Mountains (USNM 20572/35752, type of *Dorcelaphus crooki*).

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The following Applications were published on 30 September 1999 in Vol. 56, 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.), % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case No.

3116 *Gnomulus* Thorell, 1890 (Arachnida, Opiliones): proposed designation of *G. sumatranus* Thorell, 1891 as the type species.

3089 *Leucocytozoon* (Protista, Haemosporida): proposed adoption of Berestneff, 1904 as the author and of *Leukocytozoen danilewskyi* Ziemann, 1898 as the type species.

3128 *Drosophila rufifrons* Loew, 1873 and *D. lebanonensis* Wheeler, 1949 (currently *Scaptodrosophila rufifrons* and *S. lebanonensis*; Insecta, Diptera): proposed conservation of the specific names by the designation of a neotype for *D. rufifrons.*

3073 *Vespertilio pipistrellus* Schreber, 1774 and *V. pygmaeus* Leach, 1825 (currently *Pipistrellus pipistrellus* and *P. pygmaeus*; Mammalia, Chiroptera): proposed designation of neotypes.

3076 *Tanaecia coelebs* Corbet, 1941 (Insecta, Lepidoptera): proposed conservation of the specific name.

3078 *Diastylis* Say, 1818 (Crustacea, Cumacea): proposed designation of *Cuma rathkii* Krøyer, 1841 as the type species.

3131 *Hybognathus stramineus* Cope, 1865 (currently *Notropis strmineus*; Osteichthyes, Cypriniformes): proposed conservation of the specific name

3075 *Strongylus tetracanthus* Mehlis, 1831 (currently *Cyathostomum tetracanthum*) and *C. catinatum* Looss, 1900 (Nematoda): proposed conservation of usage by the designation of a neotype for *C. tetracanthum*

3084 *Musca geniculata* De Geer, 1776 and *Stomoxys cristata* Fabricius, 1805 (currently *Siphona geniculata* and *Siphona cristata*; Insecta, Diptera): proposed conservation of usage of the specific names by the replacement of the lectotype of *M. geniculata* by a neotype

3122 *Ichthyosaurus cornalianus* Bassani, 1886 (currently *Mixosaurus cornalianus*; Reptilia, Ichthyosauria): proposed designation of a neotype

3095 *Mystacina* Gray, 1843, *Chalinolobus* Peters, 1866, *M. tuberculata* Gray, 1843 and *Vespertilio tuberculatus* J. R. Forster, 1844 (currently *C. tuberculatus*) (Mammalia, Chiroptera): proposed conservation of usage of the names

3121 *Holochilus* Brandt, 1835, *Proechimys* J. A. Allen, 1899 and *Trinomys* Thomas, 1921 (Mammalia, Rodentia): proposed conservation by the designation of *H. sciureus* Wagner, 1842 as the type species of *Holochilus*

3018 *Cervus gouazoubira* Fischer, 1814 (currently *Mazama gouazoubira*; Mammalia, Artiodactyla): proposed conservation as the correct original spelling

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 30 September 1999 in Vol. 56, 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., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Opinion No.

1930 *Osilinus* Philippi, 1847 and *Austrocochlea* Fischer, 1885 (Mollusca, Gastropoda): conserved by the designation of *Trochus turbinatus* Born, 1778 as the type species of *Osilinus.*

1931 *Campeloma* Refinesque, 1819 (Mollusca, Gastropoda): conserved.

1932 *Holospira* Martens, 1860 (Mollusca, Gastropoda): *Cylindrella goldfussi* Menke, 1847 designated as the type species.

1933 *Androctonus caucasicus* Nordmann, 1840 (currently *Mesobuthus caucasicus*; Arachnida, Scorpiones): specific name conserved.

1934 *Paruroctonus* Werner, 1934 (Arachnida, Scorpiones): conserved.

1935 *Cicada clavicornis* Fabricius, 1794 (currently *Asiraca clavicornis*; Insecta, Homoptera): specific name conserved.

1936 *Thamnotettix nigropictus* Stål, 1870 (currently *Nephotettix nigropictus*; Insecta, Homoptera): specific name conserved.

1937 *Corisa propinqua* Fieber, 1860 (currently *Glaenocorisa propinqua*; Insecta, Heteroptera): specific name conserved.

1938 *Musca rosae* Fabricius, 1794 (currently *Psila* or *Chamaepsila rosae*; Insecta, Diptera): specific name conserved.

1939 *Trigonocephalus pulcher* Peters, 1862 (currently *Bothrops pulcher, Bothriechis pulcher* or *Bothriopsis pulchra*; Reptilia, Serpentes): defined by the holotype, and not a neotype; *Bothrops campbelli* Freire Lascano, 1991: specific name placed on the Official List.

1940 *Hoplocephalus vestigiatus* De Vis, 1884 (Reptilia, Serpentes): specific name placed on the Official List.

1941 *Australopithecus afarensis* Johanson, 1978 (Mammalia, Primates): specific name conserved.

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Taxonomy and evolutionary relationships of Phillips' small-eared shrew, *Cryptotis phillipsii* (Schaldach, 1966), from Oaxaca, Mexico (Mammalia: Insectivora: Soricidae)

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Abstract.—The name *Cryptotis peregrina* (Merriam, 1895) previously encompassed two separate populations of a small-eared shrew of the *Cryptotis mexicana*-group inhabiting the Sierra de Cuatro Venados and the Sierra de Miahuatlán in Oaxaca, Mexico. Analysis of museum specimens from these two populations, including the type series of *C. peregrina,* indicates that they are neither conspecific nor even sister taxa. We taxonomically restrict the name *C. peregrina* to populations in the Sierra de Cuatro Venados and adjoining Sierra Yucuyacua, whereas the name *Cryptotis phillipsii* (Schaldach, 1966) is available for the population in the Sierra de Miahuatlán. Moreover, we demonstrate that *C. phillipsii* is the most primitive member of the *C. mexicana*-group, whereas, *C. peregrina* is one of the more derived members of the group.

Choate's (1970) comprehensive revision of the small-eared shrews of the genus *Cryptotis* divided the Mexican and Central American species into three informal groupings: the "*Cryptotis mexicana*-group," the "*Cryptotis parva*-group," and a group of three "relict species." At that time, *C. mexicana* (with four subspecies), *Cryptotis goldmani* (with two subspecies), and the monotypic *Cryptotis goodwini* comprised the *C. mexicana*-group. Based on cranial and postcranial morphology (in particular, unique modifications of the forelimb) and biogeographic patterns, we (Woodman & Timm 1999) recently revised the *C. mexicana*-group, providing evidence that it may represent a natural grouping distinct from other members of the genus. Our revision recognized eight species in the *C. mexicana*-group, many of which were treated previously as subspecies (Choate 1970, Hall 1981): *C. alticola, C. goldmani, C. goodwini, C. griseoventris, C. mexicana, C. nelsoni, C. obscura,* and *C. peregrina.*

Cryptotis peregrina, which is endemic to Oaxaca, Mexico, was first described by Merriam (1895) as a subspecies of *C. mexicana* based on a series of 24 specimens collected by E. W. Nelson and E. A. Goldman in 1894 "from mountains 15 miles [south] west of city of Oaxaca" (Merriam 1895:24). Binford (1989) identified this range of mountains as the Sierra de Cuatro Venados. In addition to the type series, Choate (1970) referred specimens from the Sierra de Miahuatlán in southern Oaxaca, including the holotype and two paratypes of *Notiosorex phillipsii,* to *C. mexicana peregrina.* We initially agreed with Choate's assessment, referring material from the Sierra de Cuatro Venados and the Sierra de Miahuatlán to the species *Cryptotis peregrina* (Woodman & Timm 1999). Cranially, the shrews previously considered by Choate (1970) and subsequent authors (e.g., Hall

1981) to be subspecies of *C. mexicana* (*C. mexicana, C. nelsoni, C. obscura, C. peregrina*) are quite similar and can be difficult to distinguish. However, the foreclaws vary noticably in length and breadth among members of the *C. mexicana*-group (Choate 1970, Woodman & Timm 1999), and we showed that other aspects of the forelimb, in particular the morphology of the humerus, are distinct as well (Woodman & Timm 1999). Our phylogenetic analysis indicated that *C. peregrina* was the most plesiomorphic member of the *C. mexicana*-group.

Our study (Woodman & Timm 1999) focused mainly on the larger, broad-clawed shrews that we termed the *Cryptotis goldmani*-group, which are a subset of the *C. mexicana*-group. Initially, we were interested in the former subspecies of *C. mexicana* primarily as outgroups to aid in polarizing characters for phylogenetic analysis. In studying *Cryptotis peregrina,* we depended heavily on specimens from the Sierra de Miahuatlán in the University of Kansas Natural History Museum collection, because they were readily available to us and included the only postcranial material then known for the species. One inconsistency we noted between our study and Choate's revision was that he referred to *C.* [*m.*] *mexicana* as "having less highly developed front feet and claws" (Choate 1970:232) than *C.* [*m.*] *peregrina.* However, the specimens from the Sierra de Miahuatlán had distinctly shorter and narrower claws than *C. mexicana.* We also observed that their humeri were less modified that those of *C. mexicana,* adding to our view of their being more plesiomorphic.

Recently, we re-studied the holotype and type series of *Cryptotis peregrina* at the National Museum of Natural History and discovered that Choate's (1970) observations were correct—specimens in the type series from Sierra de Cuatro Venados all possess longer, broader claws than *C. mexicana.* In addition, we were graciously granted permission by the American Museum of Natural History to remove the humerus from the only known fluid-preserved specimen of *C. peregrina* from the Sierra Yucuyacua, a mountain range in western Oaxaca that adjoins the Sierra de Cuatro Venados. Study of these specimens indicates that the two populations of *Cryptotis* inhabiting the Sierra de Cuatro Venados\Sierra Yucuyacua complex and the Sierra de Miahuatlán, respectively, are not conspecific. Herein, we taxonomically restrict the name *Cryptotis peregrina* to shrews inhabiting the former region. The name *Cryptotis phillipsii* (Schaldach, 1966) is available for the population in the Sierra de Miahuatlán. Much of what we reported earlier in regard to *C. peregrina* (Woodman & Timm 1999) actually refers to a combination of *C. peregrina* and *C. phillipsii.* It is our purpose here to redescribe *C. peregrina* and *C. phillipsii* in light of this new information and to clarify the distinctions among the species in the *Cryptotis mexicana*-group. In addition, we present a refined hypothesis of phylogenetic relationships among the species in this group of shrews.

Methods

Our current work used the techniques and methods of our previous studies of shrews (Woodman & Timm 1992, 1993, 1999), and more detailed accounts of methodology are presented there. Species and subspecies synonomies list only published uses of names. Regional names, place names, and coordinates in Oaxaca derive from Binford (1989), Choate (1970), and our review of maps and gazetteers of the region. Terminology of dentition and dental characteristics follows Choate (1970). Anatomical terminology of the humerus and other aspects of the postcranial skeleton follows Reed (1951). Measurements used in our analyses follow Woodman & Timm (1993, 1999); abbreviations of measurements are explained in Table 1. Measurements of the skull were taken to the nearest 0.1 mm using either an ocular micrometer in a binocular microscope or a hand-held dial caliper (for condylobasal-length and cranial-breadth). Univariate statistics include mean ± standard deviation.

Multivariate analysis was carried out using Minitab 8.0. Our principle components analysis (PCA; Fig. 1, Table 2) used ten logarithm-transformed cranial measurements (condylobasal-length, breadth-of-zygomatic-plate, interorbital-breadth, breadth-across-U^1s, breadth-across-U^3s, breadth-across-M^2s, palatal-length, length-of-upper-toothrow, length-of-unicuspid-toothrow, length-of-upper-molariform-toothrow) from 12 *Cryptotis peregrina* and 14 *C. phillipsii* with complete crania.

Phylogeny and character evolution were analyzed using PAUP 4.0b2 (see Swofford 1998) and MCCLADE 3.0 (see Maddison & Maddison 1992). Phylogenetic analysis (Fig. 2) was carried out using an exhaustive search of 32 unordered and equally-weighted transition series (Table 3, Appendix I), with *Cryptotis parva parva* and *C. nigrescens* serving as outgroups for polarizing characters.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); Natural History Museum, London (BM); California Academy of Sciences, San Francisco (CAS); Escuela Nacional de Ciencias Biológicas, Mexico City (ENCB); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (UNAM); University of Kansas Natural History Museum, Lawrence (KU); Natural History Museum of Los Angeles County, Los Angeles (LACM); Museum of Comparative Zoology, Cambridge (MCZ); James Ford Bell Museum of Natural History, St. Paul (MMNH); Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City (MZFC); Texas Cooperative Wildlife Collection, College Station (TCWC); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Washington (USNM).

Results of Multivariate Analysis

Principle components analysis (PCA) of cranial variables supports the separation of *Cryptotis peregrina* and *Cryptotis phillipsii.* A plot of factor scores on factor axes 1 and 2 shows a clear distinction between these two species with minimal overlap (Fig. 1). This plot emphasizes the generally larger cranial size (factor axis 1—Table 2) of *C. phillipsii,* despite the generally similar external measurements of the two species (Table 1). In the region of size overlap between the two species on the plot, *C. peregrina* and *C. phillipsii* are separated by the combined effects of the two axes, suggesting a common, but offset trend of decreasing unicuspid-toothrow-length and palatal-length and increasing interorbital-breadth and palatal-breadth (M2B) with increasing size (Table 2).

Revised Phylogeny of the *Cryptotis mexicana*-group

Our re-analysis of phylogenetic relationships within the *Cryptotis mexicana*-group, based on 32 transition series (Table 3), resulted in a single most parsimonious tree of 67 steps (Fig. 2). Discounting differences such as the exclusion of *Cryptotis goodwini magnimana* and the inclusion of *Cryptotis phillipsii* as a species separate from *Cryptotis peregrina,* the new tree essentially matches three of the nine most parsimonious trees from our previous phylogenetic analysis of this group of shrews (Woodman & Timm 1999, fig. 13, central column of trees). The four species that comprised the *Cryptotis goldmani*-group (*C. alticola, C. goldmani, C. goodwini, C. griseoventris*) form the crown clade of the *C. mexicana*-group, whereas the species previously subsumed under the name *C. mexicana* (*C. mexicana, C. nelsoni, C. obscura, C. peregrina, C. phillipsii*) appear as individual branches at different levels of the tree. This supports our previous view that *C. mexicana* (*sensu latu*) was paraphyletic with respect to the *C. goldmani*-group.

Table 1.—Measurements of *Cryptotis mexicana*-group shrews used in this study. Statistics presented are mean ± standard deviation of the mean, and observed extremes.

	C. mexicana (Oaxaca)	*C. nelsoni*	*C. obscura*	*C. peregrina*	*C. phillipsii*
Skin measurements					
	n = 118	*n* = 9	*n* = 55	*n* = 24	*n* = 27
Head and body length (HB)					
	69 ± 4	76 ± 3	66 ± 4	72 ± 3	68 ± 6
	55–88	72–79	56–75	66–78	58–78
Tail length (TL)					
	27 ± 3	29 ± 3	26 ± 2	30 ± 2	31 ± 3
	20–34	22–33	20–32	24–33	23–36
Craniomandibular measurements					
	n = 30	*n* = 6	*n* = 32	*n* = 12	*n* = 14
Condylobasal-length (CBL)					
	18.7 ± 0.4	19.5 ± 0.3	18.4 ± 0.4	19.1 ± 0.4	19.5 ± 0.5
	17.5–19.3	19.1–20.0	17.4–19.1	18.3–19.8	18.8–20.2
Breadth-of-braincase (BB)					
	9.8 ± 0.3	10.4 ± 0.3	9.6 ± 0.2	9.9 ± 0.1	10.3 ± 0.3
	9.3–10.7	9.9–10.7	9.2–10.2	9.7–10.1	9.8–10.7
	(*n* = 28)		(*n* = 30)	(*n* = 11)	(*n* = 13)
Breadth-of-zygomatic-plate (ZP)					
	1.8 ± 0.1	2.0 ± 0.1	2.0 ± 0.1	1.6 ± 0.1	2.0 ± 0.1
	1.4–2.0	1.0–2.2	1.8–2.1	1.5–1.8	1.8–2.3
Interorbital-breadth(IO)					
	4.7 ± 0.2	5.1 ± 0.1	4.7 ± 0.1	4.7 ± 0.1	4.9 ± 0.1
	4.3–5.0	4.8–5.2	4.4–4.9	4.6–4.9	4.7–5.1
Breadth-across-first-unicuspids (U1B)					
	2.4 ± 0.1	2.8 ± 0.1	2.5 ± 0.1	2.5 ± 0.1	2.6 ± 0.1
	2.3–2.5	2.6–2.9	2.3–2.6	2.1–2.6	2.5–2.8
Breadth-across-third-unicuspids (U3B)					
	2.8 ± 0.1	3.3 ± 0.2	2.9 ± 0.1	2.8 ± 0.1	3.1 ± 0.1
	2.7–3.0	3.0–3.4	2.6–3.2	2.6–3.0	2.9–3.4
Breadth-across-second-molars (M2B)					
	5.4 ± 0.2	6.1 ± 0.2	5.3 ± 0.1	5.5 ± 0.2	5.8 ± 0.1
	5.1–5.8	5.9–6.3	5.1–5.5	5.3–5.8	5.6–6.0
Palatal-length (PL)					
	8.2 ± 0.2	8.4 ± 0.2	7.9 ± 0.2	8.5 ± 0.2	8.5 ± 0.2
	7.3–8.5	8.1–8.7	7.5–8.5	8.2–8.9	8.0–8.7
Length-of-upper-toothrow (TR)					
	7.2 ± 0.2	7.6 ± 0.2	7.1 ± 0.2	7.3 ± 0.1	7.5 ± 0.3
	6.6–7.5	7.4–7.8	6.8–7.4	7.2–7.5	7.2–8.0
Length-of-unicuspid-toothrow (UTR)					
	2.4 ± 0.1	2.4 ± 0.1	2.4 ± 0.1	2.5 ± 0.1	2.5 ± 0.1
	2.1–2.5	2.4–2.6	2.1–2.6	2.4–2.6	2.3–2.7
Length-of-upper-molariform-toothrow (MTR)					
	5.2 ± 0.1	5.6 ± 0.2	5.2 ± 0.1	5.3 ± 0.1	5.4 ± 0.2
	4.9–5.5	5.4–5.8	4.9–5.4	5.1–5.4	5.3–5.8

Table 1.—Continued.

C. mexicana (Oaxaca)	*C. nelsoni*	*C. obscura*	*C. peregrina*	*C. phillipsii*
Posterior-width-of-M^1 (WM1)				
1.6 ± 0.1	1.9	1.7 ± 0.1	1.8 ± 0.1	1.8 ± 0.1
1.5–1.8	—	1.6–1.8	1.6–2.0	1.6–2.0
(*n* = 25)	(*n* = 1)			
Length-of-mandible (LM)				
6.0 ± 0.2	6.4 ± 0.1	5.9 ± 0.2	6.2 ± 0.2	6.4 ± 0.3
5.4–6.3	6.3–6.6	5.4–6.4	5.8–6.4	5.8–7.1
Height-of-coronoid-process (HCP)				
4.3 ± 0.1	4.8 ± 0.1	4.4 ± 0.1	4.5 ± 0.1	4.8 ± 0.1
4.1–4.6	4.7–4.8	4.0–4.6	4.3–4.7	4.7–5.1
Height-of-coronoid-valley (HCV)				
2.6 ± 0.1	2.8 ± 0.1	2.6 ± 0.1	2.8 ± 0.1	2.8 ± 0.1
2.3–2.8	2.8–2.9	2.4–2.8	2.7–3.0	2.7–2.9
Height-of-articular-condyle (HAC)				
3.7 ± 0.2	3.9 ± 0.05	3.6 ± 0.2	3.8 ± 0.1	3.9 ± 0.2
3.4–3.9	3.8–4.1	3.2–3.9	3.6–4.1	3.8–4.2
Breadth-of-articular-condyle (BAC)				
2.9 ± 0.1	3.1 ± 0.1	2.9 ± 0.1	3.0 ± 0.1	3.1 ± 0.1
2.7–3.2	3.0–3.2	2.6–3.0	2.8–3.2	3.0–3.3
Articular-condyle-to-M_3 (AC3)				
4.9 ± 0.2	5.2 ± 0.1	4.6 ± 0.2	5.1 ± 0.2	5.0 ± 0.2
4.4–5.2	5.0–5.3	4.3–5.0	4.8–5.3	4.8–5.3
Length-of-lower-toothrow				
5.7 ± 0.1	6.0 ± 0.1	5.7 ± 0.1	5.9 ± 0.1	5.9 ± 0.2
5.4–5.9	5.8–6.2	5.4–5.9	5.8–6.0	5.5–6.2
Length-of-lower-molar-row (m13)				
4.3 ± 0.1	4.5 ± 0.1	4.2 ± 0.1	4.4 ± 0.1	4.4 ± 0.2
4.1–4.5	4.4–4.6	4.0–4.4	4.2–4.5	4.0–4.8
	(*n* = 6)			
Length-of-m1 (m1L)				
1.7 ± 0.1	1.8 ± 0.05	1.7 ± 0.1	1.7 ± 0.1	1.9 ± 0.1
1.6–1.9	1.8–1.9	1.6–1.8	1.6–1.8	1.6–2.0
Weight (g)				
7.4 ± 1.0	—	6.9 ± 1.1	—	8.0 ± 1.1
5.0–9.5		5.0–10.0		6.5–10.0
(*n* = 37)		(*n* = 23)		(*n* = 19)

Cryptotis phillipsii appears as the most primitive member of the *Cryptotis mexicana*-group, matching our supposition based on the morphology of its forelimb. In contrast, *Cryptotis peregrina* is much more derived and serves as a "link" between the *Cryptotis goldmani*-group of shrews and the more primitive members of the *C. mexicana*-group. Based on all but two characters (relative tail length and relative height of the coronoid process of the mandible) *C. peregrina* could, in fact, be considered a member of the *C. goldmani*-group. However, both characters are much more vari-

Table 2.—Factor loadings for the first two factor axes from principle components analysis of *Cryptotis peregrina* and *Cryptotis phillipsii* from Oaxaca. The two axes accounted for 72% of the variation. Abbreviations as in Table 1.

Variable	PC1	PC2
UTR	−0.170	0.378
PL	−0.195	0.523
IO	−0.208	−0.458
MTR	−0.334	−0.102
TR	−0.335	0.233
M2B	−0.337	−0.325
ZP	−0.371	0.221
CBL	−0.371	0.222
U1B	−0.372	−0.198
U3B	−0.373	−0.259

able among the more primitive members of the *C. mexicana*-group (Table 4) than we previously realized (Woodman & Timm 1999). For this reason, we redefine the *C. goldmani*-group below, excluding these two characters.

Systematic Biology

"*Cryptotis mexicana*-group" Choate, 1970

We (Woodman & Timm 1999) recently redescribed the *Cryptotis mexicana*-group as small to medium-sized members of the genus with long, dark dorsal pelage. All members possess variably broadened forefeet and variably broadened and elongated foreclaws; posterior border of the zygomatic plate usually positioned equal to, or

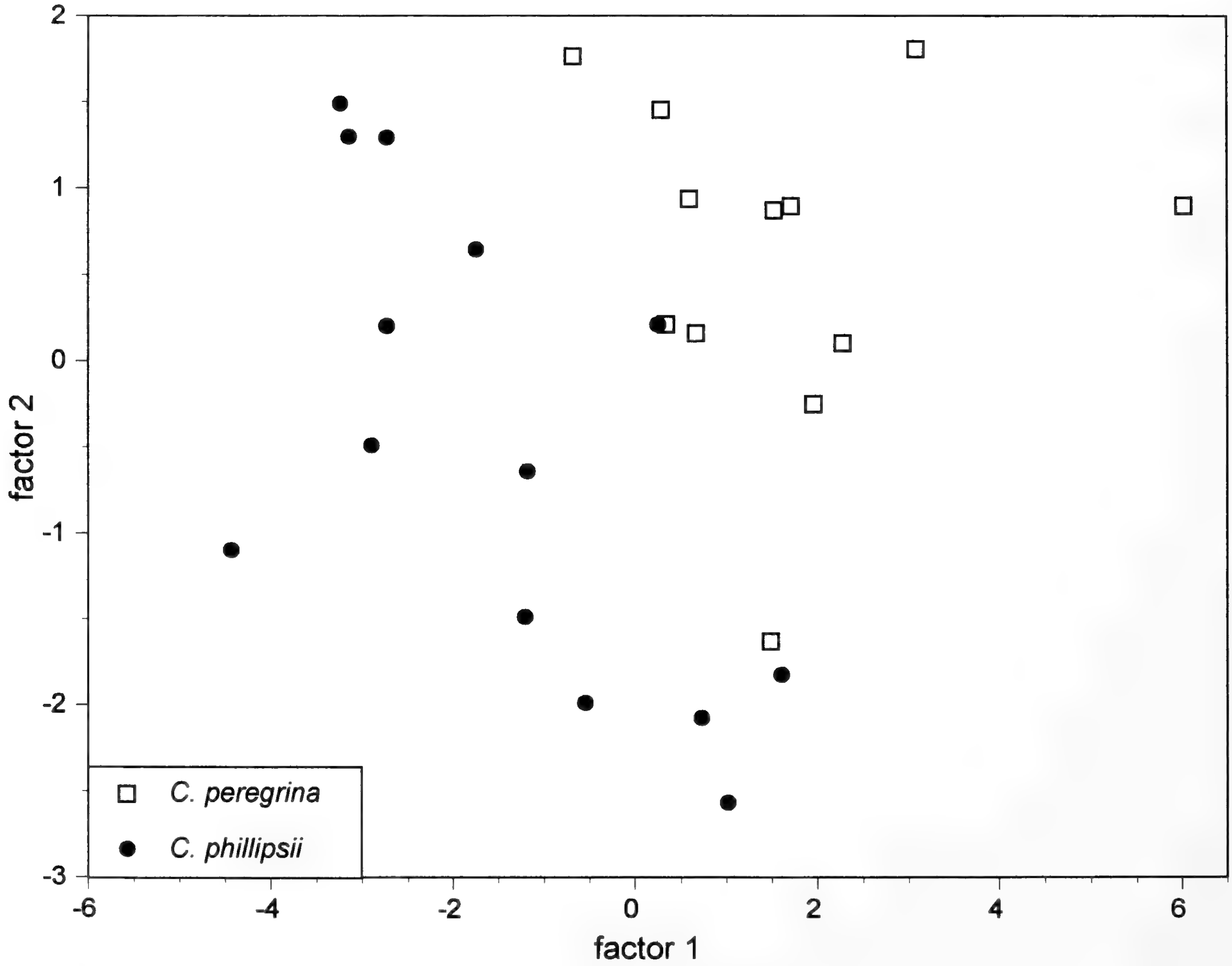

Fig. 1. Plot of factor scores from PCA of ten log-transformed measurements from 12 *Cryptotis peregrina* and 14 *Cryptotis phillipsii*. Factor axis 1 represents size (Table 2); factor loadings are negatively weighted, so the largest individuals have the smallest scores. Factor axis 2 represents a combination of palatal-length, interorbital-breadth, unicuspid-toothrow-length, and breadth-across-M^{2}s (Table 2).

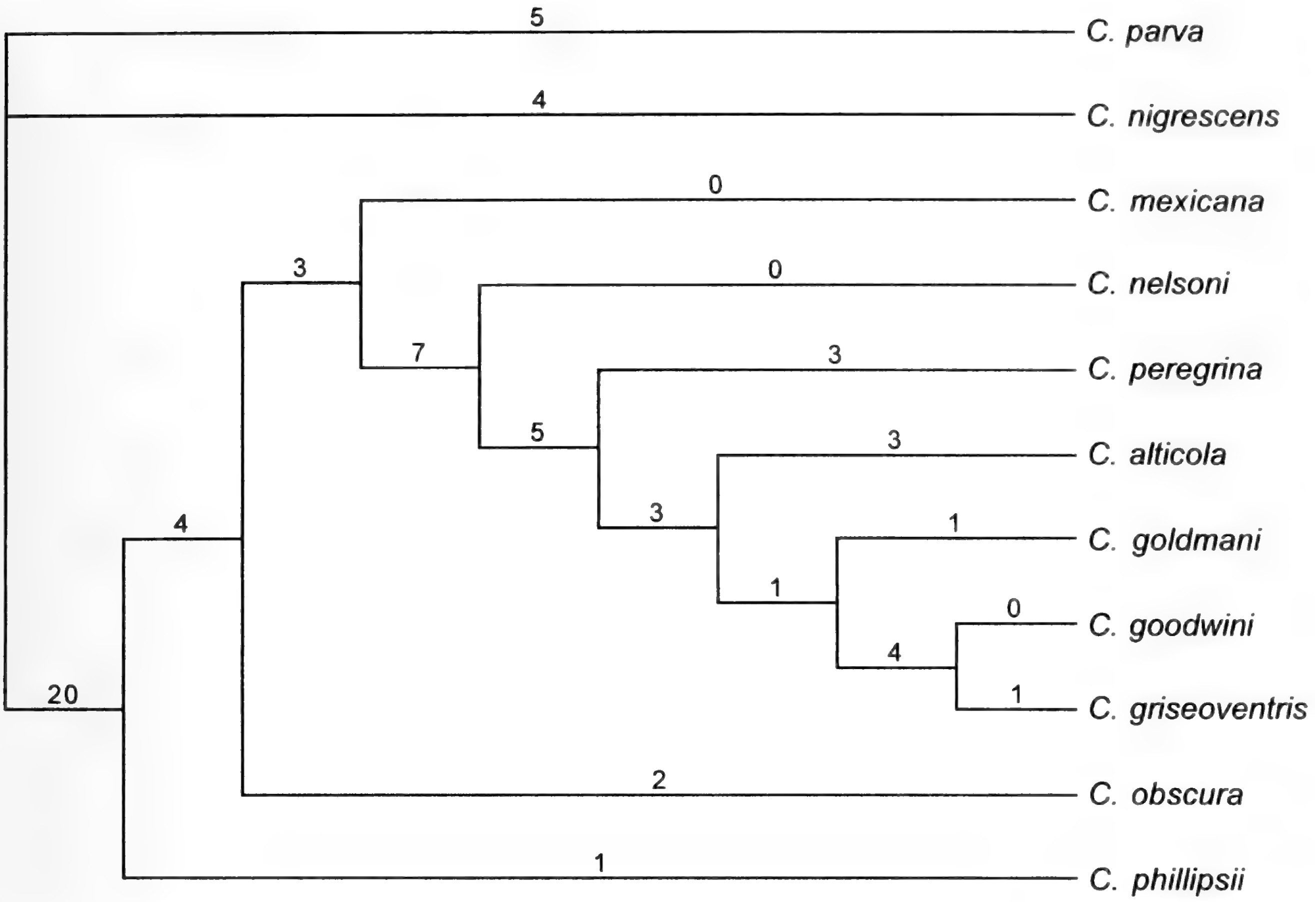

Fig. 2. Topology of the single most parsimonious tree resulting from phylogenetic analysis of the *Cryptotis mexicana*-group of shrews. *Cryptotis nigrescens* and *C. parva parva* served as the outgroups for polarizing characters. Number of transitions is shown for each branch. Tree length = 67 (minimum possible length = 49; maximum possible length = 122); consistency index = 0.731; rescaled consistency index = 0.551; retention index = 0.753; homoplasy index = 0.269.

slightly posterior to, the posterior base of the maxillary process; upper toothrow uncrowded; dentition not bulbous; anterior border of the coronoid process of the mandible joins the horizontal ramus at a relatively low angle; posterior border of lower incisor extends to posterior cingulum of P_4; relatively long distance from the coronoid process to the posterior border of M_3; tall, wide articular face of the articular process; deep lower sigmoid notch; relatively long, low P_3; relatively short, broad metacarpals; shortened and broadened humerus with elongated processes and a dorsoventrally elongate head; deeply pocketed posterior edge of the falciform process of the tibia.

Included species.—Cryptotis alticola, C. goldmani, C. goodwini, C. griseoventris, C. mexicana, C. nelsoni, C. obscura, C. peregrina, and *C. phillipsii.*

Cryptotis peregrina (Merriam, 1895)

Blarina mexicana peregrina Merriam, 1895:24.

C[ryptotis]. mexicana peregrina: Miller, 1911:222.

Cryptotis mexicana peregrina: Hall & Kelson, 1959:60; Goodwin, 1969:39 (in part); Choate, 1970:237 (in part); Hall, 1981:59 (in part).

Cryptotis mexicana mexicana: Goodwin, 1969:39 (in part).

Cryptotis peregrina: Woodman & Timm, 1999:35 (in part).

Holotype.—Skin and skull of male, USNM 68317; captured on 12 September

Table 3.—Complete character matrix for phylogenetic analysis of members of the *Cryptotis mexicana*-group and two outgroups, *Cryptotis parva parva*, and *Cryptotis nigrescens.* Transition series (TS) are explained in Appendix 1.

Taxon	Transition series																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
parva	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	2
nigrescens	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0
mexicana	2	2	1	1	2	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	0	0	2	1	1	0
nelsoni	2	2	1	?	2	1	1	1	1	0	1	1	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	0	2	?	?	1
obscura	1	1	1	?	2	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	2	1	?	0
peregrina	2	2	1	?	2	1	1	1	1	1	0	1	2	1	1	0	2	2	1	2	?	3	1	0	1	0	1	1	2	1	?	1
phillipsii	1	1	1	1	2	1	1	1	1	0	0	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	0	2	0	1	0
alticola	3	3	2	1	2	1	1	1	0	1	0	1	2	1	1	0	2	2	1	2	1	2	0	0	1	1	0	1	2	1	2	2
goldmani	3	3	2	1	2	1	1	1	1	1	0	1	2	1	1	1	2	2	1	3	1	3	0	0	1	1	0	1	2	1	2	1
goodwini	3	3	2	?	2	1	1	1	1	1	0	1	2	1	1	1	2	2	1	2	1	0	1	1	2	1	0	1	2	1	?	1
griseoventris	3	3	2	?	2	1	1	1	1	1	0	1	?	?	?	?	?	?	?	?	?	0	1	1	2	1	0	1	2	?	?	0

1894 by E. W. Nelson and E. A. Goldman (collector number 6748).

Type locality.—"mountains 15 miles [south]west of city of Oaxaca [de Juárez], Mexico (altitude, 9,500 feet)." According to Goldman (1951), the collectors spent September 10th to 19th, 1894, traveling to and from, and working at, this locality. This trip took them ca. 8 mi southwest of Oaxaca de Juárez to Cuilapan, then west into the mountains, passing Santa Inéz [Santa Inés del Monte, 16°54′30″N, 96°52′W] and climbing over the summit to a wet meadow called Nevería Herrera on the western slope.

> "These high mountains, which appeared to have no distinctive name, are somewhat isolated, the only connection with the high mountains to the east being through low hills north of Oaxaca. The upper slopes are well watered, and general conditions much as on Cerro San Felipe. Specimens were labeled 'Mountains 15 miles west of Oaxaca,' but as we later learned the direction was more nearly southwest." (Goldman, 1951:218).

Merriam (1895) reported that the specimens were obtained from a variety of elevations between 8800 [2680 m] and the summit at 9500 ft [2895 m], indicating that the type series of *Cryptotis peregrina* was collected at or near the top of the range. On topographic maps, the summit appears to be near a landmark called La Plazuela [16°56′52″N, 96°53′45″W]. Binford (1989) refers to these mountains as the Sierra de Cuatro Venados.

Distribution.—Known from 2680 to 3200 m in the Sierra de Cuatro Venados, central Oaxaca, and the Sierra Yucuyacua, western Oaxaca (Fig. 3).

Description.—Size medium to large for the genus (Table 1); tail long, averaging 30 mm, or ca. 42% (Table 4) of head-and-body length; dorsal guard hairs 6–7 mm long; forepaws enlarged; foreclaws noticeably elongate and broadened; rostrum of moderate length (PL/CBL = 44.5%, Table 4); often two well-developed dorsal foramina (44%, Table 4); foramen posterior to dorsal articular facet leading to ventral extension

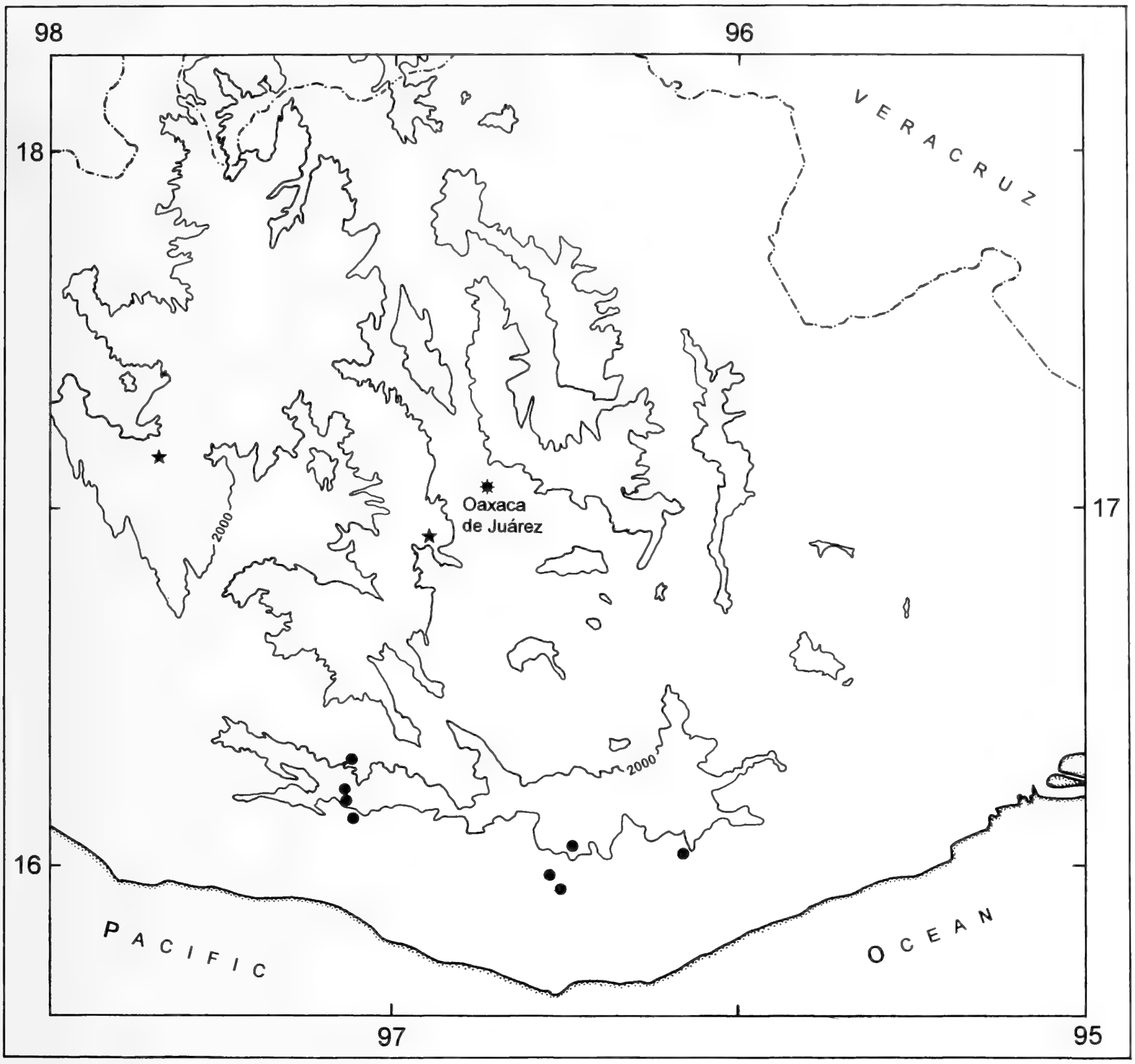

Fig. 3. Map of part of Oaxaca, Mexico, illustrating the known distribution of *Cryptotis peregrina* (★) and *Cryptotis phillipsii* (●). The 2000 m contour is shown.

of the sinus canal typically present on one or both sides of the cranium (94%, Table 4); foramen dorsal to dorsal articular facet typically absent (87%, Table 4); zygomatic plate narrow (ZP/PL = 19.3%, Table 4), anterior border usually aligned with posterior ⅓ of mesostyle-metastyle valley or metastyle of M^1; U^4 unreduced in size, surface area >½ that of U^3; U^4 usually aligned with the unicuspid toothrow and partially visible in lateral view of the skull; P^4, M^1, and M^2 slightly to moderately recessed on posterior border; protoconal basin of M^1 reduced relative to hypoconal basin; M^3 simple: usually possessing paracrista, paracone, precentrocrista (all pigmented), mesostyle, and very short postcentrocrista; M^3 lacking metacone, hypocone absent or poorly-developed, and a reduced, typically unpigmented protocone occasionally present. Articular process of the mandible generally moderately tall and wide, with a moderately broad lower articular facet; moderately high coronoid process of the mandible (HCP/ML = 73.1%, Table 4); entoconid usually present on M_3 (73%, Table 4), typically vesti-

Table 4.—Characteristics among the five species previously synonomized with *Cryptotis mexicana.*

C. mexicana (Oaxaca)	*C. nelsoni*	*C. obscura*	*C. peregrina*	*C. phillipsii*
Foramen of sinus canal				
7%	0%	19%	94%	24%
$n = 90$	$n = 8$	$n = 52$	$n = 16$	$n = 17$
Foramen dorsal to dorsal articular facet present				
13%	38%	28%	13%	82%
$n = 90$	$n = 8$	$n = 36$	$n = 15$	$n = 17$
Two distinct dorsal foramina present				
54%	50%	22%	44%	47%
$n = 95$	$n = 6$	$n = 58$	$n = 16$	$n = 19$
Posteroventral border of unicuspids				
concave	concave	straight to convex	concave	concave
Entoconid of M_3 present				
100%	100%	96%	73%	93%
68% well-developed	100% well-developed	96% well-developed	100% vestigal	83% vestigal
$n = 77$	$n = 7$	$n = 26$	$n = 22$	$n = 13$
Humerus modified				
slightly	?	slightly	extremely	slightly
Relative tail length (TL/HB × 100)				
39 ± 5	38 ± 4	40 ± 6	42 ± 3	46 ± 6
26–52	28–44	29–55	36–47	30–59
$n = 118$	$n = 9$	$n = 55$	$n = 24$	$n = 27$
Relative rostrum length (PL/CBL × 100)				
43.7 ± 0.8	43.2 ± 0.8	43.1 ± 1.1	44.5 ± 0.7	43.3 ± 0.6
41.7–45.1	42.0–44.3	41.0–45.6	43.2–46.0	42.2–44.4
$n = 30$	$n = 6$	$n = 32$	$n = 12$	$n = 14$
Relative breadth of zygomatic plate (ZP/PL × 100)				
21.6 ± 1.6	23.8 ± 1.4	24.7 ± 1.1	19.3 ± 1.0	23.4 ± 1.6
17.9–24.4	21.8–25.6	22.2–26.9	18.1–21.2	21.4–26.4
$n = 30$	$n = 7$	$n = 32$	$n = 12$	$n = 14$
Relative breadth of zygomatic plate (ZP/CBL × 100)				
9.4 ± 0.7	10.2 ± 0.6	10.6 ± 0.5	8.6 ± 0.5	10.1 ± 0.6
7.9–10.4	9.5–11.2	9.7–11.5	7.8–9.4	9.2–11.4
$n = 30$	$n = 6$	$n = 32$	$n = 12$	$n = 14$
Relative length of unicuspid toothrow (UTR/CBL × 100)				
12.7 ± 0.4	12.5 ± 0.5	13.0 ± 0.4	12.9 ± 0.3	12.7 ± 0.6
11.4–13.3	12.0–13.4	11.6–13.9	12.1–13.4	11.4–13.7
$n = 30$	$n = 6$	$n = 32$	$n = 12$	$n = 14$
Relative palatal breadth (M2B/PL × 100)				
65.9 ± 2.5	72.3 ± 0.9	67.4 ± 2.2	65.2 ± 2.5	68.7 ± 2.1
60.0–72.6	70.9–73.3	62.4–70.7	60.9–68.7	65.1–72.5
$n = 30$	$n = 7$	$n = 32$	$n = 12$	$n = 14$
Relative height of coronoid process (HCP/ML × 100)				
70.8 ± 3.5	73.8 ± 1.3	74.3 ± 3.0	73.1 ± 1.6	75.7 ± 4.1
65.1–79.6	72.3–76.2	70.2–83.6	69.4–75.0	71.6–86.2
$n = 30$	$n = 8$	$n = 32$	$n = 12$	$n = 16$

Table 4.—Continued.

C. mexicana (Oaxaca)	*C. nelsoni*	*C. obscura*	*C. peregrina*	*C. phillipsii*
Relative posterior length of mandible (AC3/ML × 100)				
80.8 ± 2.6 77.4–86.2 *n* = 30	80.2 ± 1.8 77.8–82.5 *n* = 8	77.9 ± 3.0 72.6–85.5 *n* = 32	82.1 ± 2.1 77.8–85.0 *n* = 12	78.4 ± 3.6 73.2–86.2 *n* = 16
Relative extension of articular condyle (AC3/HCP × 100)				
114.3 ± 5.1 100.0–124.4 *n* = 30	108.8 ± 1.7 106.4–110.6 *n* = 8	105.0 ± 3.7 100.0–114.3 *n* = 32	112.4 ± 2.0 109.9–115.6 *n* = 12	103.7 ± 3.9 96.1–110.6 *n* = 16

gial and unpigmented when present. Broad, curved humerus, with elongated processes (Fig. 4B).

Comparisons.—*Cryptotis peregrina* is distinctive among the species previously considered to be subspecies of *Cryptotis mexicana.* It has a narrow zygomatic plate, and it has the broadest forepaws and the longest and broadest foreclaws. The humerus is shorter, more curved, and generally more highly derived: the pectoral process is higher, lateral epicondyle more ex-

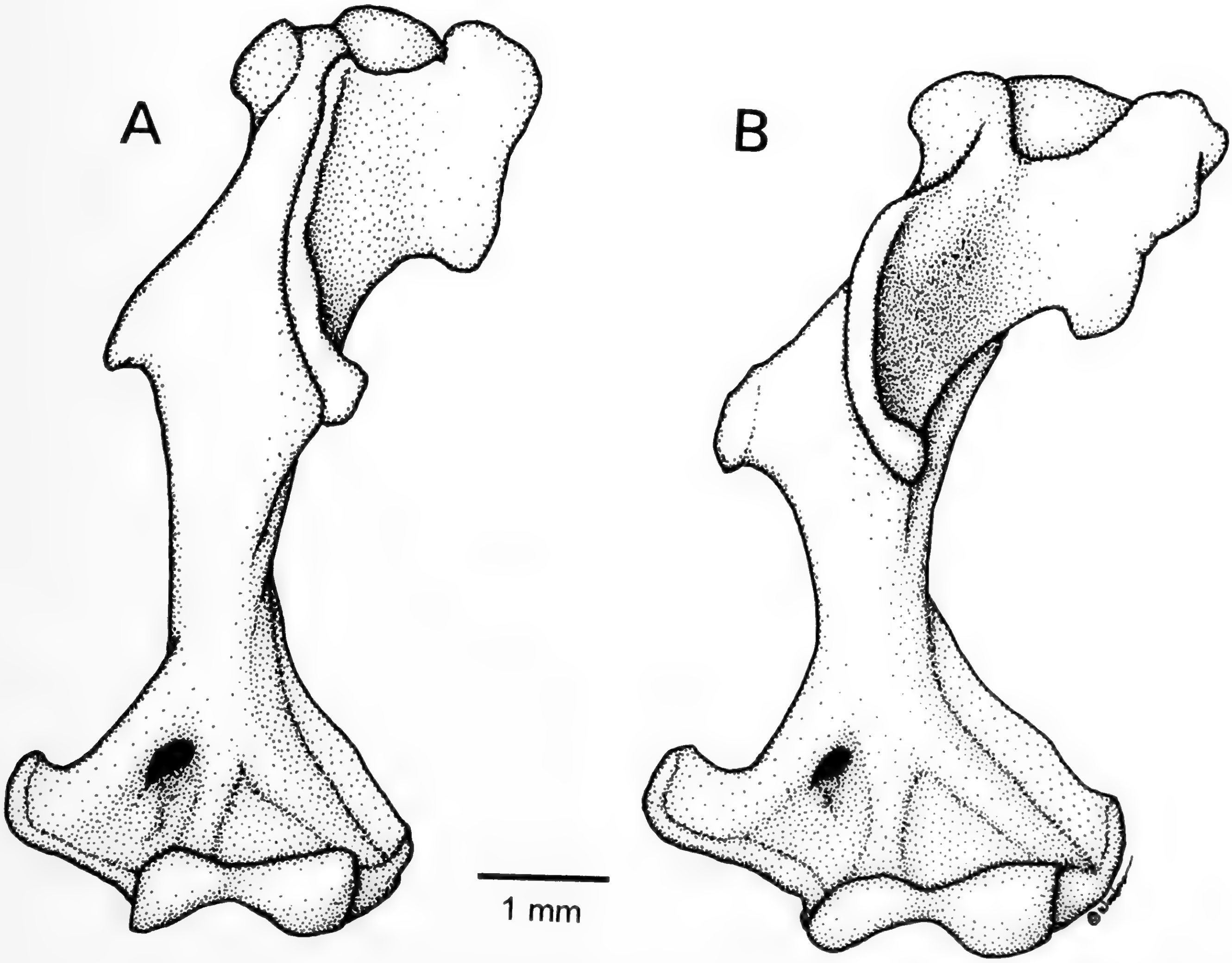

Fig. 4 Left humeri of (A) *Cryptotis phillipsii* (KU 124299) and (B) *Cryptotis peregrina* (AMNH 149965). The humerus labeled "*C. peregrina*" in Woodman and Timm (1999: Fig. 15B) is from a specimen (KU 124298) that we now recognize as *C. phillipsii.*

panded, and teres tubercle and medial epicondyle longer and more closely situated to each other. *Cryptotis peregrina* is the only species in the *C. mexicana*-group besides *Cryptotis goldmani* that usually has a well-developed foramen of the ventral branch of the sinus canal (Table 4; Woodman & Timm 1999).

Cryptotis mexicana: Cryptotis peregrina has slightly longer, broader claws and a much more derived humerus; M^3 simple, lacking metacone; entoconid of M_3 vestigial (rather than well-developed), when present.

Cryptotis nelsoni: Cryptotis peregrina has slightly longer, broader claws and a much more derived humerus; skull narrower overall; longer rostrum and much narrower palate (Table 4); M^3 simple, lacking metacone; entoconid of M_3 vestigial (rather than well-developed), when present.

Cryptotis obscura: Cryptotis peregrina has much longer, broader claws and a much more derived humerus; longer rostrum (Table 4); upper unicuspids concave on posterior surface (rather than straight or convex), appearing curved; M^3 simple, lacking metacone; more likely to have two well-developed dorsal foramina (44% vs. 22%, Table 4); entoconid of M_3 vestigial (rather than well-developed), when present.

Cryptotis phillipsii: Cryptotis peregrina has much longer and broader claws and a much more derived humerus; longer rostrum and much narrower palate (Table 4); absolutely and relatively broader zygomatic plate (Tables 1, 4); larger U^4 relative to U^3; slightly more recessed upper dentition; slightly less complex M^3; well-developed foramen of the ventral extension of sinus canal; usually no foramen dorsal to dorsal articular facet.

Cryptotis goldmani-group: *Cryptotis peregrina* is generally smaller in head-and-body-length and has a relatively longer tail (Table 1, 4); narrower zygomatic plate; more likely to possess a vestigial entoconid (rather than no entoconid) of M^3.

Remarks.—Nearly all known specimens of *Cryptotis peregrina* are part of the type series, collected in the Sierra de Cuatro Venados ca. 15 mi SW of Oaxaca de Juárez in 1894. Merriam (1895) stated that there were 25 specimens in the type series, but he did not list them individually. We were able to locate only 24 original specimens collected by Nelson and Goldman. The only other specimen of *C. peregrina* of which we are aware is a fluid-preserved individual (with the skull and left humerus removed) in poor condition, collected "N. La Muralla" in the Sierra Yucuyacua by Thomas B. MacDougall on 18 March 1952. Locality notes by MacDougall indicate this locality is at 10,500+ ft at the "top of Cerro Yucunino" (AMNH field notes, 1952). We believe (as apparently did Choate, 1970:239) that this peak is equivalent to Cerro Yucuyacua [= Piedra de Olla], based on its elevation and position relative to La Muralla and Santa María Asunción Tlaxiaco.

Goldman (1951:218) noted that the type locality was moist, with general conditions "much as on Cerro San Felipe." Areas above 8000 ft on Cerro San Felipe were covered in oak-dominated mixed forest with an herbaceous understory, and they experienced cold night-time temperatures, with frosts recorded in August. Meadows (neverías), such as the one in the vicinity of the type locality, were said to be employed by local people for making ice to be used at lower elevations. MacDougall (AMNH field notes, 1952) noted the presence of pine and oak where he captured *C. peregrina* north of La Muralla.

Specimens examined (25).—Mexico: Oaxaca: N[orth]. [of] La Muralla [16°58′N, 97°56′W], top of Cerro Yucuninó [= Cerro Yucuyacua, 17°06′N, 97°40′W], Tlaxiaco [Santa María Asunción Tlaxiaco, 17°16′N, 97°41′W], 10,500+ ft (AMNH 149965); mountains 15 mi [south] west Oaxaca de Juárez [16°30′N, 96°53′W], 9500 ft (BMNH 95.11.1.26 [= USNM 68337], USNM 68315–68336, 68338, including holotype).

"*Cryptotis goldmani*-group" Woodman & Timm, 1999

Description.—The *C. goldmani*-group is a subset of the *C. mexicana*-group that is comprised of medium-sized members of the genus with greatly broadened forefeet; extremely long, broad foreclaws; fourth upper unicuspid usually aligned with the unicuspid toothrow and partially visible in labial view of the cranium; protoconal basin of M^1 reduced relative to hypoconal basin; M^3 simple, hypocone absent or poorly developed and lacking metacone; entoconid of M_3 vestigial or absent; and extremely broad humerus with greatly elongated processes.

Included species.—*Cryptotis alticola, C. goldmani, C. goodwini, C. griseoventris,* and *C. peregrina.*

Cryptotis phillipsii (Schaldach, 1966)

Notiosorex (*Xenosorex*) *Phillipsii* Schaldach, 1966:289; Goodwin, 1969:43.

Cryptotis mexicana machetes: Musser, 1964:6; Schaldach, 1966:288; Goodwin, 1969:40 (in part).

Cryptotis mexicana peregrina: Goodwin, 1969:40 (in part); Choate, 1970:237 (in part); Hall, 1981:59 (in part).

Cryptotis peregrina: Woodman & Timm, 1999:35 (in part).

Holotype.—Skin and skull of adult female, UNAM 8445; taken 18 Dec 1964 by W. J. Schaldach, Jr. (collector number 13278). Two paratypes, KU 114226 [= UNAM 8446] and UNAM 8447.

Type locality.—"the Río Molino, 3 kilometers S.W. San Miguel Suchixtepec, altitude 2250 meters, southern Oaxaca, México" (Schaldach, 1966:289).

Distribution.—Known from 1060 to 2745 m in the Sierra de Miahuatlán, southern Oaxaca, Mexico (Fig. 3).

Description.—Size medium to large for the genus (Table 1); tail long, averaging 31 mm, or ca. 46% (Table 4) of head-and-body length; dorsal guard hairs 6–7 mm long; forepaws somewhat enlarged; foreclaws among the narrowest for members of the *Cryptotis mexicana*-group, but elongate and somewhat broadened relative to other members of the genus; rostrum of moderate length (PL/CBL = 43.3%, Table 4); often two well-developed dorsal foramina (47%, Table 4); ventral extension of the sinus canal and associated foramen typically lacking (76%, Table 4), but well-developed when present; a foramen dorsal to the dorsal articular facet usually present on one or both sides of the skull (82%, Table 4); zygomatic plate broad (ZP/PL = 23.4%, Table 4), anterior border usually aligned with posterior ½ of mesostyle-metastyle valley or metastyle of M^1; P^4, M^1, and M^2 unrecessed to slightly recessed on posterior border; surface area of U^4 typically $\leq$½ that of U^3; U^4 usually aligned with the unicuspid toothrow, but not typically visible in lateral view of the skull; protoconal basin of M^1 same size as hypoconal basin; M^3 simple, lacking metacone, hypocone poorly-developed or absent; M^3 usually possessing paracrista, paracone, precentrocrista, and mesostyle (all pigmented), and occasionally a very short postcentrocrista and a well-developed, pigmented protocone. Articular process of the mandible generally moderately tall and wide, with a moderately broad lower articular facet; coronoid process of the mandible moderately high relative to mandibular length (HCP/ML = 75.7%, Table 4); entoconid usually present on M_3 (92%, Table 4), typically vestigial (83% of those possessing entoconids), but occasionally well-developed (17%). The tall, broad, slightly curved humerus has somewhat elongated processes, but it is among the least modified within the *C. mexicana*-group (Fig. 4).

Comparisons.—*Cryptotis phillipsii* has the least modified forelimbs of any member of the *Cryptotis mexicana*-group: it has the smallest forepaws and the shortest and narrowest foreclaws; the humerus is among the longest and least curved; teres tubercle is short, medial epicondyle is short and has a straight proximal edge, and teres tubercle and medial epicondyle are broadly separated. *Cryptotis phillipsii* also has the longest tail relative to head-and-body-length (Table 4). There *may* be a local tendency for some *C. phillipsii* to develop without U^4s (12%, $n = 17$) in the region of the type locality, resulting in a reduced dentition.

Cryptotis mexicana: Cryptotis phillipsii has shorter, narrower foreclaws and a relatively longer tail; less modified humerus; broader palate (Table 4); simple M^3, lacking metacone; entoconid of M_3 usually vestigial (rather than well-developed) when present.

Cryptotis nelsoni: Cryptotis phillipsii has shorter, narrower foreclaws and a relatively longer tail; narrower palate (Table 4); simple M^3, lacking metacone; entoconid of M_3 usually vestigial (rather than well-developed) when present.

Cryptotis obscura: Cryptotis phillipsii has a relatively longer tail; upper unicuspids concave on posterior surface, appearing curved, rather than convex and cone-shaped; more likely to have two well-developed dorsal foramina (Table 4); simple M^3, lacking metacone; entoconid of M_3 usually vestigial (rather than well-developed) when present.

Cryptotis goldmani-group: *Cryptotis phillipsii* is smaller in head-and-body-length, and has much shorter, narrower foreclaws, a much less derived humerus, and a relatively longer tail; higher coronoid process (Table 4); shorter posterior portion of mandible (Table 4); much more likely to possess vestigial entoconid (rather than no entoconid) of M_3.

Remarks.—The type series of *Cryptotis phillipsii* was collected in 1964 by William J. Schaldach, Jr. and Allan R. Phillips during a trip to southern Oaxaca to obtain specimens of birds and mammals. Schaldach (1966) originally described a new species, *Notiosorex phillipsii,* on the basis of three specimens: a skin with skull and a skin without skull from Río Molino (UNAM 4445, 4447) and a skin with skull from Río Guajalote (KU 114226 = UNAM 8446). Originally identified as *Cryptotis mexicana,* the main consideration in subsequently referring these three specimens to *Notiosorex* appears to have been the presence of only three unicuspids in the upper toothrow, rather than the four unicuspids typical of *Cryptotis.* A fourth specimen (UNAM 8444), collected at Río Molino and possessing four unicuspids, was reported as *Cryptotis mexicana* (Schaldach 1966). Noting strong differences in external, cranial, and dental characters between the type series of *N. phillipsii* and specimens of *Notiosorex crawfordi* and *Megasorex gigas* that he used for comparison, Schaldach (1966) erected a new subgenus, *Xenosorex,* to distinguish the new shrew. Choate (1969) reexamined the type series of *Notiosorex phillipsii* and reported a number of distinctive cranial, mandibular, and dental characters that clearly established *N. phillipsii* as a member of the genus *Cryptotis,* despite its reduced dentition. He justifiably placed Schaldach's *N. phillipsii* as a junior synonym of *Cryptotis* [*mexicana*] *peregrina,* where it has remained until now (Choate 1970, Hall 1981, Hutterer 1993, Woodman & Timm 1999).

Cryptotis phillipsii is known from higher elevation forest, including cloud forest, in the Sierra de Miahuatlán of southern Oaxaca. The species is syntopic with *Cryptotis goldmani* at some localities, but the geographic distribution of *C. phillipsii* is not nearly as broad as that of *C. goldmani,* despite an apparently lower elevational limit.

Schaldach (1966) reported the humid, shaded ravines along the slopes of the valley of the Río Molino at the type locality contained remnant, pine- and oak-dominated cloud forest, with a dense understory of ferns, mosses, vines, and shrubs. Musser (1964) described the canyon bottom as containing moist, open forest with bromeliad-covered oaks and a dense ground cover of shrubs, ferns, and herbaceous vegetation. The higher, drier slopes were covered with a mixed secondary growth of pines and oaks. Musser (1964:6) took one *C. phillipsii,* two *Sorex saussurei oaxacae,* and 29 *Peromyscus megalops* under a "lush herbaceous ground cover" consisting largely of ferns along the steep banks of a "moist, densely vegetated streamside" with a "deep layer of wet humus and leaf litter" at 7300 ft [2225 m] near Río Molino. Paul B. Robertson (KU field notes and catalog, 1969, 1970) captured three *C. phillipsii* at Río Molino. In December 1969, he trapped one *C. phillipsii,* one *Microtus mexicanus,* two *Peromyscus aztecus,* two *P. levipes,* and four *P. megalops.* In April 1970 using a trapline "along a small rivulet," he took one *C. phillipsii* with two *Cryptotis goldmani,* one *Sorex saussurei oaxacae,* one *Microtus mexicanus,* one *Neotoma mexicana,* two *Oryzomys chapmani,* 12 *Peromyscus megalops,* and one *Reithrodontomys mexicanus.* Nearby, "among & under rocks in an overgrown field," he collected a *C. phillipsii* with two *Reithrodontomys megalotis,* three *R. sumichrasti,* and one *Sigmodon alleni.* He described the streamside vegetation at Río Molino as "hard wood" and the slopes as "almost pure pine." In addition, Schaldach (1966) reported capturing *Sorex mutabilis* (as *Sorex veraepacis*) and *Liomys pictus* at Río Molino. *Cryptotis phillipsii* and *C. goldmani* were collected in syntopy also at "lumber camp, km 158" along the Puerto Ángel Road in January 1970 by John R. Arnold and Craig Moe. *Cryptotis phillipsii* and *C. parva pueblensis* were captured syntopically 20 mi S, 5 mi E San Miguel Sola de Vega by Percy L. Clifton in June–July 1964. He described the habitat there as dense cloud forest, with *C. phillipsii* "caught under a rock in a low damp situation along a creek" (KU field notes, 1964). *Cryptotis phillipsii* also was taken in syntopy with *C. p. pueblensis* at San Miguel Suchixtepec by Thomas B. MacDougall in October 1967.

Specimens examined (36).—Mexico: Oaxaca: 20 mi S, 5 mi E Sola de Vega [San Miguel Sola de Vega, 16°31′N, 96°59′W], 4800 ft (KU 98728); 36 km (by road) N San Gabriel Mixtepec [16°06′N, 97°06′W], 1680 m (KU 124294); 27.8 km (by road) N San Gabriel Mixtepec, 1320 m (KU 124295, 124296); La Cima, Puerto Escondido road, km 184.5 [16°12′N, 97°07′W], 5750 ft (CAS 15473); Puerto Escondido road, km 193 [16°10′N, 97°07′W], 4200 ft (CAS 15474); Sinai [Finca Sinai, 16°07′N, 97°08′W], 10 km [by trail] E Nopala [Santo Reyes Nopala], 7200 ft (CAS 14940); Río Molino [16°04′N, 96°28′W], 2250–2745 m (AMNH 213758, 213759, 214152, 214803–214805; KU 121661, 124298, 124299; UNAM 8444, 8445, 8447—includes holotype); near campemento Río Molino (Hwy 175), 7300 ft (UMMZ 112572); Puerto Ángel road, km 153 [16°04′N, 96°28′W], 7100 ft (CAS 14068); San Miguel Suchixtepec [16°05′N, 96°28′W], Miahuatlán District (AMNH 214806–214808); 16 km SW [San Miguel] Suchixtepec, 2000 m (ENCB 3413, 3414); Lovene [16°02′N, 96°12′W], Miahuatlán (AMNH 178739); lumber camp, Puerto Ángel road, km 158, 8375 ft (CAS 15478); Río Guajalote [16°00′N, 96°28′W], 2000 m (KU 114226); Río Jalatengo [15°58′N, 96°27′W], Puerto Ángel road, km 178, 4275 ft (CAS 14069, 14071, 14072, 15475; UNAM 27518); Puerto Ángel road, km 195, 3475 ft (UNAM 26551); Puerto Ángel road (UNAM 27517).

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Appendix I: Transition Series Used in Phylogenetic Analysis

Transition series (TS) marked by an asterisk (*) were modified from Woodman & Timm (1999). TS 30–32 were added since that paper.

*1. length of foreclaws: short (0); elongate (1); more elongate (2); greatly elongate (3).
*2. breadth of foreclaws: narrow (0); broad (1); broader (2); extremely broad (3).
3. forefeet: small (0); enlarged, broadened (1); greatly enlarged and broadened (2).
4. metacarpals: long, narrow (0); short, broad (1).
5. posterior border of zygomatic plate: even with or anterior to anterior root of maxillary process (0); even with posterior root of zygomatic process, but separated from it by posterior border of palate (1); even with (or posterior to) and confluent with posterior root of zygomatic process (2).
6. anterior border of coronoid process: steep, forming a narrow angle with horizontal ramus of mandible (0); less steep, forming a wide angle with horizontal ramus of mandible (1).
7. articular condyle: low and broad (0); high and narrow (1).
8. lower sigmoid notch: very shallow (0); deep (1).
9. shape of unicuspids (U^1–U^3): cone-shaped, posteroventral border straight-edged or convex (0); narrow, posteroventral border concave (1).
10. protoconal basin of M^1: about equal in

size to hypoconal basin (0); reduced relative to hypoconal basin (1).

11. M^3 morphology: simple, metacone absent (0); complex, metacone present (1).
12. shape of P_3: short and high (0); long and low (1).
13. shape of humerus: long, narrow, relatively straight (0); short, robust, curved (1); short, robust, and very curved (2).
14. head of humerus: rounded (0); dorsoventrally elongate (1).
15. ventral edge of proximal face of greater tuberosity of humerus: rounded (0); with broad, deep pocket (1).

*16. pectoral process of humerus: low (0); high (1).

*17. length of teres tubercle: relatively short (0); elongate (1); greatly elongate (2).

*18. medial epicondyle of humerus: short (0); elongate (1); greatly elongate (2).

19. lateral epicondyle of humerus: small (0); expanded (1).
20. teres tubercle and medial epicondyle of humerus: far apart (0); close together (1); very close (2); extremely close (3).
21. posterior edge of falciform process of tibia: not deeply pocketed (0); deeply pocketed (1).

*22. foramen of sinus canal: absent in 100% of specimens (0); absent in >75% of specimens (1); present in >50% of specimens, but vestigial (2); present in >90% of specimens, well-developed (3).

23. dorsal foramina: two in <75% of specimens (0); two in >75% of specimens (1).
24. foramen dorsal to articular facet: present in <75% of specimens (0); present in >75% of specimens (1).

*25. entoconid of M_3: present in >90% of specimens, typically well-developed (0); present in >50% of specimens, typically vestigial (1); absent in >80% of specimens (2).

26. body size (head-and-body length): smaller, mean <69 (0); larger, mean >72 (1).
27. relative tail length (% of head-and-body length): short, mean <39% (0); long, mean >40% (1).
28. upper unicuspid toothrow: crowded, three unicuspids visible in lateral view (0); uncrowded, four unicuspids visible in lateral view (1).
29. dorsal guard hairs: short, <4 mm (0); of intermediate length, 4–5 mm (1); long, >5 mm (2).

*30. distal edge of pectoral process of humerus relative to teres tubercle: extends well distal to teres tubercle (0); extends to proximity of distal edge of teres tubercle (1).

*31. bones of hind paws: metatarsals and proximal phalanges long narrow (0); metatarsals and proximal phalanges broad (1); metatarsals and proximal phalanges short and very broad (2).

*32. posterior border of P^4, M^1, and M^2: slight to no emargination (0); noticeable emargination (1); strong emargination (2).

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Two new species of flightless rails (Aves: Rallidae) from the Middle Pleistocene "crane fauna" of Bermuda

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Abstract.—Two new species of flightless rails are described from a Pleistocene fauna in Bermuda that also includes an extinct crane (*Grus latipes*) and an extinct duck (*Anas pachyscelus*). The medium-sized *Rallus ibycus,* new species, was possibly derived from North American populations of Virginia Rail (*R. limicola*), but had a longer bill, much more robust legs, and reduced wings and pectoral girdle. The very small *Porzana piercei,* new species, except for the reduced wing and pectoral girdle, is very similar to the extant Yellow-breasted Crake (*P. flaviventer*), which now occurs only in the Neotropics, including the Greater Antilles. The fauna that included these rails developed during a long, stable glacial period of lowered sea-levels in the Middle Pleistocene, during which the entire Bermuda platform was emergent. This was followed by an abrupt and extreme interglacial about 400,000 years ago when sea-levels rose to 21 m above present levels, obliterating most of Bermuda and much of its endemic fauna, including the rails.

The island of Bermuda, situated in the western North Atlantic 1050 km east of Cape Hatteras, North Carolina, is composed almost entirely of calcareous aeolianite on the southeastern rim of a submerged, truncated summit of an extinct volcano. The aeolianite has been modified by solution to form numerous caves and fissures that are accessible to collectors either through natural openings or through limestone quarrying operations. These caves frequently contain accumulated fossils of vertebrates and invertebrates, mainly birds and terrestrial gastropods. Although much of interest to avian paleontology has been collected from Bermuda, relatively little has been published, partly for lack of a better understanding of the complexities of the island's stratigraphy and chronology, which has been greatly improved in recent years.

The first contribution to knowledge of Pleistocene birds in Bermuda was that of Wetmore (1960) who described a new genus and species of endemic crane, *Baeopteryx latipes,* and an extinct endemic duck, *Anas pachyscelus,* from the Wilkinson Quarry, Hamilton Parish. The genus *Baeopteryx* was later synonymized with typical cranes of the genus *Grus* (Fischer & Stephan 1971).

Wetmore (1960:10) mentioned that "the collection contains various bones from four species of rails, one very small, two of intermediate size, and one nearly as large as the modern clapper rail [*Rallus longirostris*]. These are not clearly marked in the present collection so that no attempt is made to describe them here in detail, particularly since complete material for one of them is now in other hands for study." Actually, among the rail material that Wetmore examined, there are remains of only two species of rails, one medium-sized and the other very small (uncataloged specimens in

USNM). Wetmore's information on Bermuda rails apparently came in part from Pierce Brodkorb, University of Florida, who had been in Bermuda collecting fossil rails with Wingate only weeks before Wetmore's publication appeared. Later, Olson (1977:353–354) briefly mentioned the still undescribed fossil rails from Bermuda. Brodkorb's collections containing the Bermuda rails passed to the Florida Museum of Natural History after Brodkorb's death in 1992, and we have now belatedly begun the process of describing them.

Some information on the relationships and adaptations of the largest species of rail to which Wetmore alluded was provided by Olson (1997). This species was not contemporaneous with the "crane fauna" and does not appear to have co-existed with any other endemic rail on Bermuda. In February 1999, we discovered a new deposit in which this species was the predominant bird. Preliminary results from amino acid racemization ratios from associated snail shells indicate that it originated during a much younger glacial period. We have postponed description of this species until the new material can be fully prepared and analyzed. Here we describe the two species that are definitely part of the "crane fauna" that we believe dates back at least to the Middle Pleistocene.

Materials and Methods

The specimens obtained by Wingate and Brodkorb in 1960 were collected in association with bones of the extinct crane *Grus latipes,* from a vertical fracture on the eastern face of the Bermuda Government quarry in Hamilton Parish that was filled with soil and snail shells of the genus *Poecilozonites* and was named the "Crane Crevice." The fossil birds, formerly part of the Pierce Brodkorb collection, are now cataloged in the Florida Museum of Natural History, University of Florida, Gainesville, and all take the prefix UF PB, which we have omitted except in the citations of the holotypes and the figure legends. There are many more specimens available than are listed among the type material. As paratypes we have listed those specimens that were used in the descriptions, are illustrated, or were used for any of the cited measurements. Measurements of long bones of the limbs usually do not include broken or juvenile specimens, which accordingly are not among the paratypes listed. Measurements were taken with digital calipers to 0.01 mm and rounded to the nearest 0.1 mm.

Comparative material examined:—Skeletons (complete unless otherwise indicated) of the following species in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), unless otherwise noted. *Amaurolimnas concolor* 613963; *Coturnicops noveboracensis* 556931; *Laterallus albigularis* 611563; *L. jamaicensis* 492195, 502495; *Pardirallus maculatus* 561272–76; *Poliolimnas cinereus* 560913; *Porzana flaviventer* 501640, 561276–78, and trunk skeletons 430043, 430931, 430979, 431339–41; *Porzana porzana* 552914; *P. albicollis* 562750; *P. atra* 562788; *P. carolina* 501052, 501671; *P. pusilla* 291704–05; *Rallus aquaticus* 431545, 553039, 553041, UF 34461; *R. limicola* 489973, 525915, 525917, UF 19598, UF 19769, UF 24324, UF 24322; *R. elegans* 499437, 525886, 610780; *R. longirostris* 525876, 525873, 525879; *R. longirostris* X *R. elegans* 525887.

Systematics

Family Rallidae

Genus *Rallus* Linnaeus

The very long, slender bill of the following species clearly places it in the genus *Rallus* in its strict sense (Olson 1973a). No flightless species of the restricted genus *Rallus* have been described previously. Such characters as are preserved in the fossils that are not obscured by flightless adaptations show no evidence of relationship to the species of *Pardirallus* (including *Or-*

tygonax), which also have long bills but are osteologically quite distinct and not especially closely related to *Rallus* (Olson 1973a).

Rallus ibycus, new species
Figs. 1–5

Holotype.—Premaxillary symphysis with anterior portion of internarial bar (pila supranasalis) UF PB5403. Collected in May 1960 by David B. Wingate.

Type locality.—Bermuda, Hamilton Parish, Government Quarry, Crane Crevice.

Chronology.—Middle Pleistocene, presumably within Oxygen Isotope Stages 13 to 20, approximately 800 to 450 kya (see discussion).

Measurements (mm) of holotype.—Length of premaxillary symphysis, 15.5.

Paratypes.—Premaxillary symphyses 5511, 5521. Pila supranasalis 5526. Crania 5401, 5512, 5518. Sterna 5402, 5430. Coracoids 5404, 5415, 5416, 5441, 5456. Humeri 5405, 5417, 5422, 5425–5426, 5428, 5457, 6063–6072, 6073, 6077, 6079. Ulnae 5406, 5423, 5440, 5458. Carpometacarpi 5407, 5419, 5424, 5439, 5459. Pelvis 5429. Femora 5409, 5432–5438, 5451, 5460, 5 uncataloged specimens. Tibiotarsi 5410, 5448–5449, 5452–5455, 5461, 5491–5492, 5498–5502, 5503, 5541–5542, 5551–5560. Tarsometatarsi 5442, 5444–5447, 5462, 5543–5546, 6001–6002, 6028–6031, 6055–6057.

Measurements (mm) of paratypes.—Rostrum: length from nasofrontal hinge estimated from 5526 and 5403 to be between 46.5 and 48.0; length of premaxillary symphysis 14.1, 15.5, 16.7. Cranium: length from naso-frontal hinge 28.0; width at postorbital processes 15.5, 15.7; width of interorbital bridge 3.3, 3.6, 3.7. Coracoid: length 15.4, 17.4, 18.2, 18.4, 19.5. Sternum: length along midline (from anterior sternal notch, not manubrium) 21.2, 21.3; width across coracoidal sulci 10.7, 12.1; depth of carina 3.7, 4.4. Carpometacarpus: length 14.0, 16.1, 16.3, 16.5, 16.9; proximal depth 3.6, 4.1, 4.2, 4.3, 4.3. Ulna: length 22.8, 24.5, 25.8, 26.9. Pelvis: sacrum length 27.3, 30.0; width across antitrochanters 15.4. See also Table 1.

Etymology.—Greek, m. *ibykos*, literally of a crane, but here a noun in apposition referring to Ibycus (fl. 528 B.C.), a lyric poet whose murder was revealed by cranes (see Anthon 1869). The name is applied to the new species from its association with the much larger fossils of cranes, the discovery of which also revealed the extinction of the rail.

Diagnosis.—Similar in overall size to *Rallus limicola* but bill longer and more slender, with a longer and more decurved premaxillary symphysis. Flightless, with the sternum and pectoral elements reduced. Hindlimb elements much more robust.

Description.—In addition to the longer, more decurved bill, this species also seems to have the orbits reduced so the frontal area in lateral view has the appearance of sloping more steeply.

Compared with *Rallus limicola*, the sternum is shorter, wider, lacks a manubrial spine, and has a deep notch between the coracoidal sulci. The carina is very low and thick anteriorly, extending laterally as a rim, which, with the anterior ridge leading from the keel, creates a deep depression on the sides of the carina.

The shaft of the coracoid is narrowed, forming a sharp ridge from the head to midshaft. The procoracoid process is smaller, more delicate and pointed. The sternocoracoidal process is much more pronounced and pointed due to the deep circular incision in the external margin.

The humerus has the head lower and smaller, the capital groove deeper, the distal end narrower, with the tricipital grooves deeper. The ulna is shorter and stouter and slightly less curved. The carpometacarpus is very reduced, short, and stout.

The pelvis in dorsal view is decidedly wider, both anteriorly and posteriorly, although the ischial area in lateral view is not as deep as in *R. limicola*.

Table 1.—Measurements (mm) of selected skeletal elements of two new species of flightless rails from the Middle Pleistocene of Bermuda.

	n	Range	Mean	*SD*
Rallus ibycus, n. sp.				
Humerus				
Length	18	28.5–36.3	32.3	2.2
Proximal width	18	6.0–7.2	6.6	0.4
Shaft width	18	1.7–2.2	1.9	0.1
Distal width	18	4.0–4.8	4.4	0.2
Femur				
Length	16	34.9–41.5	37.9	2.6
Proximal width	15	5.7–6.9	6.4	0.3
Distal width	15	5.7–7.1	6.3	0.5
Tibiotarsus				
Length from proximal articular surface	28	45.7–55.5	50.5	3.4
Distal width	27	4.7–5.8	5.2	0.3
Tarsometatarsus				
Length	19	27.1–34.3	30.2	2.4
Proximal width	18	5.1–5.9	5.4	0.3
Distal width	18	5.1–6.1	5.6	0.3
Porzana piercei, n. sp.				
Humerus				
Length	54	19.7–23.2	21.4	0.7
Tibiotarsus				
Length from proximal articular surface	8	33.6–38.1	35.5	1.6
Distal width	7	3.1–3.4	3.3	0.1
Tarsometatarsus				
Length	25	19.9–23.9	22.3	0.9
Proximal width	25	3.1–3.6	3.4	0.1
Distal width	24	3.4–3.8	3.6	0.1

All of the elements of the hindlimb are extremely robust compared with *R. limicola,* with heavier shafts and more expanded articulations. The head of the femur is proportionately larger. The tibiotarsus and tarsometatarsus are proportionately shorter. The cnemial crests of the tibiotarsus are better developed, the fibular crest is longer, and the distal tendinal opening is larger. The tarsometatarsus has the trochleae more splayed, with the inner trochlea less elevated and retracted than in *R. limicola.*

Remarks.—The most likely progenitor of *R. ibycus* would be the Virginia Rail, *Rallus limicola,* a common migratory species in eastern North America that has been found as a "frequent but scarce vagrant" in Bermuda (Amos 1991:121). Rails described as being similar to *R. limicola* are known from the Pliocene and Pleistocene of North America (Olson 1977). The Eurasian Water Rail, *Rallus aquaticus,* is a less likely ancestor on geographic grounds, and also because of its larger size.

Genus *Porzana* Vieillot

The following new species of flightless rail from Bermuda is characterized by very small size and a short "crake-like" bill that invites comparison with the New World species of *Porzana, Laterallus,* and *Coturnicops.* Of particular concern is the Neotropical Yellow-breasted Crake, usually

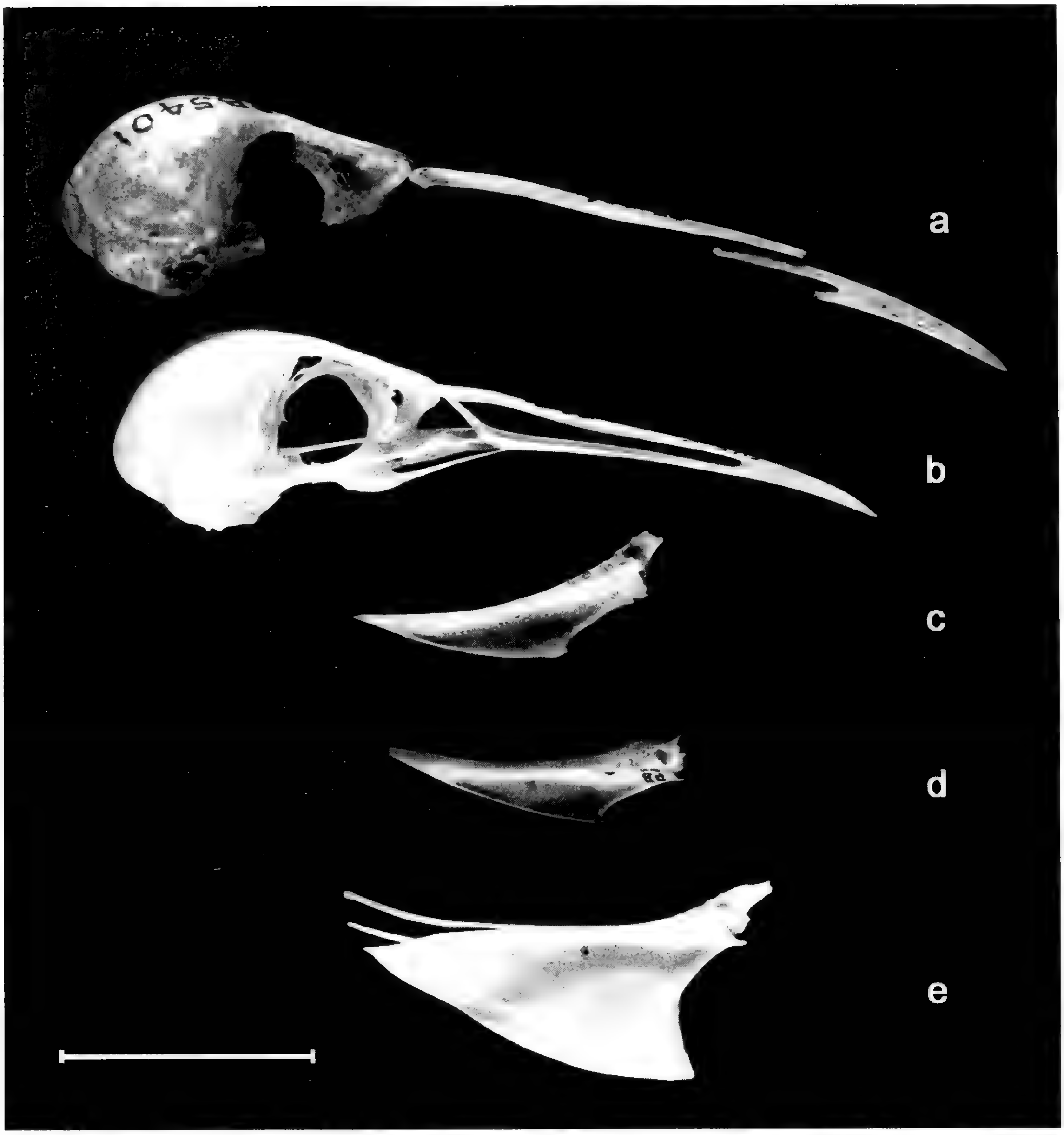

Fig. 1. Comparison of skulls (a–b) and sterna (c–e) of *Rallus* in lateral view. a, *Rallus ibycus,* new species (premaxillary symphysis, holotype UF PB5403; pila supranasalis UF PB5526; cranium UF PB 5401); b, e, *R. limicola* female USNM 525915; c, d, *R. ibycus* UF PB5430, UF PB5402. Scale bar = 2 cm.

known as *Porzana flaviventer,* for which Ridgway (1920) once erected the monotypic genus *Hapalocrex* (type *Rallus flaviventer* Boddaert). This species has little resemblance to the various species of *Porzana* with which it has been placed in most current literature. Using mostly external characters, Olson (1970) suggested that it be placed in the genus *Poliolimnas* with the Australo-Malayan species *P. cinereus.* Although a few authors have accepted Olson's conclusion (e.g., Short 1975), it has otherwise either been widely ignored or even sharply attacked (Mees 1982).

In an extensive morphological analysis of the Gruiformes emphasizing the Rallidae, Livezey (1998) found the relationships among the "crakes" and supposed allies to be difficult to resolve and even more difficult to reconcile with traditional taxonomy. The preliminary results of an extensive sampling of mitochondrial DNA sequences of the Rallidae indicate that the genus *Porzana* as now generally construed (e.g., del Hoyo et al. 1996), is an unnatural assemblage (Beth Slikas, National Zoological Park, pers. comm.). Until the taxonomic difficulties among the crakes can be better

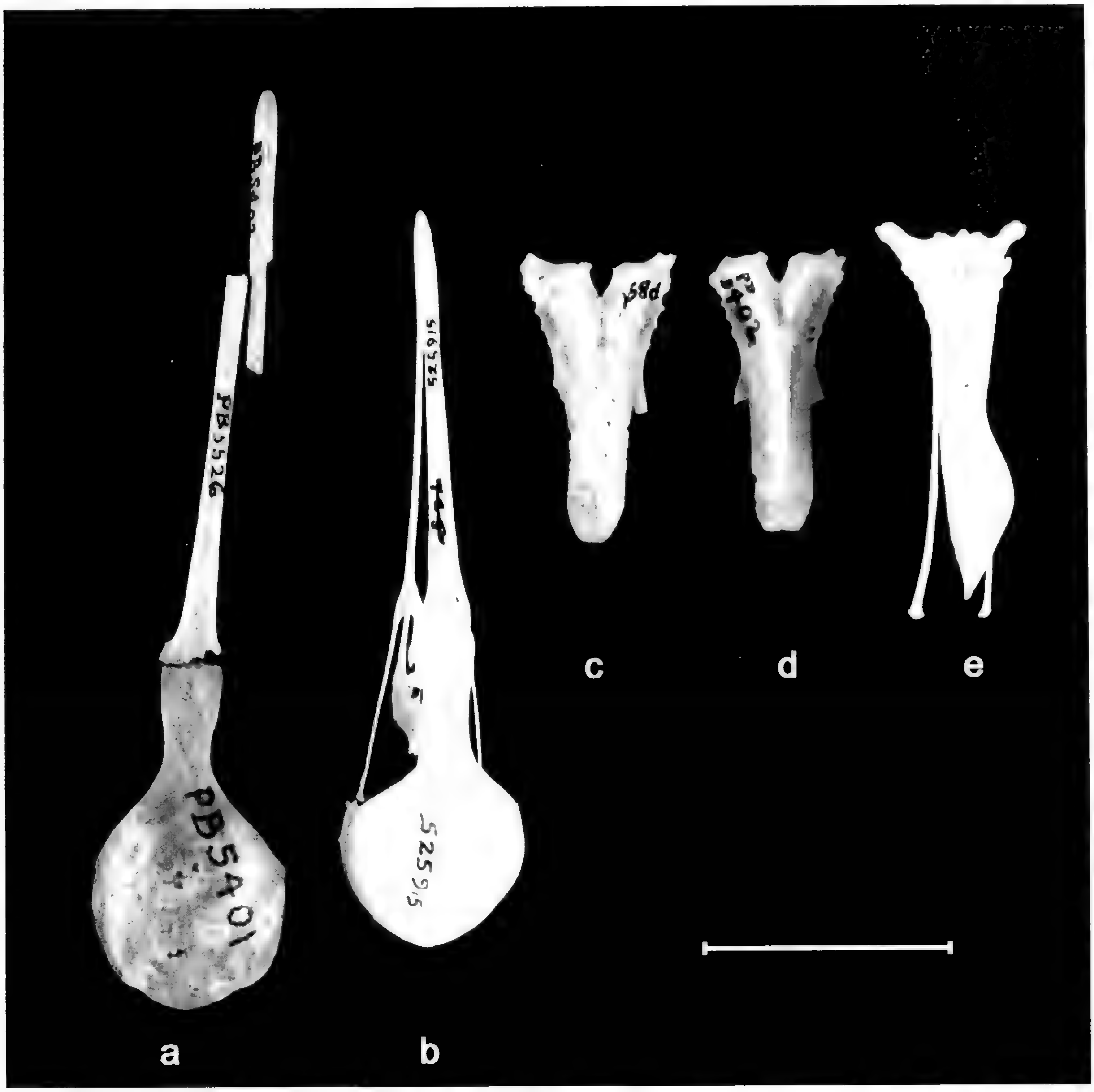

Fig. 2. Comparison of skulls (a–b) in dorsal view and sterna (c–e) in ventral view of *Rallus*. a, *Rallus ibycus*, new species (premaxillary symphysis, holotype UF PB5403; pila supranasalis UF PB5526; cranium UF PB 5401); b, e, *R. limicola* female USNM 525915; c, d, *R. ibycus* UF PB5430, UF PB5402. Scale bar = 2 cm.

resolved, we have chosen to continue with general usage in including *flaviventer* in the genus *Porzana*.

The fossil species from Bermuda compares as follows with other crakes from which it might have been derived. In *Laterallus* the nostril is shorter and higher, the premaxillary symphysis is shorter, and the interorbital bridge is wider. In species of *Porzana* except *P. flaviventer,* the nostril is longer and the premaxillary symphysis is shorter (except in *P. pusilla,* which has a long symphysis). In *Coturnicops* the bill is extremely short and deep, quite unlike the fossil species. In the relatively short nostril, long premaxillary symphysis, and narrow interorbital bridge, the small Bermuda rail agrees perfectly with *Porzana flaviventer.*

A striking feature is the proportions of the hindlimb. When the hindlimb elements of *Porzana flaviventer* are compared with those of *Laterallus jamaicensis* it is seen that whereas the tibiotarsi are of nearly equal length, the femur in *P. flaviventer* is much shorter and all the elements are stouter. In *Coturnicops noveboracensis* the tibiotarsus is shorter yet the femur is longer than in *P. flaviventer.* Compared with other

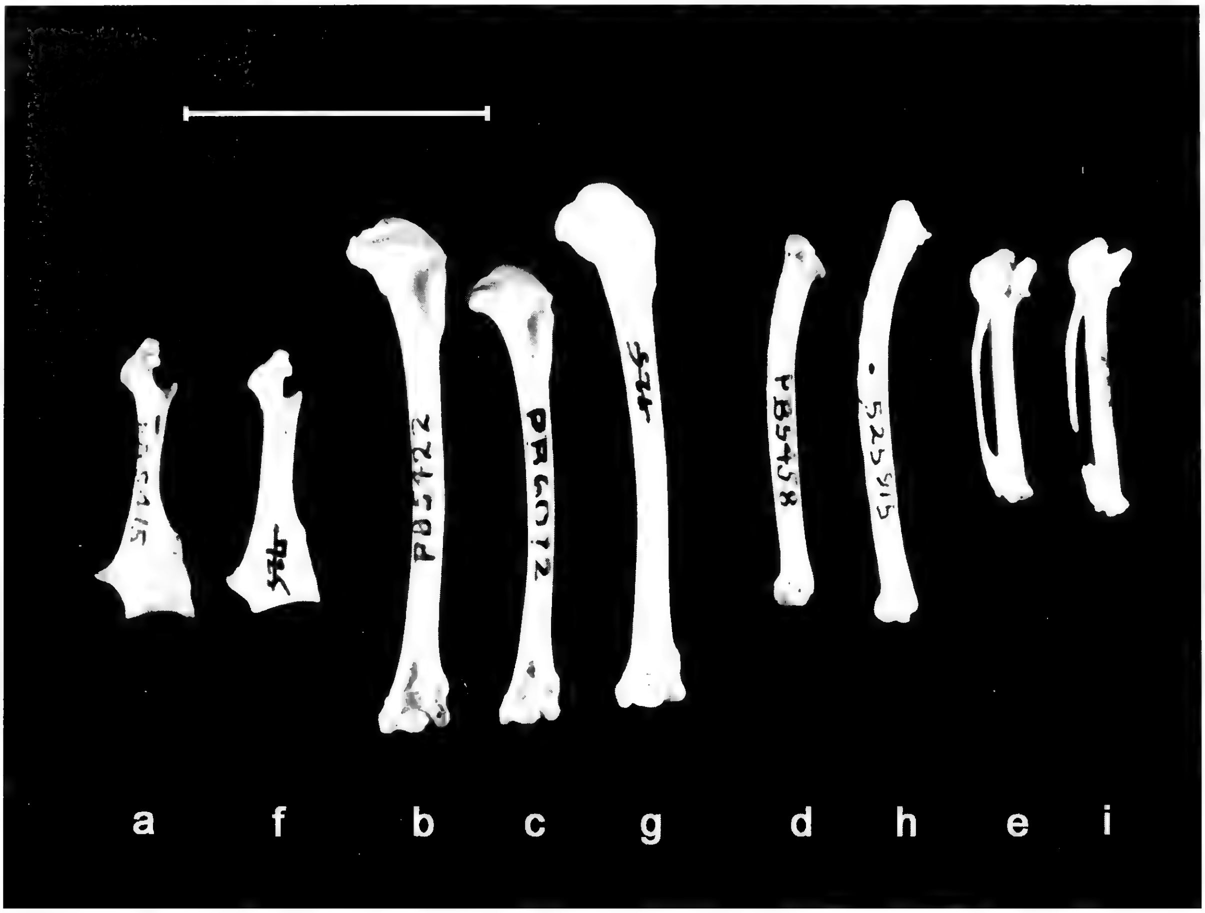

Fig. 3. Comparison of pectoral and wing elements of *Rallus ibycus,* new species (a–e) with *R. limicola* (f–i, female USNM 525915). a, f, right coracoids in ventral view (a, UF PB5415); b, c, g, left humeri in palmar view (b, UF PB5422; c, UF PB6072); d, h, left ulnae in internal view (d, UF PB5458); e, i, left carpometacarpi in internal view (e, UF PB5407). Scale bar = 2 cm.

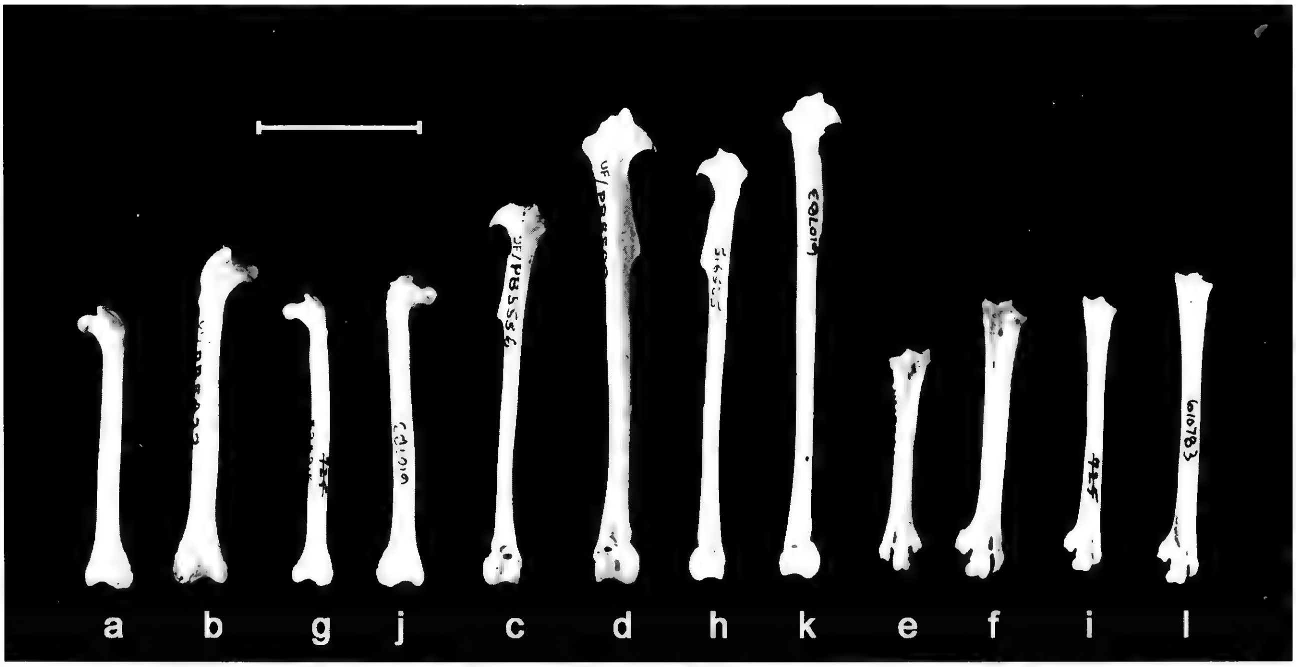

Fig. 4. Comparison of hindlimb elements in anterior view of *Rallus ibycus,* new species (a–f) with *R. limicola* (g–i, USNM 525915 female; j–l, USNM 610783 male). a, left femur UF PB5438; b, right femur UF PB5432; c, right tibiotarsus UF PB5556; d, left tibiotarsus UF PB5500; e, right tarsometatarsus UF PB5462; f, left tarsometatarsus UF PB5544. Scale bar = 2 cm.

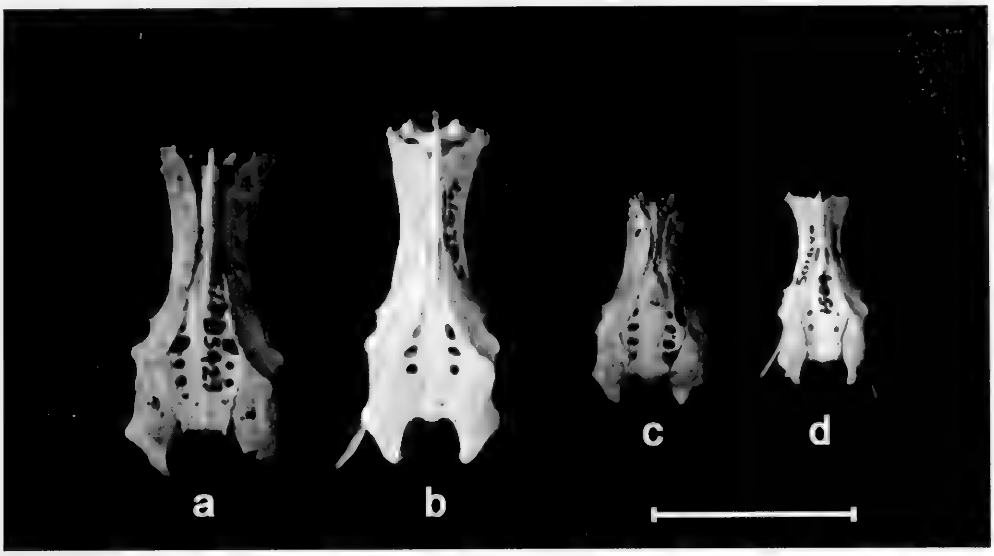

Fig. 5. Pelves of rails in dorsal view. a, *Rallus ibycus*, new species (UF PB5429); b, *R. limicola* (USNM 610783 male); c, *Porzana piercei* new species (UF PB5490); d, *P. flaviventer* (USNM 501640). Scale bar = 2 cm.

species of *Porzana,* the hindlimb elements of *P. flaviventer* are more likewise more robust, with the femur being proportionately shorter. As with the cranial elements, the hindlimb in the small Bermuda rail is most similar to that of *P. flaviventer.* The labels that Pierce Brodkorb left with the specimens indicate that he, too, had concluded that the small Bermuda rail was derived from *P. flaviventer.* The diagnosis of the new species is therefore based on its differences from that species.

Porzana piercei, new species
Figs. 5–9

Holotype.—Complete rostrum UF PB5413. Collected in March 1960 by Pierce Brodkorb and David B. Wingate.

Type locality.—Bermuda, Hamilton Parish, Government Quarry, Crane Crevice.

Chronology.—Middle Pleistocene, presumably within Oxygen Isotope Stages 13 to 20, approximately 800 to 450 kya (see discussion).

Measurements (mm) of holotype.—Length from nasofrontal hinge to tip, 16.8; length of premaxillary symphysis, 5.8.

Paratypes.—Rostra 5421, 5536–5540. Crania 5412, 5527–5528, 5533. Mandible 5481. Sternum 5414. Scapula 5482. Coracoids 5464, 5474, 5483. Humeri 5465, 5484, 5618, 5620, 5620 bis, 5621–5624, 5624 bis, 5625–5629, 5631–5633, 5635–5640, 5640 bis?, 5641–5643, 5645–5648, 5650–5651, 5653, 5654–5671, 5686, 6195. Ulnae 5466, 5485. Carpometacarpi 5476, 5487. Pelvis 5490. Femora 5468, 5478, 5488, 1 uncataloged. Tibiotarsi 5469–5471, 5510, 5547–5550. Tarsometatarsi (all rights except 5590 & 1 uncataloged with it) 3489, 5575–5585, 5587–5590 + 1 uncataloged, 5594, 5606–5607, 5617, 6060.

Measurements (mm) of paratypes.—Scapula: length 17.4. Coracoid: length 10.5, 10.7, 11.7. Ulna: length 16.6, 17.5. Carpometacarpus: length 11.0, 11.2. Pelvis: sacrum length 18.2, 19.0; width across antitrochanters 11.1, 11.6. Femur: length 25.0, 25.2, 26.2, 26.2; proximal width 3.8, 4.1, 4.2, 4.2; distal width 3.7. 3.9, 3.9, 4.1. See also Table 1.

Etymology.—Dedicated to the late Pierce Brodkorb who was instrumental in collecting rail material on Bermuda and who first recognized the affinities of this species.

Diagnosis.—Very similar to *P. flaviventer* but differing in having the skull and bill somewhat larger and in being flightless, with the sternum and pectoral apparatus reduced.

Description.—Compared with *P. flaviventer* the cranium is wider, the foramen magnum larger, and the rostrum is wider with a shorter, wider premaxillary symphysis. The single specimen of mandible, a symphysis with the left dentary, is abraded at the tip but the symphysis is wider and deeper and the bone appears larger than in *P. flaviventer.*

The single available sternum lacks the lateral processes but clearly indicates a flightless species, as the body of the bone is much shorter, but slightly wider, with a much reduced carina that is lower and more posteriorly situated than in *P. flaviventer.* The sternocoracoidal processes are narrower and angled less dorsally in anterior view. The intercoracoidal notch is wider and the manubrial spine lacking.

The coracoids are reduced with more slender shafts and more delicate heads. The only available scapula has the articular end and anterior portion of the shaft wider, the acromion less pointed, and the glenoid facet larger.

The humeri are only slightly smaller than in *P. flaviventer* but have a weaker shaft, a wider capital groove, and a reduced bicipital crest. The ulnae hardly differ except in the slightly weaker shafts. The carpometacarpi differ only in slightly smaller size and proportionately shorter intermetacarpal space.

The pelvis is wider in dorsal view and the postacetabular portion is proportionately shorter. Apart from being slightly more robust, it is difficult to detect any differences in the hindlimb elements from those of the living species, particularly given the very limited comparative material available for the latter.

Remarks.—This species differs very little morphologically from *Porzana flaviventer.* Although clearly flightless, the degree of reduction of the wing and pectoral girdle is relatively slight compared with many other flightless rails, probably indicating recency of derivation.

The Yellow-breasted Crake, *P. flaviventer,* is a very small, delicate rail that typically inhabits relatively large bodies of water with dense, emergent vegetation. Similar habitats were unlikely to have been present in Bermuda, so the birds must have been able to adapt to different ecological conditions, just as other aquatic rails have adapted to even harsher insular environments on Ascension, St. Helena, and Laysan Islands (Olson 1973b). The modern distribution of *P. flaviventer* includes the Greater Antilles and the Neotropical mainland from southern Mexico to Argentina. An extralimital record from Antigua suggests that the species may have occurred in the Lesser Antilles at least up until about 4300 years ago (Pregill et al. 1988:15).

The Yellow-breasted Crake has never been found historically in Bermuda (Amos 1991). Although it is possible that *P. piercei* was derived from populations of that species in the Greater Antilles, it seems equally plausible that the distribution of *P. flaviventer* may have extended into North America during periods of the Pleistocene, as was shown for the Neotropical rail *Laterallus exilis* (Olson 1974), in which case colonization of Bermuda may have been directly from the North American mainland.

Discussion

Of critical importance is determining the age of the Bermudian avifauna that included at least a crane and a duck with reduced powers of flight and the two species of flightless rails described here. Of these fossils Wetmore (1960:1) could say no more than that "it is certain that they are old, and for the present it is my assumption that they date back to the Pleistocene." Brodkorb (*in* Olson 1977:354) thought that they were "post-Nebraskan, probably Aftonian or Kansan." We now know, however, that the periodicity of sea-level and climatic changes associated with glacial cycles in the Pleistocene was much more complex than the traditional view of the four Nebraskan through Wisconsinan glacial periods, with their intervening interglacials (e.g., Hearty 1998).

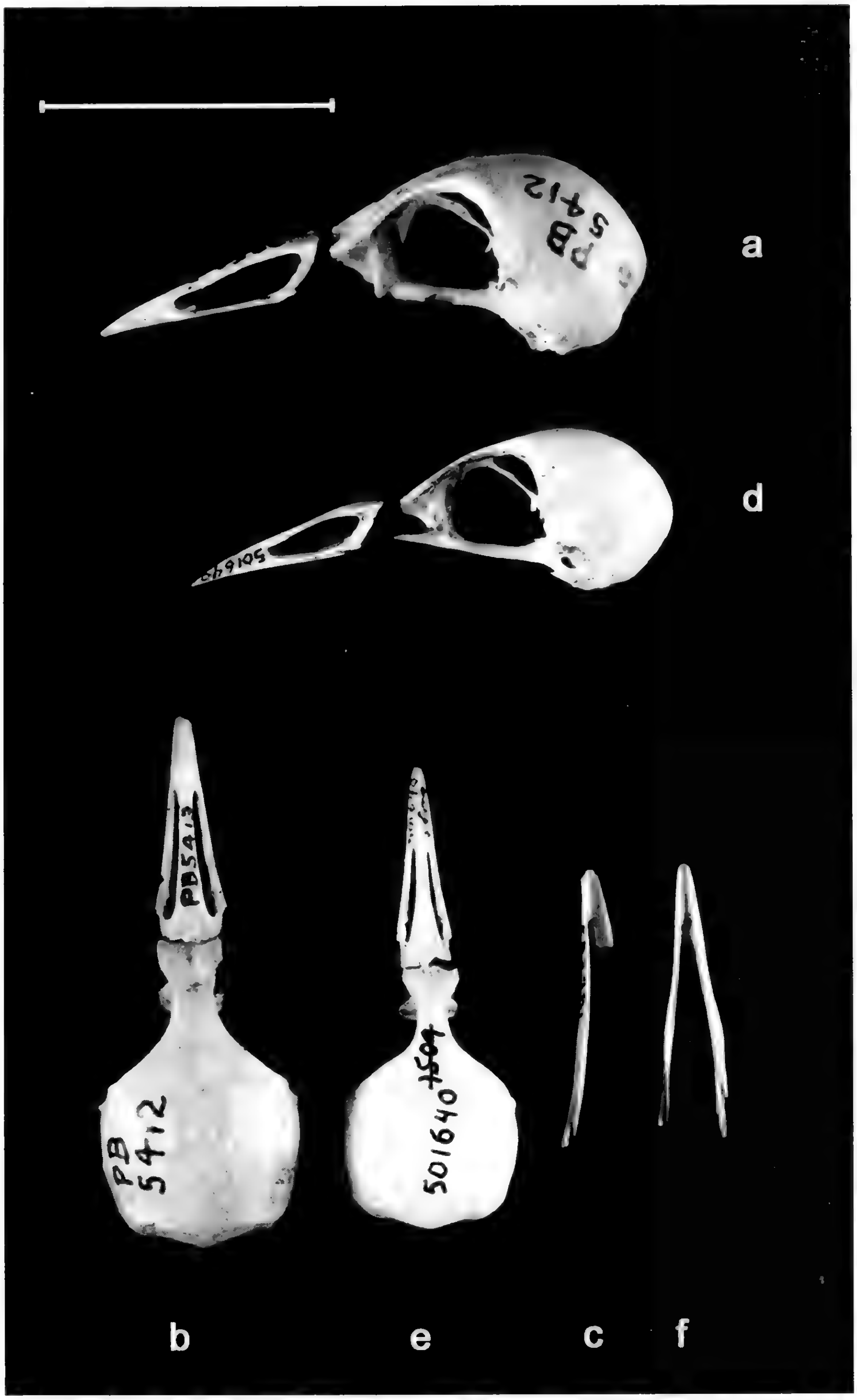

Fig. 6. Comparison of skulls (a–d, lateral view; b–e, dorsal view) and dorsal views of mandibles (c, f) of *Porzana piercei,* new species (a–c) with a very small female *P. flaviventer* USNM 501640 (d–f). a–b, rostrum, holotype UF PB5413, and cranium UF PB5412; c, UF PB5481. Scale bar = 2 cm.

There are as yet no direct radiometric dates on the "crane fauna" of Bermuda but circumstantial evidence points very strongly towards a long period of lowered sea levels in the Middle Pleistocene. The "crane fauna" certainly did not survive into the Holocene as there is no mention of any such birds in the accounts of early settlers nor are there fossils of these birds in any late Quaternary deposits on the island. To have evolved and sustained such a diverse endemic avifauna, especially including a bird as large as a crane, which would have required extensive savanna-like habitat, the

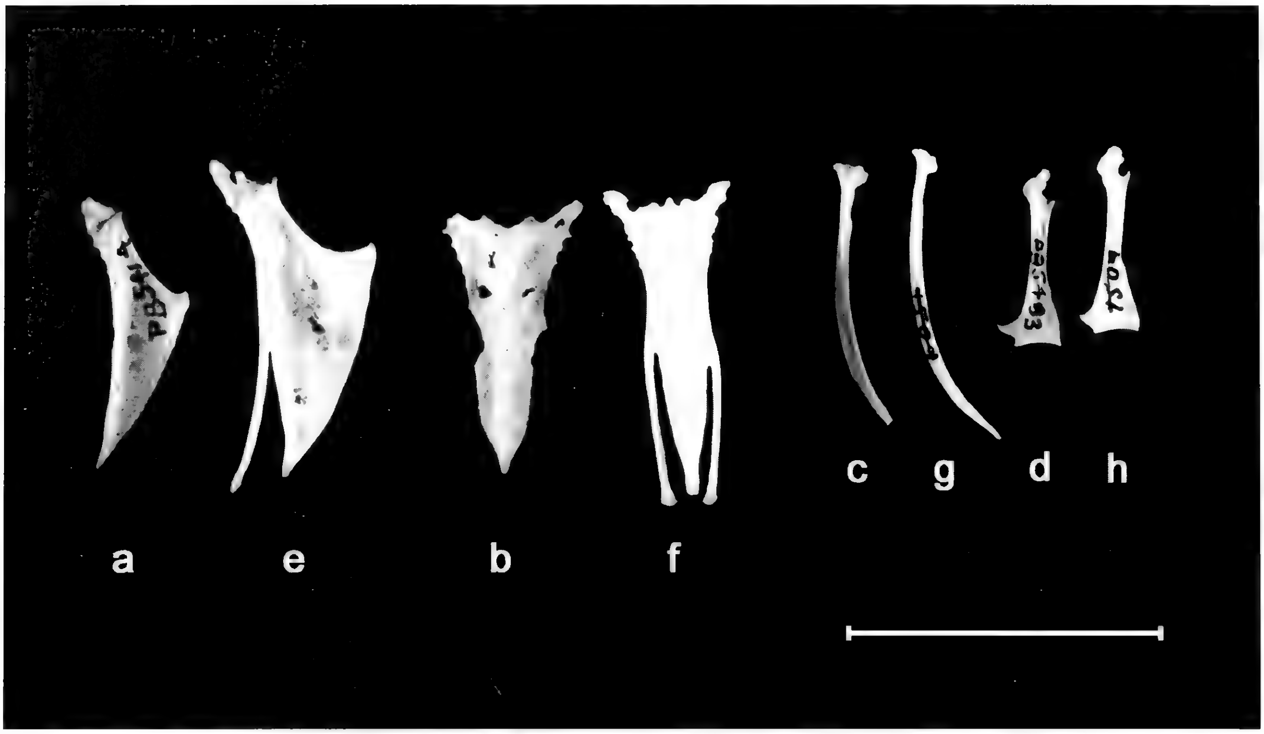

Fig. 7. Comparison of elements of the pectoral girdle of *Porzana piercei,* new species (a–d) with a very small female *P. flaviventer* USNM 501640 (e–h). a–b, sternum UF PB5414 in lateral and ventral views; c, right scapula in dorsal view; UF PB5482; d, left coracoid in ventral view UF PB5483. Scale bar = 2 cm.

land area of Bermuda would have had to be at a maximum for a long period, indicating a glacial period of lowered sea-level of exceptional duration. Thus, Brodkorb's suggestion of Aftonian, which was an interglacial period between the Kansan and Nebraskan glacial epochs, can be ruled out.

Interglacials on Bermuda were periods of marine buildup of carbonate sands on the flooded Bermuda platform, whereas glacial periods were marked by sea-levels well below the surface of the platform when deposition of "terra rossa" soils occured (Hearty & Vacher 1994). Thus, we would

Fig. 8. Comparison of wing elements of *Porzana piercei,* new species (a–d) with a very small female *P. flaviventer* USNM 501640 (e–g). a–b, left humeri in anconal view UF PB5637 and UF PB5632; c, right ulna in internal view UF PB5485; d, right carpometacarpus UF PB5487. Scale bar = 2 cm.

Fig. 9. Comparison of hindlimb elements in anterior view of *Porzana piercei,* new species (a–f) with *P. flaviventer* (g–i, USNM 501640 small female; j–l, USNM 561276 unsexed). a, right femur UF PB5478; b, right femur UF PB5488; c, right tibiotarsus UF PB5470; d, right tibiotarsus UF PB5510; e, right tarsometatarsus UF PB9229; f, right tarsometatarsus UF PB5590. Scale bar = 2 cm.

expect deposition of fossils associated with "terra rossa" soils in caves and fissure fills to have taken place mainly during periods of lowered sea levels. The longest and most stable period of lowered sea-levels in the Quaternary history of Bermuda was from Oxygen Isotope Stage 13 back to about Stage 21 (Hearty & Vacher 1994:687, table 1), which spanned a period from about 450 kya to about 800 kya. Although sea-levels fluctuated during this time, as shown by the various isotope stages, the amplitude of the fluctuations was greatly reduced. Thus, even during the highest stands, the sea was at or below the level of the Bermuda platform through the preponderance of this interval, during which the subaerial portion of the platform would have been at its maximum extent. It was during this time that deep limestone dissolution (karstification) and the accumulation of a massive "terra rossa" soil, the Castle Harbour Geosol, occurred (Hearty & Vacher 1994).

This span of several hundred thousand years of maximum island emergence and relatively stable terrestrial conditions would probably have been the only time during Bermuda's Pleistocene history when the "crane fauna" could have developed. Subsequent events also provide a very convincing explanation for the disappearance of this fauna, for it is now known that during interglacial Stage 11, 380 to 440 kya, sea levels rose much higher than had previously been documented (Hearty et al. 1999), reaching a height of over 20 m above present level. This would have reduced the land area of Bermuda by two orders of magnitude, so that only a few small islets would have remained. In terms of the terrestrial biota, this event would essentially have wiped the slate clean, eliminating the crane, duck, and rails. A new period of colonization and adaption during the next glacial period probably resulted in a substantially different avifauna.

Acknowledgments

We would like to thank the manager and staff of the Bermuda Government quarry for alerting Wingate to the extraordinary deposits of avian fossil material that were exposed by quarrying operations in 1959 and 1960, and for their considerable cooperation and assistance during collection of specimens. We would also like to acknowledge the late Pierce Brodkorb for his part in collecting, numbering, and studying the fossil rail material from Bermuda. We thank Marc Frank and David W. Steadman, Florida Museum of Natural History, Gainesville, for information, arrangements, access to fossil and modern collections, lending specimens, and other considerations. For an understanding and appreciation of aspects of the geology of Bermuda we are indebted to Paul J. Hearty, who also provided many useful comments on the manuscript. Helen James generated the statistics in Table 1 from our measurements; the photographs are by John Steiner and Victor E. Krantz, Smithsonian Photographic Services, and these were made ready for publication by Brian Schmidt, Division of Birds, to all of whom we are especially grateful. This is Contribution #26, Bermuda Biodiversity Project (BBP), of the Bermuda Aquarium, Natural History Museum and Zoo.

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A new species of *Anthias* (Teleostei: Serranidae: Anthiinae) from the Galápagos Islands, with keys to *Anthias* and eastern Pacific Anthiinae

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Abstract.—*Anthias noeli,* new species, is described from 17 specimens collected off the Galápagos Islands in the eastern Pacific, keys to the species of *Anthias* and to the species of eastern Pacific Anthiinae are provided, and comments are presented on hermaphroditism in the Anthiinae. The specimens of the new species, described herein, constitute the first authentic record of *Anthias* from the Pacific; the genus is otherwise known only from the Atlantic where it is represented by seven species. The following characters in combination allow the separation of *Anthias noeli* from its congeners: soft rays in the dorsal fin 15 (rarely 16); tubed lateral-line scales 38 to 46; caudal-peduncle scales 22 to 25; lower jaw naked or with only a few scales posteriorly; gular region naked; total gillrakers on first gill arch 37 to 41; dorsal, anal, pelvic, and caudal fins each with some produced soft rays; anal fin angulate posteriorly; depressed anal-fin length 32 to 43% SL; longest dorsal-fin spine (fourth or fifth) 14 to 20% SL; upper caudal-fin lobe (39–60% SL) longer than lower (38–57% SL); no teeth on tongue.

During recent collecting trips to the Galápagos Islands, investigators aboard submersibles from the Harbor Branch Oceanographic Institution (Fort Pierce, Florida) have captured a number of new species, including 17 specimens of the new anthiine serranid described herein. Anthiines are small to medium size brightly colored fishes that occur worldwide in shallow to moderate depths of tropical, subtropical, and temperate seas. They are usually associated with coral reefs or rocky bottoms that provide refuge from predators. Individuals of most species feed upon zooplankton near the bottom and hastily seek shelter when approached by predators. Anthiines are often seen in aggregations, with males attending large harems. As far as is known, they are protogynous hermaphrodites, with many species being sexually dichromatic and some being sexually dimorphic, especially in fin structure.

There are approximately 185 valid described species in the serranid subfamily Anthiinae, classified variously in at least 25 genera; additionally, there are a number of other known undescribed species of Anthiinae in museum collections, and there are undoubtedly other species that remain to be discovered.

Katayama & Amaoka (1986) restricted *Anthias* to include only Atlantic forms, removing Indo-Pacific species more appropriately regarded as representatives of *Pseudanthias, Franzia,* and *Mirolabrichthys.* Although not clearly stated, it appears that Katayama & Amaoka (1986:217–219, 221) considered *Anthias* to include the following species: *anthias, asperilinguis, helenensis, menezesi, nicholsi, salmopunctatus, tenuis,* and *woodsi.* We modify their concept of the genus *Anthias* to exclude *salmopunctatus* and *tenuis,* which, as shown by Baldwin (1990), appear to be sister species and warrant placement in a genus distinct from *Anthias.* In addition, we include in *Anthias* both the new species described herein and *cyprinoides* formerly assigned to *Holanthias* by Katayama & Amaoka (1986).

Although we are not aware of any character that is clearly synapomorphic for the species of *Anthias,* all eight are extremely similar morphologically and appear to form a natural group. Herein we provide a diagnosis and description of the genus that distinguishes species of *Anthias* from all other serranid fishes.

Methods

Institutional abbreviations follow Leviton et al. (1985), except for HBOM (=Harbor Branch Oceanographic Museum). The methods used here are those of Anderson & Heemstra (1980), as modified by Anderson et al. (1990). Some of those methods are reiterated or clarified below. Tubed lateral-line scales were counted on both sides of each specimen of the new species; other scale counts, except those around the caudal peduncle, were made on either side, depending on condition of the specimen. Counts of caudal-peduncle scales were of the number of scales around the narrowest part of the peduncle. In making counts of rows of cheek scales and counts of scale rows and scales above and below the lateral line, small scales at orbit and at bases of dorsal and anal fins were excluded. (Scales excluded from those counts are distinctly and abruptly smaller than adjacent scales in the counted series.) Scales above the lateral line were counted in a ventroposterior direction from origin of dorsal fin to, but excluding, the lateral-line scale. Scales below the lateral line were counted in a dorsoanterior direction from origin of anal fin to, but excluding, the lateral-line scale. Gillrakers (including rudiments, when present) on the first gill arch were counted on the right side. We follow Mabee (1988) and use "supraneural" instead of "predorsal" to refer to the short series of bones anterior to the pterygiophores that support the dorsal fin, and we conform with Johnson & Patterson (1993: 557) and Patterson & Johnson (1995) in using the term "epineurals" for the intermuscular bones that conventionally have been called "epipleurals" in perciform fishes. Measurements are given as percentages of standard length (SL), except internarial distance which is also presented as the quotient of the snout length divided by the distance between the nares. Osteological data were recorded from radiographs. Standard methods for wax histology were used in preparing the gonadal sections for microscopic examination.

Anthias Bloch

Anthias Bloch, 1792 (type species *Labrus anthias* Linnaeus, 1758, by absolute tautonomy).

Aylopon Rafinesque, 1810 (type species *Labrus anthias* Linnaeus, 1758, by virture of the fact that a replacement name retains the type of the prior name; *Anthias* incorrectly regarded as preoccupied by *Anthia* Weber, 1801, a genus of Coleoptera).

Diagnosis.—A genus of Anthiinae distinguishable from all other genera of the family Serranidae by the following combination of characters. No tooth plate on second epibranchial. Vertebrae 26 (10 precaudal + 16 caudal). Formula for configuration of supraneural bones, anterior neural spines, and anterior dorsal pterygiophores 0/0/2/1+1/1/ (using notation of Ahlstrom et al., 1976), except *A. nicholsi* rarely with slightly different placement of supraneural bones. Principal caudal-fin rays 15 (8 + 7); branched rays 13 (7 + 6). Dorsal-fin rays X, 13 to 16 (usually X, 14 or 15, most frequently X, 15). Anal-fin rays III, 6 to 8 (usually III, 7). Pleural ribs on vertebrae 3 through 10. Epineurals associated with first 11 to 13 vertebrae. Scales ctenoid, with only marginal cteni (i.e., no ctenial bases present proximal to marginal cteni—see Hughes 1981; this type of scale called peripheral ctenoid by Roberts 1993); no smaller accessory scales (secondary squamation) at bases of body scales. Most of head, including maxilla scaly. Lateral line complete, extending to at least base of caudal fin (running parallel to dorsal body contour a few scale rows ventral to dorsal-fin base, curving rather abruptly ventral to posterior end of dorsal-fin base to run near midlateral axis of body). No supramaxilla. Anterior and posterior nares closely set on each side of snout; posterior border of anterior naris produced into a short flap, but never into a long filament. No fleshy papillae on border of orbit. Posterior margin of bony opercle with three spinous processes. Branchiostegal rays seven. Dorsal fin single, not deeply notched between spinous and soft portions. First caudal vertebra without parapophyses. Preopercle serrate, but without antrorse spines. Vomer and palatines with teeth; vomerine tooth patch without a well-developed posterior prolongation.

Description.—Characters included in the generic diagnosis form a part of the generic description and are not repeated. Premaxillae protrusile. Posterodorsal border of maxilla not covered by elements of circumorbital series when mouth closed. Outer teeth in jaws mostly conical; inner teeth mostly villiform or cardiform; some enlarged as canines. Endopterygoids usually toothless. Tongue usually without teeth (except present on tongue in almost all *A. menezesi* and *A. cyprinoides*). Pectoral fin approximately symmetrical, with 16 to 22 rays. Pelvic-fin rays I, 5. Gillrakers well developed, total on first arch 37 to 48. Lateral-line scales 31 to 48. Caudal-peduncle scales 16 to 25. No trisegmental pterygiophores associated with dorsal and anal fins. No spur on posteriormost ventral procurrent ray (see Johnson 1975); penultimate ventral procurrent caudal-fin ray not shortened basally. Parhypural with well-developed hypurapophysis. Autogenous hypurals 5—no hypural fusions. Epurals 3. Uroneurals 1 pair (posterior pair absent). Modified scales (interpelvic process) overlapping pelvic-fin bases along midventral line.

Those species of *Anthias* in which the larvae have been described lack several characters found in the larvae of some American anthiines, viz., specialized larval scales and serrae on supraoccipital crest, pterotic ridge, articular, frontal ridge, parietal ridge, and fin spines. In addition, the known larvae of *Anthias* have a single serrate supraorbital ridge dorsal to each eye, in contrast with the larvae of at least two species of American anthiines that have three serrate supraorbital ridges on each side (Baldwin 1990).

Key to the Species of *Anthias*

1a. Lateral-line scales 31–34; sum of lateral-line scales plus total number of gillrakers on first gill arch, in individual specimens, 71–76; caudal-fin lobes moderate (length of upper lobe 31–49% SL) . . . .*Anthias nicholsi* Firth, 1933 (western North Atlantic)

1b. Lateral-line scales 36–48; sum of lateral-line scales plus total number of gillrakers on first gill arch, in individual specimens, 75–88; caudal-fin lobes moderate to well produced (length of upper lobe 32–110% SL) 2

2a. Longest dorsal-fin spine (usually the third) 13–30% SL, 19–30% SL in specimens more than ca. 100 mm SL; third dorsal-fin spine typically with well developed filament which may be up to 17% SL; lower caudal-fin lobe usually longer than upper . . . . *Anthias anthias* (Linnaeus, 1758) (eastern Atlantic, including the Mediterranean and Adriatic seas)

2b. Longest dorsal-fin spine 10–20% SL; fin membrane usually extending as a short filament at tip of each dorsal spine, but never produced to the extent seen in *A. anthias*; upper caudal-fin lobe usually longer than lower 3

3a. Soft dorsal-fin rays usually 14 (15 in 1 of 17 specimens); midline of gular region and lower jaw well covered with scales; pelvic-fin length 27–41% SL .... *Anthias woodsi* Anderson & Heemstra, 1980 (western North Atlantic)

3b. Soft dorsal-fin rays usually 15 (rarely 16); gular region naked; lower jaw naked or only partly covered with scales; pelvic-fin length 33–76% SL 4

4a. Pectoral-fin rays 19–21 (usually 20 or 21); longest dorsal-fin spine 10–13% SL; upper caudal-fin lobe 32–44% SL; pelvic-fin length 33–39% SL; known only from the eastern South Atlantic 5

4b. Pectoral-fin rays 17–20 (usually 18 or 19); longest dorsal-fin spine 12–20% SL; upper caudal-fin lobe 39–>70% SL; pelvic-fin length 33–76% SL; not known from the eastern South Atlantic 6

5a. Caudal-peduncle scales ca. 18; posterior margin of anal fin rounded; upper caudal-fin lobe 37–44% SL; no teeth on tongue .... *Anthias helenensis* Katayama & Amaoka, 1986 (eastern South Atlantic north of the Island of St. Helena)

5b. Caudal-peduncle scales 20–24; posterior margin of anal fin angular; upper caudal-fin lobe 32–37% SL; tongue usually with one or two small patches of teeth .... *Anthias cyprinoides* Katayama & Amaoka, 1986 (eastern South Atlantic west of the Island of Pagalu)

6a. Total gillrakers on first gill arch 41–48; tongue usually with teeth, teeth usually in narrow elongated patch ... *Anthias menezesi* Anderson & Heemstra, 1980 (western South Atlantic)

6b. Total gillrakers on first gill arch 37–41; tongue usually without teeth 7

7a. Soft dorsal fin and usually soft anal fin without produced rays; caudal-peduncle scales 17 or 18; lateral-line scales 36–41; two of largest individuals examined (out of the 10 known specimens) with teeth on tongue .... *Anthias asperilinguis* Günther, 1859 (western North Atlantic)

7b. Two or more soft dorsal-fin rays and one or more soft anal-fin rays produced; caudal-peduncle scales 22–25; lateral-line scales 38–46; no teeth on tongue ...... *Anthias noeli,* new species (Galápagos Islands, eastern Pacific)

Anthias noeli, new species
Rosy Jewelfish
Figs. 1–5; Tables 1, 2

Material examined.—Seventeen specimens, 62.1 to 173 mm SL; all collected off the Galápagos Islands in the eastern Pacific Ocean in depths of 184 to 351 m.

Holotype: USNM 353113 (167 mm SL, ♂); seamount SE of Isla San Cristobal–01°06.48′S, 89°06.70′W; 202 m; *Johnson-Sea-Link-I* dive no. 3937; Gilmore & Santos, 6 Nov 1995.

Paratypes: USNM 351335 (2, 127–150; ♀, ♂); off NE Isla Darwin–01°42′N, 92°00′W; 351 m; *Johnson-Sea-Link-II* dive no. 3103; McCosker & Pawson, 18 Jul 1998. CAS 86573 (1, 132; ♂); off Isla Darwin–01°41.39′N, 91°58.88′W; 335 m; *Johnson-Sea-Link-I* dive no. 3963; McCosker et al., 20 Nov 1995. USNM 351334 (2, 86–110; ♂, ♂); off Isla Marchena–00°24′N, 90°26.3′W; 303 m; *Johnson-Sea-Link-II* dive no. 3109; Baldwin & McCosker, 21 Jul 1998. GMBL 95-34 (1, 139; ♀) & HBOM 107:08471 (1, 123; ♀); off Cabo Douglas, Isla Fernandina–00°17.60′S, 91°39.00′W; 299 m; *Johnson-Sea-Link-I* dive no. 3956; Robison & Santos, 16 Nov 1995. CAS 201896 (1, 173; ♂); off Isla Plazas (=Plaza Sur in Fig. 2)–00°31′24″S, 90°09′0″W; 308 m; *Johnson-Sea-Link-II* dive no. 3096; McCosker & Day, 7 Jul 1998. USNM 351333 (2, 132–170; ?, ♂); 2 miles E of Isla Plazas (=Plaza Sur in Fig. 2)–00°32.25′S, 90°09.02′W; 308 m; *Johnson-Sea-Link-II* dive no. 3096; McCosker & Day, 7 Jul 1998. CAS 86807 (1, 163; ♂); seamount SE of Isla San Cristobal–01°06.03′S, 89°12.20′W; *Johnson-Sea-*

Table 1.—Data on morphometric characters for *Anthias noeli.* Standard lengths are in mm; other measurements, in percentages of standard length.

Character	*n*	Min.	Max.	Mean	Holotype
Standard length	17	62.1	173	—	167
Head, length	17	36.8	43.4	39.4	37.6
Snout, length	17	6.0	9.2	7.7	8.4
Orbit, diameter	17	11.3	15.1	13.5	11.4
Postorbital length of head	17	17.0	20.4	18.8	18.4
Upper jaw, length	17	17.0	19.0	17.9	18.2
Maxilla, width	17	5.9	7.4	6.6	7.0
Bony interorbital, width	17	7.6	9.1	8.3	8.6
Internarial distance	17	0.7	1.2	1.0	0.9
Body, depth	17	35.0	42.1	38.5	40.4
Body, width	17	13.1	19.1	15.9	17.6
Predorsal length	17	31.8	36.6	34.1	33.7
Prepelvic length	17	35.7	43.7	39.1	38.2
Preanal length	17	59.4	66.3	63.3	64.0
Caudal peduncle, length	17	21.9	26.7	24.6	25.6
Caudal peduncle, depth	17	11.8	13.6	12.6	13.6
Dorsal-fin base, length	17	54.4	61.7	57.0	61.7
Pectoral fin, length	17	28.2	33.4	31.2	31.4
Pelvic fin, length	11	32.6	55.1	42.7	53.7
Anal-fin base, length	17	16.1	18.5	17.3	18.2
Anal fin, length	15	32.3	42.9	37.0	41.9
Upper caudal-fin lobe, length	12	38.8	60.4	49.2	46.9
Lower caudal-fin lobe, length	13	38.2	57.4	46.8	46.3
First dorsal spine, length	14	6.1	8.5	7.0	7.4
Third dorsal spine, length	15	13.1	17.8	15.3	14.9
Fourth dorsal spine, length	11	14.3	19.9	16.6	14.7
Tenth dorsal spine, length	15	10.7	12.6	11.7	12.2
Longest dorsal spine, length	13	14.3	19.9	16.5	15.2
Longest dorsal soft ray, length	11	26.1	44.7	36.0	38.3
Pelvic spine, length	15	15.4	19.8	17.3	17.1
First anal spine, length	16	7.2	10.4	8.2	7.7
Second anal spine, length	14	12.0	20.4	15.6	14.4
Third anal spine, length	16	12.8	17.1	14.7	12.8
Longest anal soft ray, length	15	24.0	31.8	27.4	31.8

Link-I dive no. 3934; McCosker et al., 5 Nov 1995. UF 110990 (2, 68–134; ♀, ♀); seamount SE of Isla San Cristobal–01°06.23′S, 89°06.91′W; 184–215 m; *Johnson-Sea-Link-I* dive no. 3935; Robison & Liberatore, 5 Nov 1995. ANSP 177770 (3 specimens, 62.1–106 mm SL; ?, ♀, ♂); off Devil's Crown, Isla Floreana–01°12.50′S, 90°25.56′W; 232 m; *Johnson-Sea-Link-I* dive no. 3945; McCosker & Liberatore, 9 Nov 1995.

Diagnosis.—A species of *Anthias* distinguishable from all other species of the genus by the following combination of characters. Dorsal-fin rays X, 15 or 16 (usually X, 15). Anal-fin rays III, 6 or 7 (usually III, 7). Pectoral-fin rays 18 to 20 (most frequently 19). Lateral-line scales 38 to 46 (usually 39–44). Total gillrakers on first gill arch 37 to 41 (usually 38–40; no rudimentary rakers). Sum of lateral-line scales plus total number of gillrakers, on individual specimens, 78 to 85. Caudal-peduncle scales 22 to 25 (usually 23 or 24). Caudal fin lunate to deeply forked (larger individuals tending to have more lunate fins). Dorsal, anal, pelvic, and caudal fins each with some produced soft rays. Upper caudal-fin lobe longer than lower. Anal fin angulated posteriorly. Gular region without

Table 2.—Frequency distributions of numbers of fin rays, scales, and gillrakers on first gill arch in *Anthias noeli*. Counts for the holotype are indicated by asterisks.

Character	15	16	6	7	18	19	20	Mean
Dorsal soft rays	16*	1						15.06
Anal soft rays			1	16*				6.94
Pectoral-fin rays,								
Left side					1	14*	2	19.06
Right side					2	10	4*	19.12

	38	39	40	41	42	43	44	45	46	Mean
Tubed lateral-line scales,										
Left side	1	2	2	3	1	4	3*	—	1	41.82
Right side		1	2	4	4*	1	4	1		42.06

	22	23	24	25	Mean
Circum caudal-peduncle scales	1	7	5*	2	23.53

	10	11	12	Mean	27	28	29	30	Mean
Gillrakers									
Upper limb	4	12*	1	10.82					
Lower limb					5*	7	4	1	28.06

	37	38	39	40	41	Mean
Total gillrakers (upper limb + lower limb)	1	6*	5	4	1	38.88

scales. Endopterygoids and tongue without teeth.

Description.—Characters presented in the generic and species diagnoses and the generic description form part of the species description and are not repeated unless necessary for clarification. Data for morphometric characters appear in Table 1; those for some countable characters in Table 2. Mouth nearly terminal, lower jaw exceeding upper jaw very slightly. Maxilla falling short of vertical through posterior border of orbit. Maxilla usually widened distally, with a small shelf or rostrally directed hook on labial border (as in *Anatolanthias apiomycter*—see Anderson et al. 1990:926, fig. 2). Internarial distance 6–12, usually 7–10, times in snout length. Vertical limb of preopercle serrate; horizontal limb smooth or with several small serrae near angle; angle with a single spine, a serrated spinous process, or relatively large serrae. Distal margins of interopercle and subopercle usually smooth or nearly so, occasionally with several small serrae.

Premaxilla with inner band of very small teeth and outer series of larger, mostly anteriorly directed, conical teeth; near symphysis, two to several teeth along medial margin of inner band enlarged as posteriorly directed conical teeth; outer row of larger conical teeth usually preceded by one or two enlarged canine teeth. Dentary with row of slender conical teeth along lateral edge of jaw; this row including one to three teeth, usually enlarged into recurved canines, at a point approximately one third length of row from its anterior end; band of very small teeth extending anteriorly from this row and reaching to near symphysis; one to several teeth on inner edge of band near symphysis enlarged and directed posteriorly; one or two enlarged exserted canines near symphysis.

Branchiostegal rays seven—anterior three inserting along ventral edge or ven-

Fig. 1. Holotype of *Anthias noeli*, new species, USNM 353113, 167 mm SL; Galápagos Islands, eastern Pacific Ocean. Photograph by Donald Hurlbert, National Museum of Natural History, Smithsonian Institution.

tromedial aspect of hyoid arch, posterior four inserting on lateral surface of arch. Pseudobranch well developed, with ca. 22 to 33 filaments; number of filaments increasing with increase in SL (No. filaments = a + b[SL]; where a = 17.03, b = 0.08, r^2 = 0.7522).

Most of head, including most of dorsum of snout, interorbital region, and maxilla, scaly. Lateral aspect of snout, lachrymal, branchiostegals, branchiostegal membranes, and gular region naked (one specimen with a few scales on lachrymals). Dentary usually naked, but some specimens with a few scales posteriorly. Rows of scales on cheek 8 to 11 (usually 9 or 10; difficult to count). Dorsal and anal fins mostly scaleless, except columns of very small scales frequently present proximally on interradial membranes between soft rays, particularly on larger specimens. Rows of scales between lateral line and mid-base of spinous dorsal fin 2 or 3. Scales between origin of dorsal fin and lateral line 6 to 8. Scales between origin of anal fin and lateral line 17 to 20.

Longest dorsal-fin spine fourth or fifth. Second anal-fin spine more robust than first or third. Procurrent caudal-fin rays 9 (rarely 10) dorsally, 8 or 9 ventrally. Dorsal-fin membrane produced into a short filament posterior to each spine. Two or more soft dorsal-fin rays, one or more soft anal-fin rays, first two (and on occasion third) soft pelvic-fin rays (second longest), and caudal-fin lobes produced. Pectoral fin reaching posteriorly to at least as far as vertical through base of third anal spine, frequently as far as vertical through base of second anal soft ray or beyond; dorsalmost pectoral-fin ray always unbranched, ray next to dorsalmost ray and ventralmost ray occasionally unbranched. Pelvic fin reaching posteriorly at least to base of first anal soft ray to as far as well beyond posterior end of anal-fin base. Pelvic fin inserted beneath anterior part of pectoral-fin base.

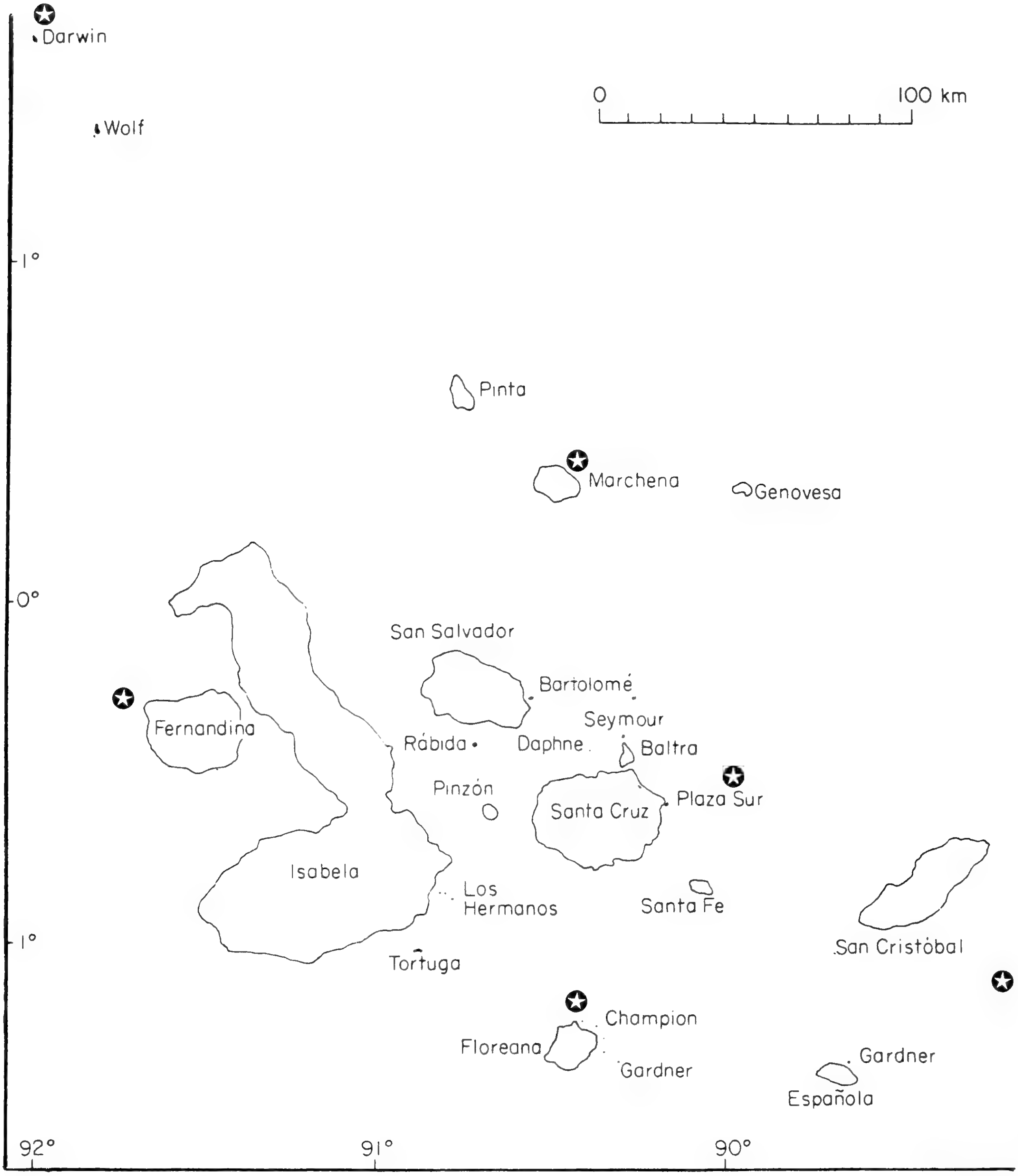

Fig. 2. Map of Galápagos Islands, eastern Pacific Ocean, showing localities of capture of *Anthias noeli,* new species. Modified from Grant 1984.

Coloration.—Description based on color photographs, taken shortly after capture, of two paratypes (CAS 201896, 173 mm SL; USNM 351333, 170 mm SL; see Fig. 3), and color notes, made by the second author in the field, of two other paratypes (USNM 351335, 127 & 150 mm SL). Head mostly rosy, a yellow streak extending across lachrymal and part of cheek and a broad yellow stripe extending from posterior margin of eye to posterior tip of opercle. Jaws rosy except small patch of yellow on upper lip near premaxillary symphysis. Iris yellow. Body mostly rosy dorsally, paler ventrally, a few yellow stripes or blotches on lateral and ventral aspects of body; black blotch present at anterior base of spinous dorsal fin. Membrane covering dorsal-fin spines yellow except rosy distally; interradial membranes mostly rosy; soft dorsal fin mostly rosy, except membranes separating three anteriormost dorsal soft rays mostly yellow or yellow distally and last four rays pale purple. Anal-fin spines and interradial membranes yellow; anterior soft anal-fin rays and interradial membranes yellow basally, yellow and rosy distally; posterior portion of soft anal fin rosy to pale purple. Pectoral fin rosy. Pelvic fin mostly pale rose, some yellow basally and on membrane between first and second rays. Caudal fin mostly rosy, some yellow on outer rays of dorsal and ventral lobes; produced distal ends of caudal-fin lobes rosy or lilac to purplish in color.

Coloration in alcohol.—Dark spot anterior to base of spinous dorsal fin usually persisting; dorsum of head frequently dusky; fins mostly pallid; remainder of fish straw-colored.

Sexuality.—Histological examination of the gonads of all specimens of the new species (except for two for which no gonadal tissue could be found) showed that six individuals (68.0–139 mm SL) are females and nine (86.0–173 mm SL), including the five largest (150–173 mm SL), are males, suggesting that *Anthias noeli* is protogynous (see section on hermaphroditism in anthiines).

Sexual dimorphism.—In specimens more than about 120 mm SL, females (4 specimens, 123–139 mm SL) have shorter pelvic fins (33–36% SL vs. 43–55% SL), shorter longest dorsal soft rays (31–33% SL vs. 38–45% SL), shorter longest anal soft rays (24–28% SL vs. 28–32% SL), and shorter depressed anal-fin lengths (33–37% SL vs. 37–42% SL) than do males (5 specimens, 150–173 mm SL).

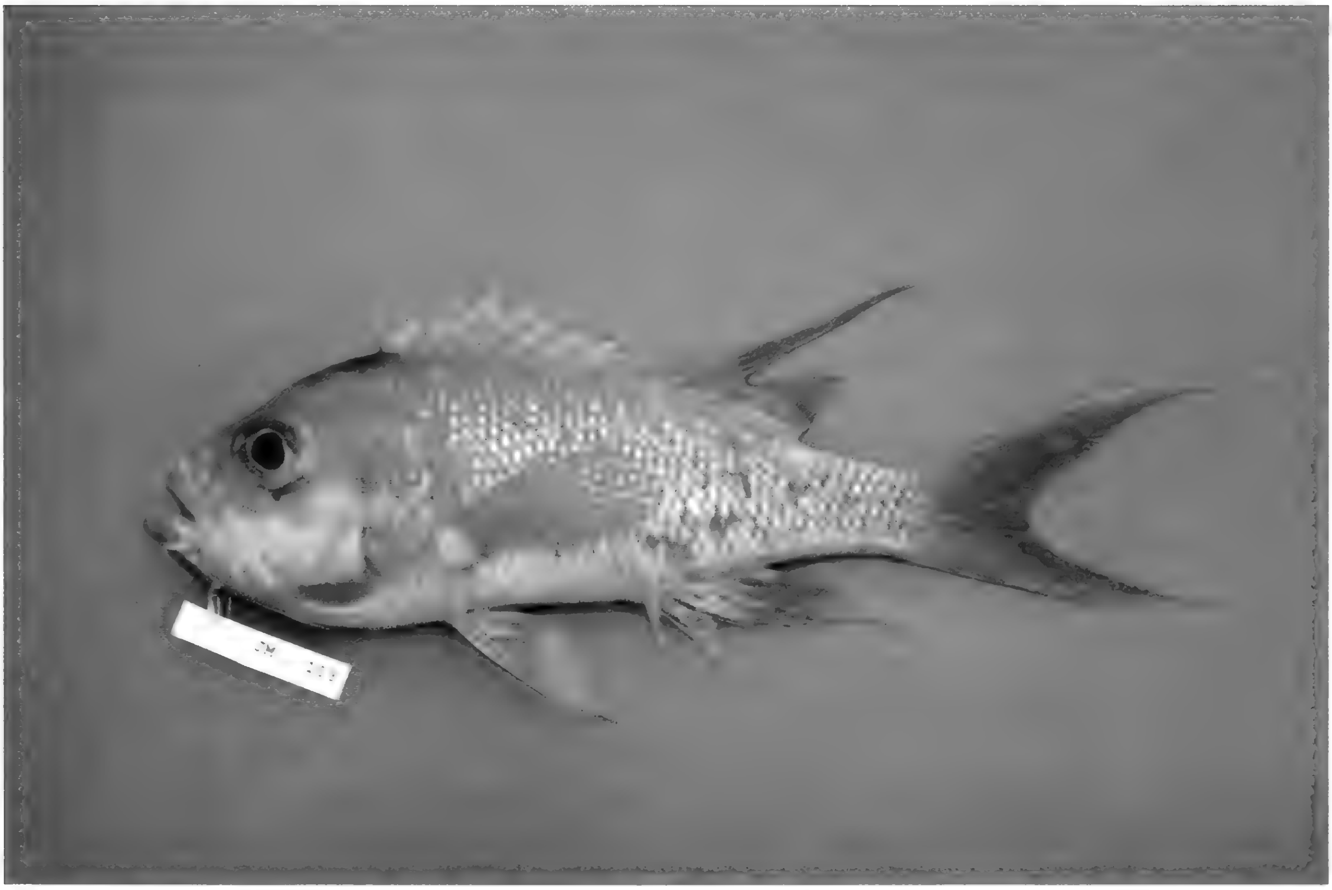

Fig. 3. Paratype of *Anthias noeli*, new species, USNM 351333, 170 mm SL; Galápagos Islands, eastern Pacific Ocean.

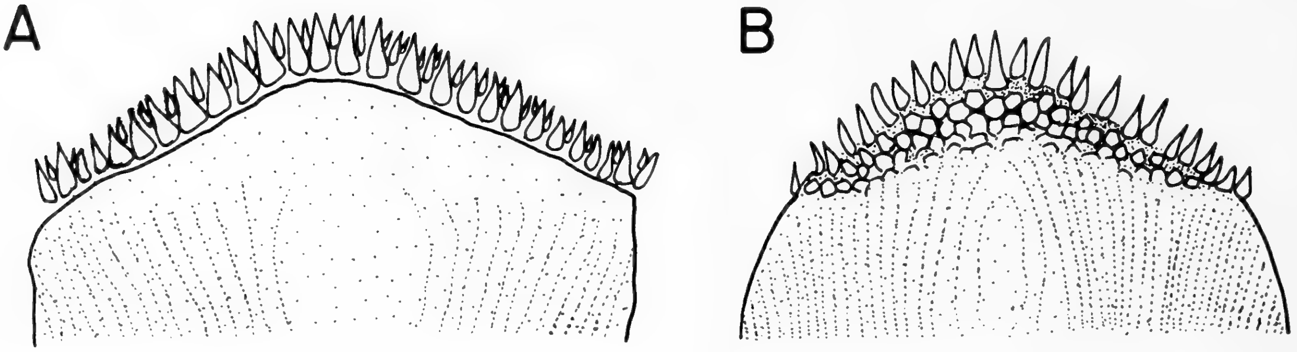

Fig. 4. Scales of anthiine fishes (posterior fields of scales towards the top of the page). A, ctenoid scale with only marginal cteni, as in species of *Anthias*; B, ctenoid scale with ctenial bases present proximal to marginal cteni.

Comparisons.—Anthias noeli is separable from other species of *Anthias* as follows: longest dorsal-fin spine fourth or fifth, third dorsal-fin spine with at most a short filament, and upper caudal-fin lobe longer than lower caudal-fin lobe in *A. noeli* versus longest dorsal-fin spine usually third, third dorsal-fin spine typically with well developed filament (up to 17% SL), and lower caudal-fin lobe usually longer than upper caudal-fin lobe in *A. anthias*; two or more soft dorsal-fin rays and one or more soft anal-fin rays produced and 22 to 25 caudal-peduncle scales in *A. noeli* versus soft dorsal fin and usually soft anal fin without produced rays and 17 or 18 caudal-peduncle scales in *A. asperilinguis*; upper caudal-fin lobe length 39 to 60% SL, 18 to 20 (usually 19) pectoral-fin rays, and tongue without teeth in *A. noeli* versus upper caudal-fin lobe length 32 to 37% SL, 20 or 21 pectoral-fin rays, and tongue usually with teeth in *A. cyprinoides*; 22 to 25 caudal-peduncle scales and anal fin angulated posteriorly in *A. noeli* versus ca. 18 caudal-peduncle scales and anal fin rounded posteriorly in *A. helenensis*; 37 to 41 total gillrakers on first gill arch and tongue without teeth in *A. noeli* versus 41 to 48 total gillrakers on first gill arch and tongue usually with teeth in *A. menezesi*; 38 to 46 lateral-line scales in *A. noeli* versus 31 to 34 in *A. nicholsi*; 15 or 16 (usually 15) soft dorsal-fin rays and gular region and dentary without scales (some specimens with a few scales on dentary posteriorly) in *A. noeli* versus 14 or 15 (usually 14) soft dorsal-fin rays and midline of gular region and dentary well covered with scales in *A. woodsi.*

In addition, *Anthias noeli* is distinguishable from the other species of Anthiinae found in the eastern Pacific by the following combination of characters: scales ctenoid, with only marginal cteni (i.e., no ctenial bases present proximal to marginal cteni; see Fig. 4A); maxilla scaly; dentary naked or with only a few scales posteriorly; gular region without scales; vomer with teeth; no teeth on tongue; anterior naris relatively close to posterior naris (internarial distance 6–12, usually 7–10, times in snout length); posterior border of anterior naris produced into a short flap, but never into a long filament; preopercle without antrorse spines; urohyal without anteriorly projecting spine; dorsal-fin rays X, 15 or 16 (usually X, 15); anal-fin rays III, 6 or 7 (usually III, 7); lateral-line scales 38 to 46; total gillrakers on first gill arch 37 to 41; diameter of bony orbit 11 to 15% SL. The most recent comparative treatment of the adults of eastern Pacific anthiines is that of Fitch (1982), which covers only four of those species, all found in the northern hemisphere. To facilitate identification of all 13 species of eastern Pacific Anthiinae, we present a key to those taxa (see below).

Distribution.—Anthias noeli is known only from the Galápagos Islands, eastern

Pacific Ocean, in depths ranging from 184 to 351 meters (see Fig. 2).

Etymology.—The specific name, *noeli,* is for Noel Archambault, IMAX® cameraman/stereographer, who lost his life on 26 June 1998 in a tragic plane crash in the Galápagos during one of the expeditions on which the new species was collected. Noel was a pioneer of modern 3-D film technology. It is appropriate to name in his memory a new species collected using the modern submersible technology that is allowing the exploration of oceanic regions previously inaccessible to scientific study.

Key to the Eastern Pacific Species of Anthiinae

1a. Scales ctenoid, with only marginal cteni (i.e., no ctenial bases present proximal to marginal cteni; Fig. 4A) 2

1b. Scales ctenoid with ctenial bases present proximal to marginal cteni (Fig. 4B) or in one species (*Trachypoma macracanthus*) scales cycloid 7

2a. Maxilla scaly 3

2b. Maxilla naked 5

3a. Vomer edentate; anterior naris somewhat remote from posterior naris; internarial distance 2.8–3.1 times in snout length .. *Anatolanthias apiomycter* Anderson, Parin, & Randall, 1990 (Nazca Ridge)

3b. Vomerine dentition well developed; anterior naris relatively close to posterior naris; internarial distance more than 5.0 times in snout length 4

4a. Posterior border of anterior naris produced into a filament, usually reaching posterior naris when reflected; ventral surface of dentary and midline of gular region with scales; bony orbit diameter 7–11% SL (8–11% SL in specimens <160 mm SL, 7–9% SL in specimens >165 mm SL); teeth usually present on tongue .... *Pronotogrammus multifasciatus* Gill, 1863 (southern California and the Gulf of California to northern Peru and the Galápagos Islands)

4b. Posterior border of anterior naris without a filament, but produced into a short flap that almost always fails to reach posterior naris when reflected; dentary usually without scales, occasionally with a few scales posteriorly; gular region without scales; bony orbit diameter 11–15% SL (12–15% SL in specimens <140 mm SL, 11–13% SL in specimens >150 mm SL); no teeth on tongue ... *Anthias noeli,* new species (Galápagos Islands)

5a. Lateral-line scales 60–71 (usually 62–68); specimens more than about 70 mm SL with sharp spine projecting anteriorly from ventral border of urohyal .... *Hemanthias signifer* (Garman, 1899) (southern California to northern Peru)

5b. Lateral-line scales 36–57 (usually 54 or fewer); urohyal without anteriorly projecting spine 6

6a. Lateral-line scales 36–40; total gillrakers on first arch 38–43; longest dorsal-fin spine most frequently the sixth, never the third; third dorsal-fin spine with short filament, but filament never well produced; middle rays of upper and lower lobes of caudal fin not longest in fin .... *Pronotogrammus eos* Gilbert, 1890 (mid-Gulf of California [28°N; Fitch 1982] to Colombia [6.5°N])

6b. Lateral-line scales 49–57; total gillrakers on first arch 31–35; longest dorsal-fin spine—the third; third dorsal-fin spine with well produced filament (at least in larger individuals); middle rays of upper and lower lobes of caudal fin longest in fin .... *Hemanthias peruanus* (Steindachner, 1875) (Hipólito Bank [27°N], Baja California Sur, in the Pacific and Cabo Lobos [ca. 30°N], Sonora, in the Gulf of California to Trujillo [8°S], Peru, and the Galápagos Islands [Fitch 1982; Grove & Lavenberg 1997])

7a. Spines in dorsal fin XI-XIII; ventral border of preopercle with strong antrorse spines 8

7b. Spines in dorsal fin X; ventral border of preopercle without antrorse spines, except in *Hypoplectrodes semicinctum* and occasionally in *Plectranthias exsul* 10

8a. Scales cycloid; spines in dorsal fin XII; soft rays in anal fin 6 . . . . *Trachypoma macracanthus* Günther, 1859 (widely distributed in the South Pacific, including Easter Island and the Desventuradas Islands off the coast of Chile [Randall & Cea Egaña 1984; Pequeño & Lamilla 1996a,b; Rojas & Pequeño 1998a])

8b. Scales ctenoid; dorsal spines XI or XIII; soft rays in anal fin 8 or 9 . . . 9

9a. Dorsal-fin rays XI, 17 or 18 . . . . *Acanthistius pictus* (Tschudi, 1846) (coasts of Peru and Chile)

9b. Dorsal-fin rays XIII, 14 or 15 . . . . *Acanthistius fuscus* (Regan, 1913) (Easter Island and Sala y Gómez Island [Rojas & Pequeño 1998a])

10a. Soft rays in dorsal fin 19–22 11

10b. Soft rays in dorsal fin 15 or 16 12

11a. Preopercle with 2 or 3 antrorse spines (one spine usually at angle or on ventral margin near angle, other spine[s] on ventral margin); total gillrakers on first gill arch 17–20; lateral-line scales 48–55 (most frequently 48–51) . . . . *Hypoplectrodes semicinctum* (Valenciennes, 1833) (Juan Fernández Islands and San Félix Island [in the Desventuradas Islands] off the coast of Chile, and possibly Easter Island [Anderson & Heemstra 1989; Pequeño & Lamilla 1996b; Rojas & Pequeño 1998a])

11b. Preopercle serrate, but without antrorse spines; total gillrakers on first gill arch 34–37; lateral-line scales 58–65, usually 61–64 (counts only from eastern Pacific specimens) . . . . *Caprodon longimanus* (Günther, 1859) (widely distributed in the Pacific—including Easter Island and the Nazca Ridge and from the Desventuradas and Juan Fernández islands off the coast of Chile, and "along the coast of South America" [Pequeño & Lamilla 1996a:931, 1996b])

12a. Scales on dorsum of head not extending anterior to nares (Randall 1996: 117); longest soft dorsal-fin ray ca. 26–35% SL; total gillrakers on first gill arch 26–28; in life, two orange-red bars on body (one just anterior to anal fin, the other terminating ventrally posterior to anal fin) . . . . *Plectranthias parini* (Anderson & Randall, 1991) (Sala y Gómez Ridge and Easter Island [Randall 1996])

12b. Scales on dorsum of head extending anteriorly almost to upper lip, except for triangular premaxillary groove (Randall 1996:117); longest soft dorsal-fin ray ca. 16–>26% SL; total gillrakers on first arch 26–31 (usually 28 or 29); in life, brilliant red oblong area extending from bases of posterior rays of soft dorsal fin ventrally to just below midline and then posteriorly over middle of caudal peduncle to reach midventral line near base of caudal fin . . . . *Plectranthias exsul* Heemstra & Anderson, 1983 (Juan Fernández Islands and Nazca Ridge; also reported from Desventuradas Islands by Rojas & Pequeño 1998a)

Plectranthias lamillai

Rojas & Pequeño (1998b) described a new species of *Plectranthias, P. lamillai,* from a single specimen (MNHNC P.7055, 139.6 mm SL) collected off Alejandro Selkirk Island in the Juan Fernández Islands off the coast of Chile. In the description provided by Rojas & Pequeño (1998b), we could find no characters that seem to reliably distinguish it from *Plectranthias exsul,* also known from off the Juan Fernández Islands. As a consequence, the first author made a detailed examination of the holotype of *P. lamillai* (now 136 mm SL) and compared it closely with two specimens of *P. exsul* (USNM 176577—a paratype, 158 mm SL, and USNM 312927, 122 mm SL) and found that the holotype agrees well with the original description of *P. exsul* and, with one exception, with the specimens of *P. exsul* with which it was directly compared. The interorbital region of the paratype of *P. exsul* examined in comparison is more flattened than that of the holotype of *P. lamillai*; this we attribute to ontogenetic differences or perhaps to sexual dimorphism. In contrast, the 122-mm specimen of *P. exsul* is essentially identical in head and body shape to the holotype of *P. lamillai*. It should be noted that the drawing with the original description of *P. lamillai* (see Rojas & Pequeño 1998b:fig 2) is not a particularly good representation of the holotype, especially of the head. *Plectranthias lamillai* and *P. exsul* have somewhat different patterns of coloration, but we think that the different patterns displayed are best interpreted as variations on a common theme. In view of the preceding and pending a more complete investigation, we deem it best to consider *P. lamillai* Rojas & Pequeño, 1998, as a junior synonym of *P. exsul* Heemstra & Anderson, 1983.

Comments on Hermaphroditism in Anthiine Serranids

Protogyny has been reported in species representing a number of anthiine genera, including *Hypoplectrodes* (*H. huntii* [as *Ellerkeldia huntii*] and *H. maccullochi*; Jones 1980 and Webb & Kingsford 1992, respectively), *Hemanthias* (*H. vivanus* and *H. peruanus*; Hastings 1981 and Coleman 1983, respectively), *Pronotogrammus* (*P. martinicensis* [as *Holanthias martinicensis*]; Coleman 1981), *Pseudanthias* (*P. squamipinnis* [as *Anthias squamipinnis*]; Fishelson 1970 and Shapiro in a series of studies on the behavioral aspects of sex reversal—e.g., Shapiro 1986), *Sacura* (*S. margaritacea*; Reinboth 1963), and *Anthias* (*A. anthias*; Reinboth 1964). In addition, Heemstra (1973) provided evidence for protogyny in *Pseudanthias conspicuus* (as *Anthias conspicuus*), and Robins & Starck (1961) stated that *Plectranthias garrupellus* is probably protogynous. Thresher (1984) presented a summary (current through about 1981) of the information available on the reproductive biology of anthiines.

One might assume, from the publications on anthiines cited above, that all of them are protogynous and monandric. Similarly, based on a number of studies, groupers (Serranidae: Epinephelinae), in general, have been considered to display monandric protogyny, but Sadovy & Colin (1995:961) found that sexuality in *Epinephelus striatus* (the Nassau grouper) "is essentially gonochoristic, with potential for sex change" and that "the juveniles pass through a bisexual stage of gonadal development," thus illustrating the importance of not making a priori assumptions about the reproductive biology of serranid fishes. In a study of the Serranidae of the eastern Gulf of Mexico, Bullock & Smith (1991) presented evidence for protogyny in the anthiine *Hemanthias leptus,* but, based on finding a ripening male of 86 mm SL (p. 21, fig. 8b) and a sexually mature male of 61 mm SL (p. 207, pl. Id), entertained the idea that *H. leptus* may be diandric, acknowledging, however, that additional study is needed to confirm this.

In the subsection entitled Sexuality (under *Anthias noeli,* new species), we have presented evidence suggesting that *Anthias noeli* is protogynous. To gather a better appreciation of sexuality in the genus *Anthias,* William A. Roumillat, at our request, examined histological sections of the gonads of 20 specimens of the western Atlantic *A. nicholsi* and found 12 females (52.0–125 mm SL), one individual (73.0 mm SL) transforming from female to male, and seven secondary males (99.9–134 mm SL). These data strongly suggest that *Anthias nicholsi* is protogynous. *Anthias noeli* displays patterns of gonadal morphology similar to those seen in *A. nicholsi* (Fig. 5), lending further support to our contention that *A. noeli* is probably protogynous.

Sadovy & Shapiro (1987) gave criteria for diagnosing various types of hermaphroditism in fishes. Features that they identified as strongly indicating protogyny are: "membrane-lined central cavities in testes; transitional individuals; atretic bodies in stages 1, 2, or 3 of oocytic atresia within testes; sperm sinuses in the gonadal wall;

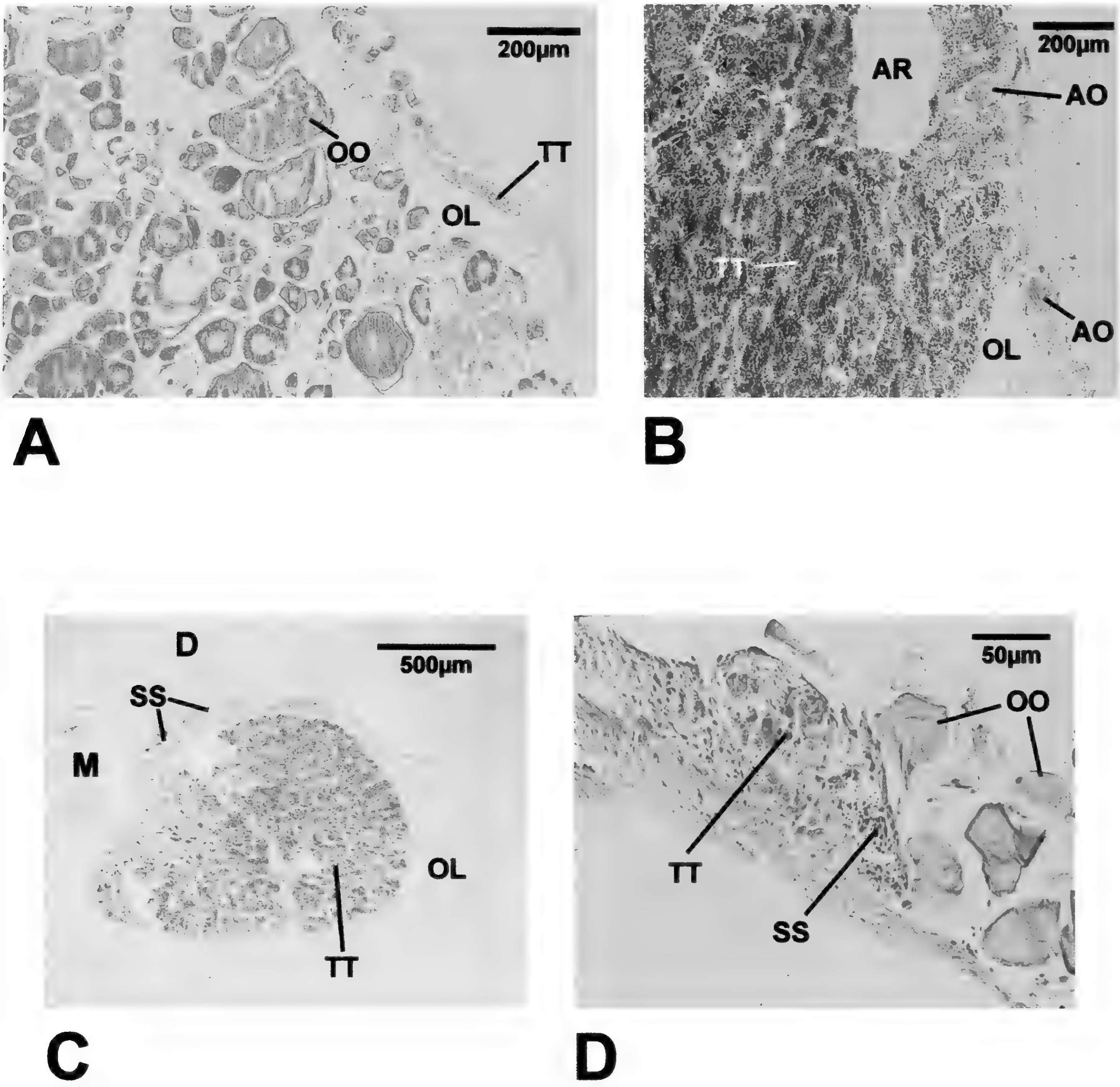

Fig. 5. Gonadal sections of specimens of *Anthias* stained with hematoxylin and eosin-Y. A, *A. noeli,* new species, HBOM 107:08471, 123 mm SL, mature female; B, *A. noeli,* new species, CAS 201896, 173 mm SL, secondary male; C, *A. noeli* new species, CAS 86573, 132 mm SL, secondary male; D, *A. nicholsi,* GMBL 59-32, 73.0 mm SL, individual transforming from female to male. Abbreviations: AR = artifact; AO = atretic oocyte; D = dorsal; M = medial; OL = ovarian lumen; OO = oocyte; SS = sperm sinus; TT = testicular tissue. Photomicrographs by William A. Roumillat, digital imagery by Karen Swanson, South Carolina Department of Natural Resources, Charleston.

and experimental production of transitional or sex-reversed individuals through manipulation of the social system" (Sadovy & Shapiro 1987:150). In our studies we found, with the assistance of Bill Roumillat, that *Anthias nicholsi* fulfills all of those criteria, except the last one which requires live material, and that *A. noeli* meets all but the last and the one involving transitional individuals (sensu Sadovy & Shapiro 1987: 147–148) which were not observed. We feel that it is reasonable to conclude that both species are protogynous.

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Description of two new blenniid fish species: *Entomacrodus lemuria* from the western Indian Ocean and *E. williamsi* from the western Pacific Ocean

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Abstract.—*Entomacrodus lemuria* is described from specimens from Madagascar, Mauritius, and Renunion, and *E. williamsi* is described from specimens from Halmahera (Indonesia), Madang (Papua New Guinea), and Duff Islands (Santa Cruz Islands, Solomon Islands). New distribution records are provided for *E. sealei,* a widely distributed Pacific plate endemic, and *E. corneliae,* a Marquesas Islands endemic. All four species are members of the Nigricans Group of *Entomacrodus,* which group is distinguished from all other blenniids in having the lateral thirds of the ventral margin of the upper lip crenulate and the middle third entire. Within the group, these four species form a subgroup distinguished by having most of the five preopercular pore positions represented externally by pairs or multiples of pores, as opposed to rarely having more than one or two positions with pairs or multiples of pores.

Springer (1967) revised the circumtropical shorefish genus *Entomacrodus.* There have been no new species described in the genus since that publication. Springer (1972:13) provided additional information on the Indo-Pacific species, including mention of a variant color pattern in a single specimen from Madang Harbor, Papua New Guinea. He tentatively identified the variant as *Entomacrodus sealei* Bryan & Herre, 1903, which is otherwise unknown from the island of New Guinea. Springer (1982:19) reported a second specimen of the variant from Ternate, Indonesia, where typical specimens of *E. sealei* are also unknown. He believed that the distribution of the variant, from two localities near the western margin of the Pacific plate, was allopatric to that of typical *E. sealei,* a widely distributed Pacific plate endemic (Springer 1982: fig. 8). Recently, in a single collection, J. T. Williams and associates obtained five specimens of the putative variant together with a large number of typical specimens of *E. sealei.* The sympatry of the two forms convinces us that two species are involved, and we formally describe the unnamed one herein. We have also obtained numerous specimens recently collected from Mauritius, Reunion, and Madagascar of another undescribed species that also appears to be related to *E. sealei,* and we describe that species herein.

In recent years there has been much interest in documenting (inventorying) the fish faunas of many parts of the world. Concomitantly, there has been much collecting and specimens have become available from many localities previously unsampled. Since 1967, there has been an extensive accumulation of *Entomacrodus* specimens in museum collections, and the genus is in need of a new revision. We are unable to undertake that project in the forseeable future, but believe that when there is reasonable certainty that undescribed species ex-

Table 1. Frequency distributions for number of preopercular pore positions represented by pairs or multiples of pores in specimens ≥25 mm SL of the Nigricans Species Group of *Entomacrodus*. There are five pore positions.

		Number of positions with pairs or multiples of pores						
Species	N	0	1	2	3	4	5	$\bar{x}$
cadenati	84	84	-	-	-	-	-	0.00
textilis	55	54	1	-	-	-	-	0.02
caudofasciatus	149	145	4	-	-	-	-	0.03
vomerinus	113	109	3	1	-	-	-	0.04
nigricans	343	314	26	3	-	-	-	0.09
chiostictus	487	184	164	96	29	12	2	1.02
williamsi	7	-	-	1	2	1	3	3.71
lemuria	47	-	1	2	13	16	15	3.89
sealei	99	-	-	-	7	17	75	4.69
corneliae	14	-	-	-	-	-	14	5.00

ist, their descriptions are warranted without delay.

Although the species of *Entomacrodus* have not been analyzed cladistically, some of the seven species groups Springer (1967: 12–13) recognized in the genus are probably monophyletic. One of these, the Nigricans Group, was defined on the basis of the morphology of the ventral margin of the upper lip: the central third of the margin is entire and the lateral third of the margin on each side is crenulate. This morphology does not occur in any other blennioid and, thus, serves as a reasonable basis for an hypothesis of monophyly of the group. Based on this character, the two new species are both members of the Nigricans Group.

Methods

Including the two new species, there are ten species in the Nigricans Group. There are very few characters that distinguish these species, and primary among them are a few particulars of the color pattern and sensory pores. For this reason, our descriptions are brief and limited to little more than the essentials necessary to differentiate the taxa.

Unless defined herein, methods are those of Springer (1967). All counts of vertical fin-ray elements were made from radiographs. When split to the base and supported by a single pterygiophore, the posteriormost anal-fin ray was counted as 1 (Method A of Springer 1967:5).

Preopercular pore positions: There are five sensory canal foramina on the lateral surface of the preopercle (Springer 1968: fig. 7; Smith-Vaniz & Springer 1971:fig. 16). Each of these foramina is represented by (connected to) one or more pores in the skin immediately external to the foramen. We term each such representation a "preopercular pore position" or simply "position" when in context (Fig. 1). Springer (1967) recognized six pore positions, but his ventroanteriormost position does not exit from the lateral surface of the preopercle and is excluded from our definition. The pores are small and often difficult to see; however, the number of these positions with two or more pores is an important character

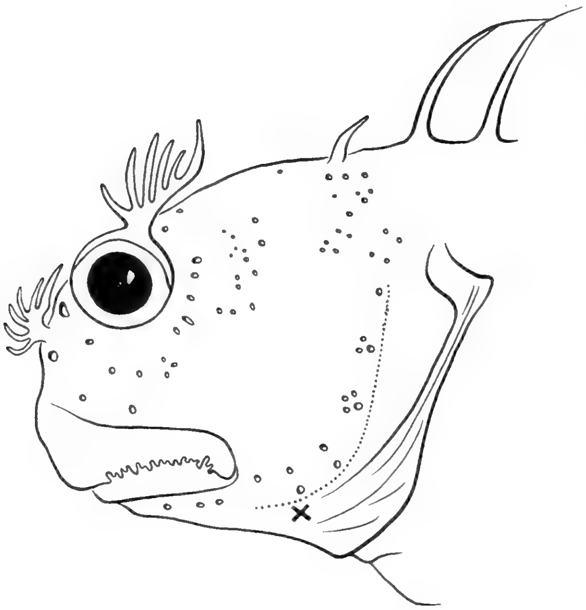

Fig. 1. Diagrammatic illustration of head pores in *Entomacrodus*. External limits of preopercle margin indicated by dotted line; x below ventralmost preopercular pore position; pore position types shown from ventralmost to dorsalmost: paired, paired, multiples, multiples, simple.

for distinguishing species of the Nigricans Group (Table 1). In specimens shorter than 24 mm SL the pore positions may consist only or mostly of single pores in all species of the Nigricans Group; however, in *E. lemuria,* all of the five specimens 18.2–22.7 mm SL, we checked for this character, had two to five positions with pairs of pores, and the smallest specimen had four positions with pairs of pores. To be on the conservative side, we restrict our characterization of pore positions to specimens 24 mm SL and longer (Table 1).

Color pattern: Many features of the color pattern in the Nigricans Group species are highly variable intraspecfically, others are reasonably consistent within and among the species. Some of the variation is the result of poor preservation, but much variation exists in well-preserved specimens. Among the most variable markings are the presence (or absence) and expression of the dusky bars on the body sides, and some of the dusky markings on the head and dorsal and anal fins. These markings, even in specimens that appear to exhibit full expression of color pattern, are of little use for diagnosing species. The more consistent banding of the caudal fin is also of no use. We have found that only aspects of the color pattern of the humeral area dorsal to the pectoral-fin axil and the upper lip are of importance. For these reasons, we restrict our color-pattern descriptions to these two features. The reader desiring more detail is referred to our illustrations and those of the Nigricans Group species in Springer (1967: pls. 18–27).

Institutional abbreviations are those listed in Eschmeyer (1998:16–22).

Materials

Unless noted otherwise, data reported are taken from specimens cited in Springer (1967, 1972).

Nigricans Species Group

Diagnosis.—Species of *Entomacrodus* with: central third of ventral margin of upper lip entire and lateral thirds crenulate; supraorbital cirri branched; nuchal cirri simple; posteriormost dorsal-fin spine reduced, not visible externally; segmented dorsal-fin rays 13–17 (rarely 13, strongly modally 14 or 15 in all but one species: modally 16 in *E. vomerinus* from the southwestern Atlantic); segmented anal-fin rays 14–18 (rarely 14 and only in *E. nigricans,* from the Caribbean; strongly modally 16 in all but *E. vomerinus,* modally 17, and 18 only in *E. vomerinus*); vertebrae 10+23–26 (strongly modally 34 in all but *E. vomerinus,* modally 35). Small species, largest specimen (always male) ranging from 53–105 mm SL, attaining more than 70 mm only in *E. lemuria* (72.1 mm) and *E. vomerinus* (105 mm).

Species Subgroups and Species Distributions

The ten species of the Nigricans Group appear to fall into three subgroups based on the number of preopercular pore positions

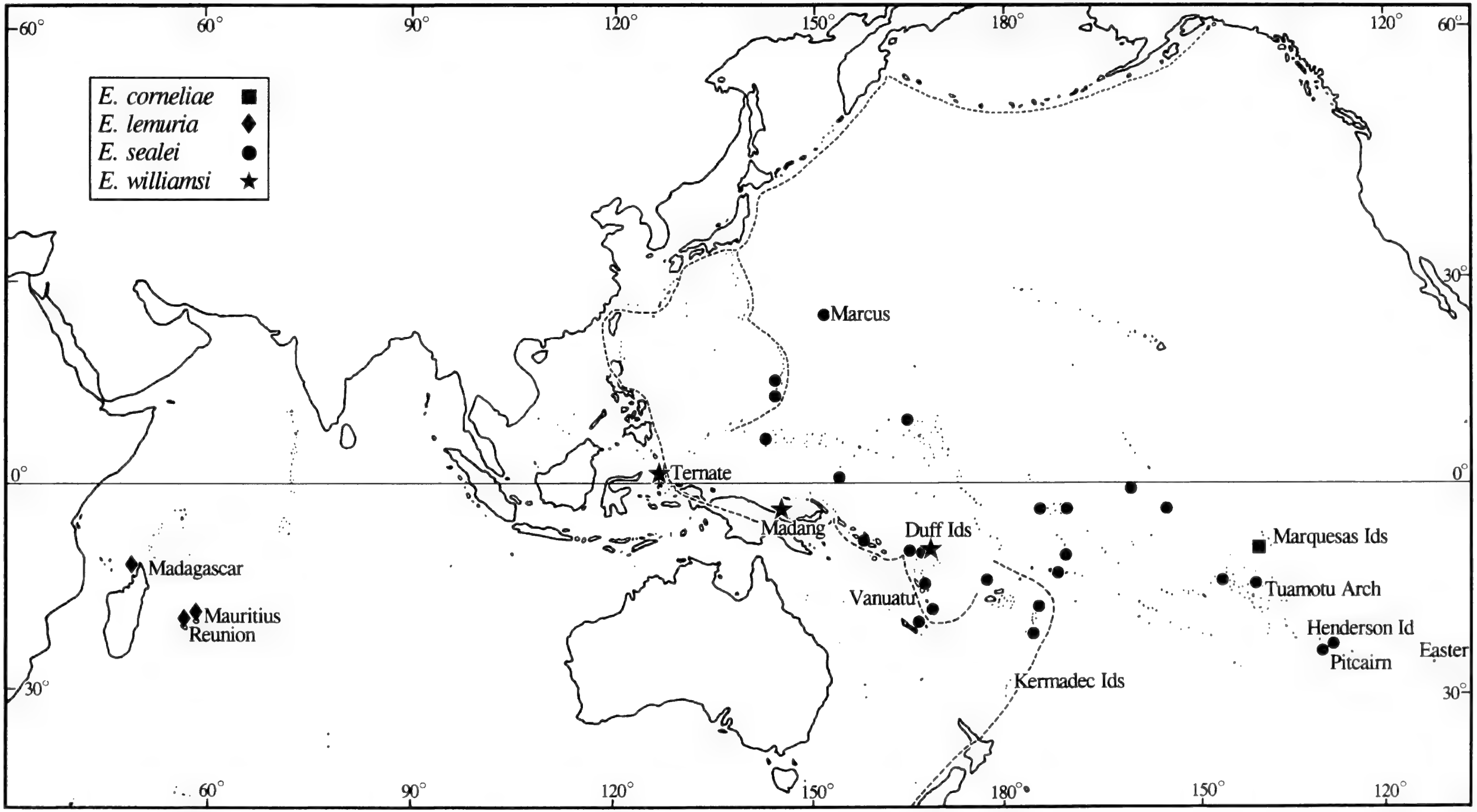

Fig. 2. Distribution of the species of Subgroup 3 of the Nigricans Species Group of *Entomacrodus*. Dashed lines indicate western margins of Pacific and Philippine lithospheric plates and eastern margin of Philippine plate, which is coincident with western margin of Pacific plate.

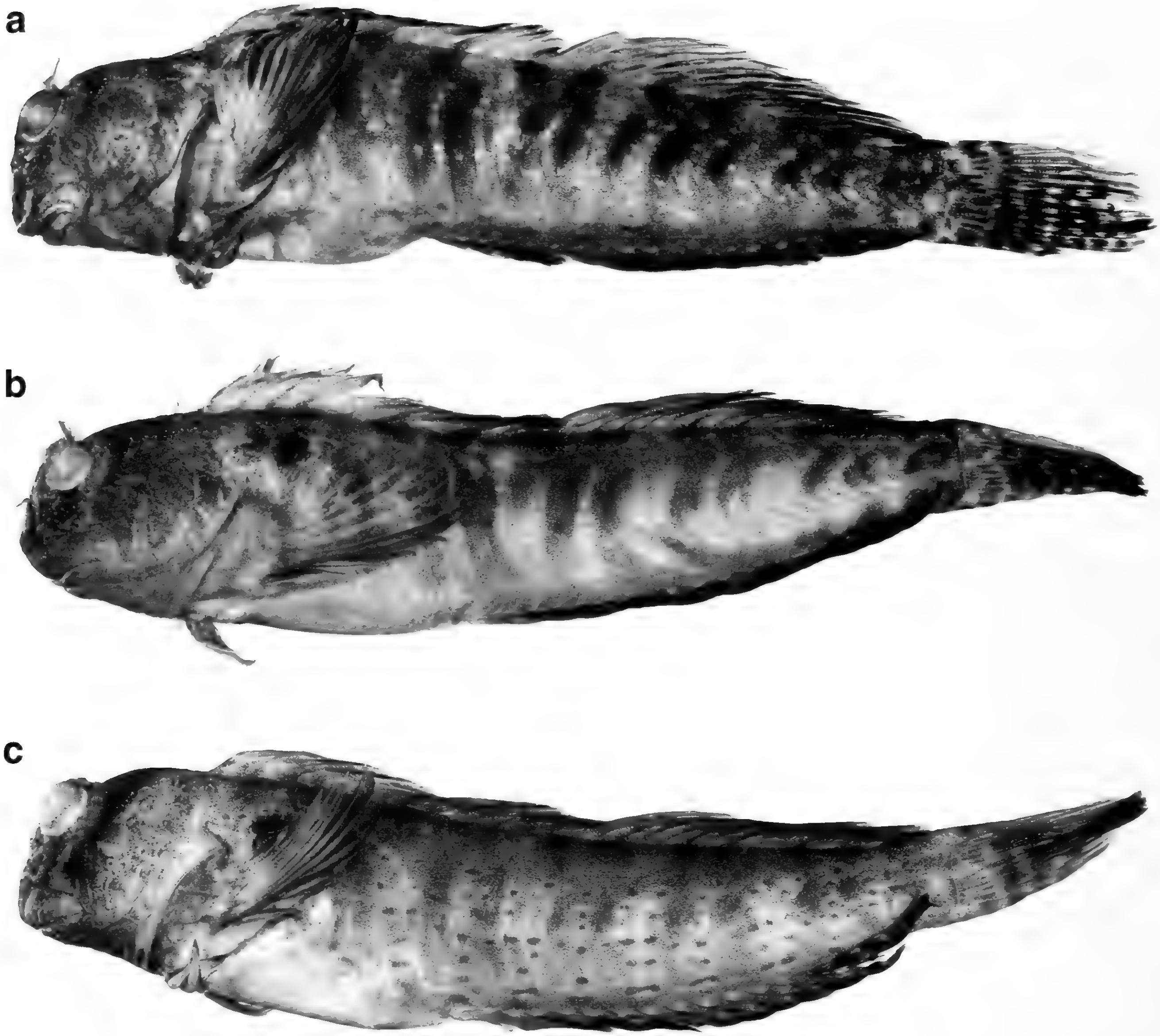

Fig. 3. *Entomacrodus lemuria,* Reunion: a, SMNS 20827, holotype, 59.8 mm SL (pectoral fin obscures humeral spot); b & c, SMNS 213272, 61.5 and 57.4 mm SL.

with pairs or multiples of pores (Table 1). The monophyly and inter- and intrarelationships of these subgroups are problematic, but the distributions of each subgroup and the species within each subgroup seem to correlate more strongly with geography than might be expected by chance and may hint at the naturalness of the groups.

Subgroup 1 comprises five species, of which 91.5–100% of the specimens have all pore positions represented by single pores, and no specimen has more than two positions represented by pairs or multiples of pores. Subgroup 2 comprises only one species, in which 37.8% of the specimens have only simple pore positions, and based on the mean number of positions with paired or multiple positions (Table 1) is more similar to Subgroup 1 than Subgroup 3. Subgroup 3 comprises four species, in which no specimen has only simple pore positions. Subgroup 1 includes all four of the Atlantic species and one eastern Indian Ocean-western-and-central Pacific species: *E. cadenati* Springer (tropical eastern Atlantic, except St. Helena and Ascension), *E. textilis* (Quoy & Gaimard) (Ascension and St. Helena), *E. nigricans* Gill (Caribbean Sea, Bermuda, Bahamas), *E. vomerinus* (Valenciennes) (southwestern Atlantic), and *E. caudofasciatus* (Regan), eastern Indian Ocean east to Henderson Island, Pacific Ocean.

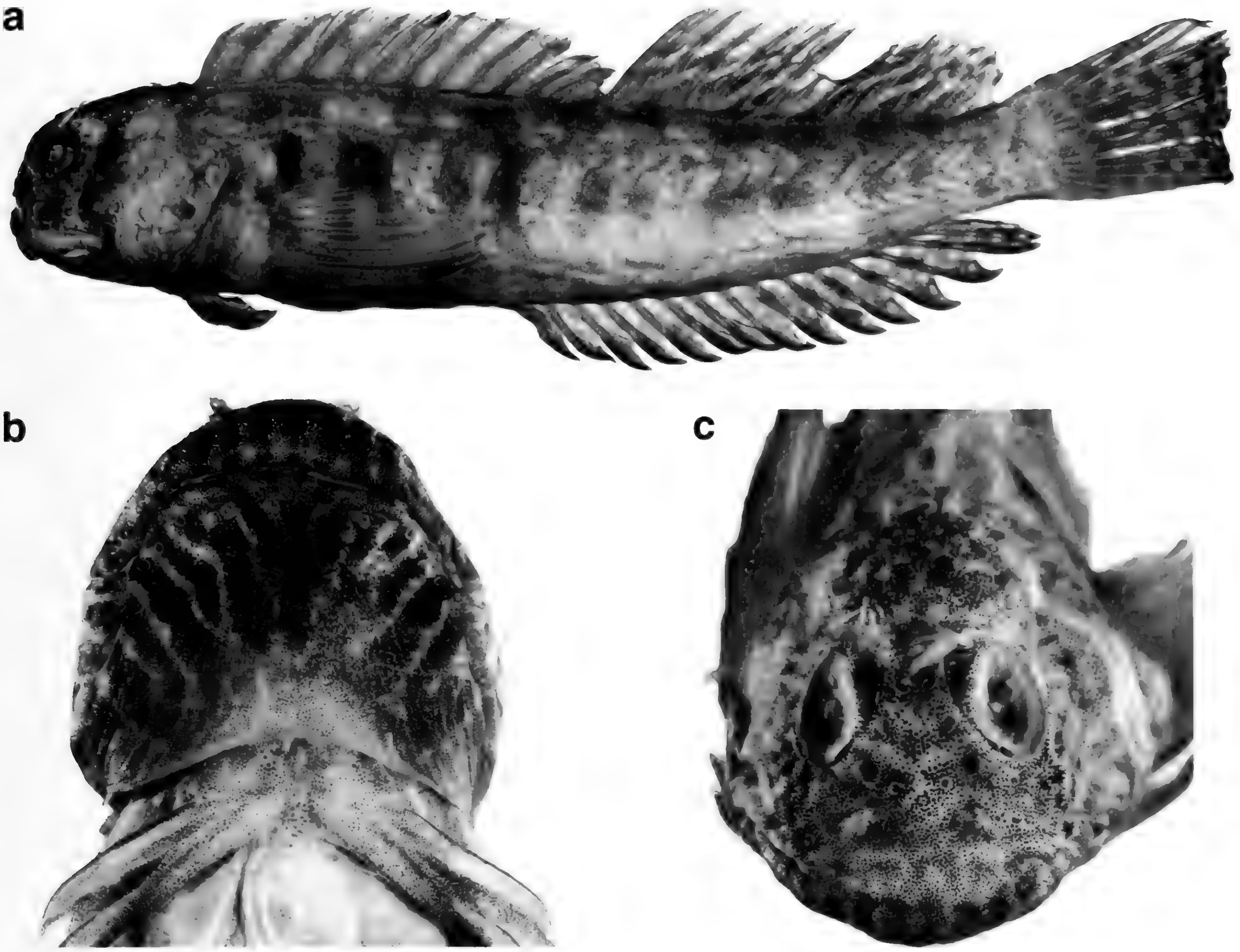

Fig. 4. *Entomacrodus lemuria,* Mauritius: a, USNM 341905, 66.3 mm SL (note damage to second dorsal fin); b & c, USNM 339747, 43.9 mm SL, ventral and anterior views of head.

Subgroup 2 comprises only *E. chiostictus* (Jordan & Gilbert) (eastern Pacific).

Subgroup 3 (Fig. 2) comprises only Pacific or Indian Ocean species: *E. corneliae* (Fowler) (Marquesas Islands endemic), *E. sealei* (widely destributed Pacific plate endemic, but absent from Marquesas Islands), and the two new species, *E. williamsi* (western margin of Pacific plate) and *E. lemuria* (southwestern Indian Ocean).

Within Subgroups 1 and 3, all the species are allopatric except for one co-occurrence of *E. sealei* and *E. williamsi* near the westernmost limits of *E. sealei.* Considering all the species together, the only other occurrence of sympatry is that of the widely distributed *E. caudofasciatus* with *E. sealei.*

If the sister species of *E. lemuria* is *E. sealei,* or *E. sealei* and one or both of the other two Group 3 species, the distribution pattern shown by *E. lemuria* and its sister taxa is another example of eastern Indian Ocean-Pacific plate disjunct distributions reported by Springer & Williams (1990). Those authors hypothesized that the broad gap between the two distributions was the result of extinction and explained the genesis of widely distributed Pacific plate endemic species, such as *E. sealei.*

Entomacrodus lemuria, new species

Figs. 3 & 4

Entomacrodus sp. Fricke, 1999:478, Réunion; Mauritius.

Holotype.—SMNS 20827, male, 59.8 mm SL, Réunion, west coast, 250 m N Boucan-Canot, 5 km WSW St. Paul, 21°01′35″S, 55°13′36″E, intertidal area of

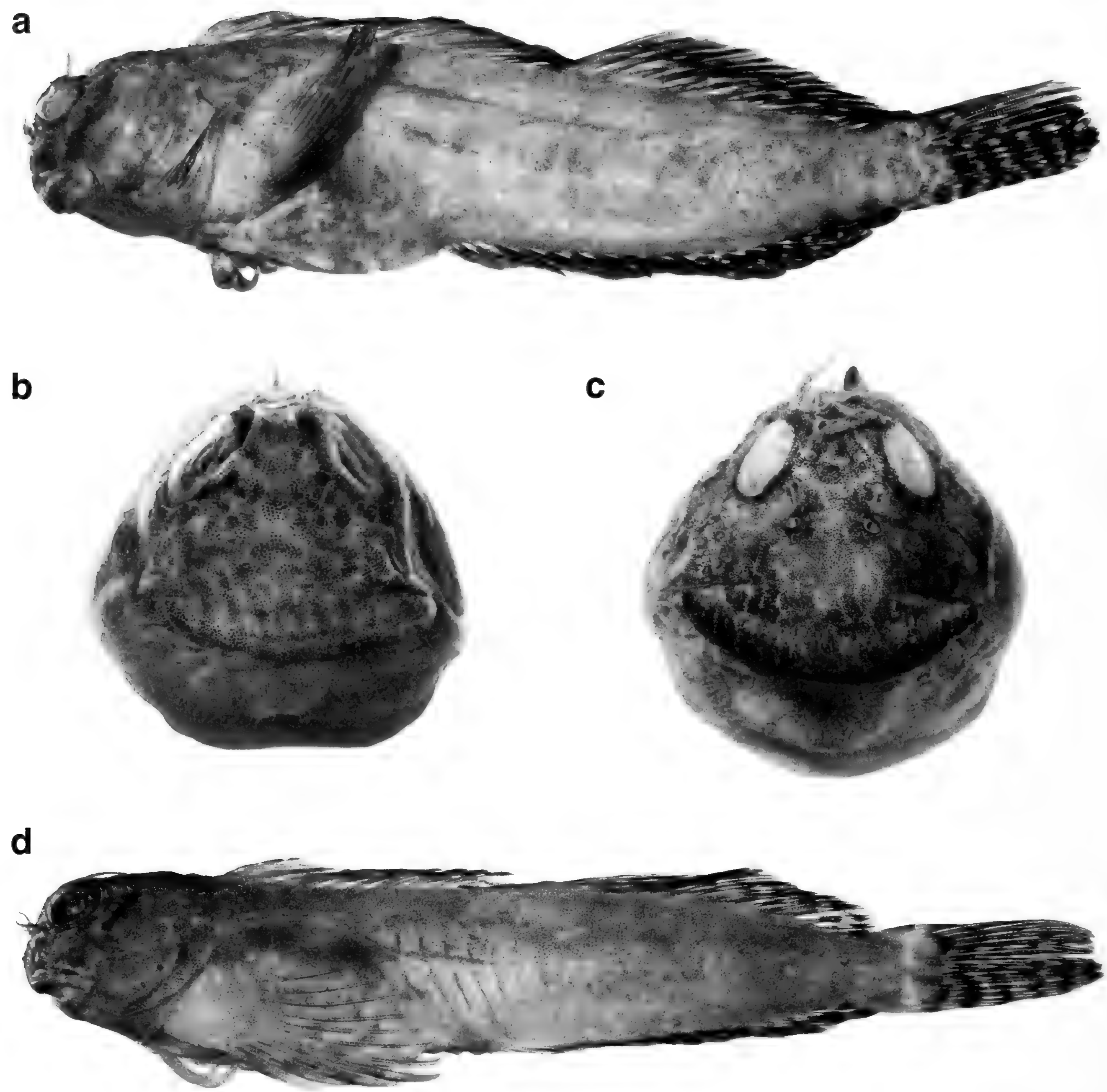

Fig. 5. *Entomacrodus williamsi*, Duff Islands, Santa Cruz Islands, Solomon Islands: a & c, USNM 356864, holotype, 59.8 mm SL lateral and frontal views of head; b & d, USNM 357792, 37.7 mm SL, frontal view of head and lateral view.

narrow fringing reef, near black rocks on shore, R. Fricke and S. Ribes, 18 Dec 1998.

Paratypes.—SMNS 21372, 4 specimens, 43.4–61.4 mm SL, collected with the holotype; AMS I.39536-001 (5:40.9–61.5 mm SL), CAS 209025 (5:25.6–60.0 mm SL), ROM 71976 (5:29.7–54.7 mm SL), RUSI 60472 (5:42.5–63.3 mm SL), USNM 339747 (57:18.1–67.9 mm SL), all Mauritius, W coast, Albion, off rocks at end of Victoria Avenue, surge zone, 0–5 m, A. C. Gill, P. C. Heemstra, M. Smale, and D. G. Smith, 15 May 1995, field no. PCH 95-M23; USNM 341905 (4:23.7–66.3 mm SL), same data as preceding, except: tide pools, between 25 April and 17 May 1995, field no. PCH 95-M9; USNM 357266 (29.5 mm SL), Madagascar, Nosy Be, near Andilama Beach Hotel, J. Paxton et al., 7 Nov 1988, *Vityaz* cruise 17, field no. JP 88-9.

Diagnosis.—Ventral margin of upper lip crenulate on lateral thirds; entire on central third; nape cirri present, simple; orbital cirri branched; 1 to 5, usually 3 to 5, preoper-

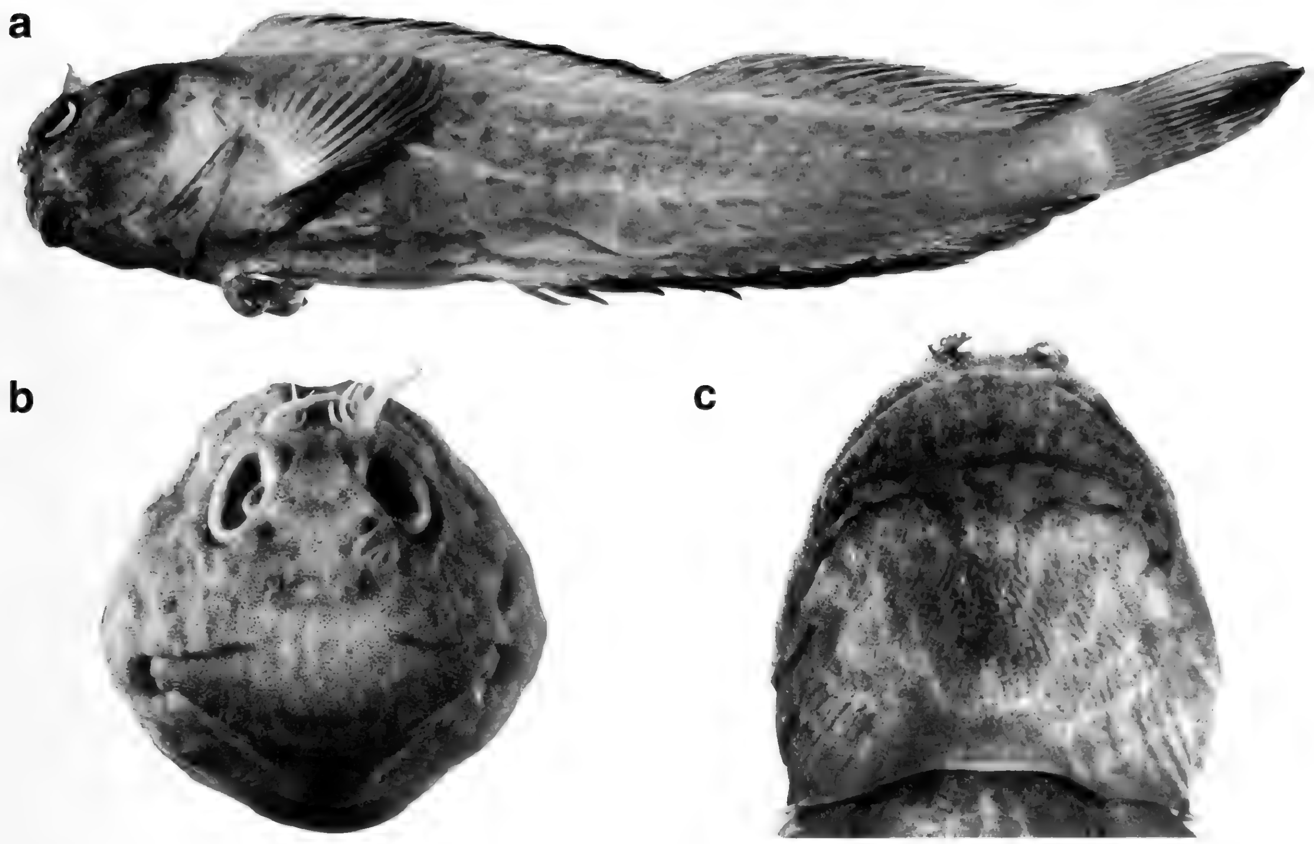

Fig. 6. *Entomacrodus corneliae,* Marquesas Islands, Nuku Hiva: AMS I.21773010, a, lateral view; b & c, frontal and ventral views of head.

cular pore positions with pairs or multiples of pores; subquadrate dark blotch present in humeral area on body (Figs. 3b, c; 4a); upper lip frequently with up to 15 alternating dark and 15 pale bands of subequal width, up to 7 of each above central, ventrally entire portion of lip (Fig. 4c, d); prominent, irregular dark mark on head just posterior to midpostorbital sensory pores (Figs. 3 & 4a).

Description (* denotes character state of holotype).—Dorsal fin XIII,14 (*n* = 4), XIII,15* (36), or XIV,17 (1). Anal fin II,16* (33) or II,17 (7), last ray split to base* (37) or simple (3, of which all have 17 segmented rays). Vertebrae: precaudal 10+23 (1), 24 (32), or 25* (6); pleural ribs 11* (30); epineural ribs 13* (9), 14 (6), 15 (11), 16 (0), 17 (1). Segmented pelvic-fin rays 4* (40). Pectoral-fin rays 13/14 (2), 14/14* (37), or 14/15 (1). Dorsal procurrent caudal-fin rays/ventral procurrent caudal-fin rays 7/6 (2), 7/7* (10), 8/7 (18), 8/8 (4), or 9/8 (1); segmented caudal-fin rays 13* (27), of which middle 9 are branched, dorsalmost and ventralmost 2 are simple.

Orbital cirrus branched (usually only on medial edge of stoutest cirrus), free cirrus tips 3–8, number tending to increase with size, variable bilaterally (holotype has 6/5). Nape cirri 1* on each side, rarely with 1 or 2 tiny branches. Nasal cirri palmate, 5 to 10 on each side (holotype with 8/9).

Lateral-line a continuous posteroventrally curving tube extending posteriorly to vertical from base of 9th to 13th dorsal-fin spine (10th*), continuing along body midside as series of 1 to 8 (5*) tiny, disconnected, bipored tubes extending to vertical from 11th dorsal-fin spine to 5th segmented ray (2nd segmented ray*). Preopercular pore positions (Table 1) with 1 to 5* positions with pairs or multiples of pores.

Color pattern: Highly variable ranging from almost lacking distinctive markings to being well marked. Some indication of the degree of color-pattern variation is indicated in Fig. 3, all specimens taken in the same

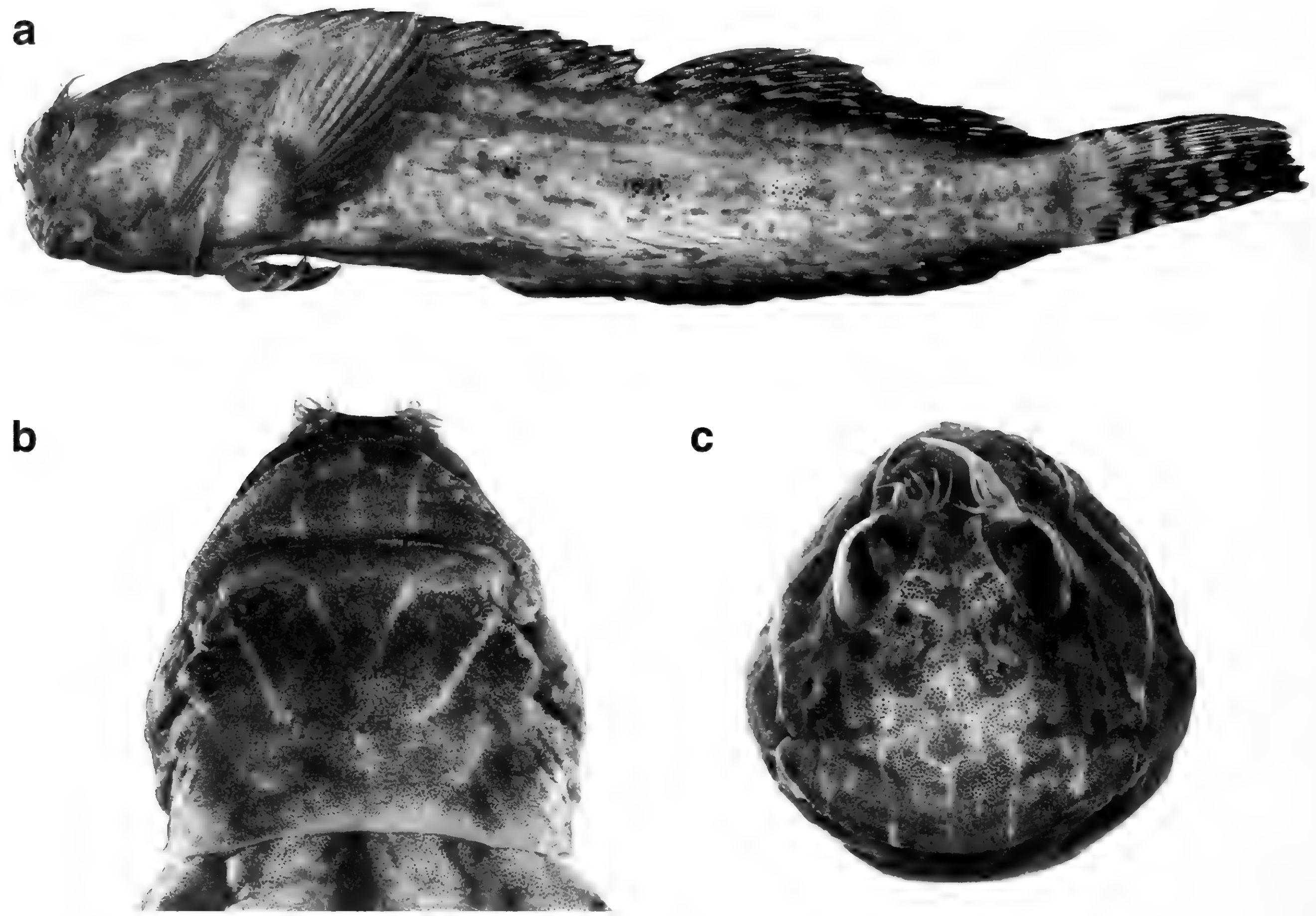

Fig. 7. *Entomacrodus sealei*, Eua, Tonga Islands: USNM 335206, 57.8 mm SL, a, lateral view; b & c ventral and frontal views of head.

collection. Most noticeable and consistent marking a diagnostic subquadrate to ovoid dark spot on body just dorsoposterior to pectoral-fin axil. Other markings may include: irregular dark spot on sensory pore series posterior to eye; snout above lip and sides of head with irregular pattern of dark and pale markings; underside of head with up to about 6 dusky chevrons separated by narrower pale bands; upper lip often with series of up to 15 dark bands alternating with up to 15 pale bands (dark lip bands, when present, 5 or 6 on central part of lip in area over noncrenulate portion of upper lip. Body with 4 or 5 pairs of dusky bands on sides, with offset dorsal portions.

Comparisons.—Entomacrodus lemuria is the only species of Subgroup 3 that has as the darkest marking on the body, a subquadrate to ovoid spot in the humeral area. *Entomacrodus sealei* occasionally has a dark slash in the humeral region, but it is much more slender than the humeral spot of *E. lemuria.* The humeral spot is essentially the only difference between *E. lemuria* and *E. williamsi.* Among the other two members of Subgroup 3, *E. lemuria* also differs from *E. sealei* (Fig. 7) in having more dark and pale lip bands, including more in the region above the noncrenulate portion of the upper lip, and in having the pale bands only a little less slender than the dark bands (versus almost consistently 7 or 8, each, dark and pale alternating bands, midlip dark bands much broader than pale bands, no more than 4 of each in area above noncrenulate portion of lip). *Entomacrodus lemuria* differs from *E. corneliae* (Fig. 6) in having only one prominent irregular dark spot on the head posterior to midpostorbital sensory pores (versus 2 such dark marks).

Etymology.—From Lemuria, a hypothetical continent, supposed to have existed in the Indian Ocean and now represented by

Madagascar and some adjacent islands; here used as a noun in apposition.

Entomacrodus williamsi, new species
Fig. 5

Holotype.—USNM 356864, male, 52.8 mm SL, Solomon Islands, Santa Cruz Islands, Duff Islands, Lakao, NW end at Temomoa Pt, 09°47′54″S, 165°05′18″E, small cove, surge channels in big boulders, in heavy surge, 0–10 m, 24 Sep 1998, J. T. Williams et al.

Paratypes: USNM 357792, 4 specimens, 36.5–38.1 mm SL, collected with holotype. USNM 206400, 37.6 mm SL, Papua New Guinea, Madang Harbour, S edge of Massas Island, 0–2.4 m, 2 Jun 1970, B. B. Collette, field no. BBC 1501. USNM 356244, 32.4 mm SL, Indonesia, Moluccas, Ternate, Ternate [city], 0.2–0.5 m, 1–2 July 1979, H. Singou, field no. HS-F610.

Description (* denotes character state of holotype).—Dorsal fin XIII,14 (*n* = 1) or XIII,15* (6). Anal fin II,15 (1), II,16* (5) or II,17 (1), last ray split to base* (5) or simple (2, of which 1 has 15 and 1 has 17 segmented rays). Vertebrae: precaudal 10+24* (7); pleural ribs 11* (7); epineural ribs 14* (5) or 15 (1). Segmented pelvic-fin rays 4* (7). Pectoral-fin rays 13/14 (1) or 14/14* (6). Dorsal procurrent caudal-fin rays/ventral procurrent caudal-fin rays 8/2 (1), 8/7 (2), 8/8* (2), or 9/8 (1); segmented caudal-fin rays 13* (7), of which middle 9 are branched, dorsalmost and ventralmost 2 are simple* (6, one specimen damaged).

Orbital cirrus usually branched (usually only on medial edge of stoutest cirrus), free cirrus tips 1–6 (1 or 2 probably abnormal), variable bilaterally (holotype has 5/6). Nape cirri 1* on each side (1 specimen with cirrus forked on one side). Nasal cirri palmate, 4 to 7 on each side (holotype with 6/7).

Lateral-line a continuous posteroventrally curving tube extending posteriorly to vertical from base of 9th to 12th dorsal-fin spine (11th*), continuing along body midside as series of 2 to 6 (*5) tiny, disconnected, bipored tubes extending to vertical from 13th dorsal-fin spine to 5th segmented ray (4th ray*). Preopercular pore positions (Table 1) with 2 to 5 positions with pairs or multiples of pores (5*; see Table 1).

Comparisons.—The lack of a dark humeral spot in *E. williamsi* is essentially the only difference between it and *E. lemuria.* There are very few specimens of *E. williamsi,* and none of these exhibits distinctive markings on the body, which may have been present in life. If lack of pattern on the body of preserved specimens is typical, this would constitute another difference from *E. lemuria,* and the other two species. Among the other two species of Subgroup 3, *E. williamsi* also differs from *E. sealei* (Fig. 7) in having more dark and pale lip bands, including more in the region above the noncrenulate portion of the upper lip and in having the pale bands only a litte less slender than the dark bands (versus almost consistently 7 or 8, each, dark and pale alternating bands, midlip dark bands much broader than pale bands, no more than 4 of each in area above noncrenulate portion of lip), and from *E. corneliae* (Fig. 6) in having only one prominent irregular dark spot on the head posterior to midpostorbital sensory pores (versus 2 such dark marks).

Etymology.—Named for our colleague Jeffrey T. Williams, in recognition of his outstanding efforts in collecting Indo-Pacific fishes.

Entomacrodus corneliae (Fowler, 1932)
Fig. 6

Additional material (all of the few known specimens are from the same locality): Marquesas Islands, Nuku Hiva: AMS I.21773010 (9).

Entomacrodus sealei Bryan & Herre, 1903
Fig. 7

New distribution records for *E. sealei* include: Loyalty Islands: Lifou Island, SMNS

21712 (1 specimen). Vanuatu: Tanna, USNM 344230 (13); Epi, USNM 356399 (7). Fiji: Rotuma, USNM 283060 (1). Tonga: Eua, USNM 329699 (>30), 335206 (12); Tongatapu, USNM 337428 (1); Vava'u Group, Hunga, USNM 339314 (8); Vava'u, USNM 340229 (2). Solomon Islands: Santa Cruz Islands, Duff Islands, Lakao, USNM 356857 (92); Taumako, USNM 357098 (12); Russell Islands, Mbanika (or Banika), NMNZ P.26004 (1). Tuamotu Archipelago: Rangiroa, BPBM 14007 (8). Pitcairn Islands: Henderson Island: BPBM 17091 (10).

Acknowledgments

For the loan of specimens we thank J. E. Randall (BPBM), M. McGrouther (AMS), and C. Roberts (NMNZ). Several USNM colleagues provided a variety of services: K. Darrow prepared the distribution map; K. Murphy provided technical assistance; J. Clayton, L. Palmer, and S. Raredon handled loan and accession actions. T. B. Griswold produced the photographs for Figs. 3–7. The U.S.N.M. Office of Biodiversity Programs Grant to V. G. Springer and J. T. Williams provided funds for Williams's expedition to the Santa Cruz Islands (1998), during which important material was collected. U.S.N.M. Research Opportunities Fund grant. no. 1233F57A to D.G. Smith (USNM) supported his participation in an expedition to Mauritius, during which one of the new species was collected. A draft of this manuscript was reviewed by J. T. Williams.

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Ammodytoides leptus, a new species of sand lance (Teleostei: Ammodytidae) from Pitcairn Island

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Abstract.—*Ammodytoides leptus* is described from 23 specimens from Pitcairn Island. It has more lateral-line scales than any other known species of *Ammodytoides* or *Bleekeria* (119–123 vs. 88–118). It is thinner than *A. pylei, A. kimurai,* and *A. gilli* (body depth 8.6–9.5% SL vs. 9.5–11.7%).

During his expedition to the eastern South Pacific on board the schooner *Westward* (Randall 1978, 1999), the second author collected the first sand lance recorded from the South Seas at Pitcairn Island in January 1971. The purpose of this paper is to describe this sand lance and assess its relationships to other members of the genus *Ammodytoides* as defined by Ida et al. (1994), including two additional species described by Ida & Randall (1993) and Randall et al. (1994) and *A. gilli* redescribed by Collette & Robertson (2000).

Materials and Methods

Type specimens of the new species have been deposited in the Bernice P. Bishop Museum, Honolulu (BPBM), the National Museum of Natural History, Washington, D.C. (USNM), the Australian Museum, Sydney (AMS), the Museum of Comparative Zoology, Cambridge (MCZ), and the National Science Museum, Tokyo (NSMT). Institutional abbreviations for sources of comparative material follow Leviton et al. (1985). Measurements follow Ida and Randall (1993) and Randall et al. (1994). Generic nomenclature follows Ida et al. (1994). All proportions are presented as percent of standard length (SL).

Ammodytoides leptus, new species
Fig. 1

Ammodytes sp. Randall 1999:24 (an undescribed species from Pitcairn).

Diagnosis.—A species of *Ammodytoides* with dorsal-fin rays 50–53; anal-fin rays 24–25; pectoral-fin rays 16–17; pelvic fins absent; lateral line incomplete, pored lateral-line scales 114–118 + 4–6 unpored scales = 119–123; gill rakers on first arch (6–7) + (22–25) = 29–32; vertebrae (34–36) + (26–27) = 61–63, including hypural plate.

Description.—Body elongate, depth 8.6–9.5%, width 5.6–6.3%; head length 23.3–25.1%; snout length 6.7–7.3%; orbit diameter 4.1–4.5%; fleshy interorbital distance 3.5–3.7%; upper jaw length 7.8–8.6%; least caudal peduncle depth 4.7–5.1%; caudal peduncle length 6.6–8.3% SL; predorsal distance 24.0–28.5%; preanal distance 63.3–66.2%; caudal-fin length 13.6–14.5%; caudal fin concavity 6.3–7.1%; pectoral-fin length 9.0–10.1% (Table 1).

Scales small, thin, and cycloid, arranged in straight diagonal rows; head naked, no row of small scales on upper part of opercle, scales extending anteriorly to supratemporal lateral-line canal; about 10–12 rows of predorsal scales; fins naked except caudal fin, which has scales extending about

Table 1.—Proportional measurements of type specimens of *Ammodytoides leptus* expressed in percent of standard length.

	Holotype	Paratypes							
Standard length (mm)	96.2	89.1	86.9	86.4	85.3	82.9	81.3	79.8	75.8
Body depth	8.6	9.2	9.5	9.3	9.0	8.8	8.7	8.9	9.0
Body width	6.2	5.8	6.3	6.1	5.6	5.6	6.0	5.6	5.9
Head length	23.3	24.8	24.4	24.1	24.2	24.6	24.6	24.4	25.1
Snout length	6.8	6.7	7.0	7.1	6.9	7.0	7.0	7.0	7.3
Orbit diameter	4.2	4.2	4.1	4.1	4.1	4.1	4.2	4.4	4.5
Interorbital space	3.7	3.7	3.7	3.7	3.6	3.7	3.7	3.5	3.7
Upper jaw length	7.8	8.0	7.9	8.1	7.9	8.2	8.2	8.0	8.6
Caudal peduncle depth	4.7	4.7	4.7	4.9	4.9	4.8	4.8	5.0	5.1
Caudal peduncle length	8.3	7.4	—	6.9	6.8	6.6	6.8	6.8	6.9
Predorsal length	26.2	24.0	24.7	24.3	28.5	25.2	24.7	24.4	24.1
Preanal length	65.7	65.7	66.2	66.2	63.3	65.1	65.7	65.8	65.0
Caudal fin length	14.4	13.6	13.7	13.9	14.2	14.5	13.7	13.5	14.1
Caudal concavity	7.1	6.7	6.7	6.8	6.6	6.6	6.3	6.8	—
Pectoral fin length	10.1	9.5	9.5	9.6	9.0	9.4	9.6	9.3	9.8

three-fourths distance to posterior margin; lateral line high on body, ascending from gill opening to three scales below origin of dorsal fin, passing posteriorly parallel to upper edge of body, pored scales ending high on body, about 4–6 scales from caudal-fin base. Suborbital lateral-line canal interrupted, with four preorbital and four postorbital pores (as in *A. pylei*; Randall et al., 1994: fig. 2A).

In life, dorsum grayish green, sides silvery and ventrum iridescent; fins hyaline, caudal yellowish. Specimens brown in preservative.

Comparisons.—*Ammodytoides leptus* has more lateral-line scales than any other known species of *Ammodytoides* or *Bleekeria* (119–123 vs. 88–118). It is thinner than *A. pylei, A. kimurai,* and *A. gilli* (body depth 8.6–9.5% vs. 9.5–11.7%, Table 2). It resembles *A. gilli* and differs from *A. pylei* and *A. kimurai* in several morphometric characters, larger eye (4.1–5.1% vs. 2.8–3.7%), longer upper jaw (7.8–9.5% vs. 6.6–7.9%), longer predorsal distance (24.0–28.5% vs. 21.8–24.7%), and longer caudal fin (12.8–16.0% vs. 10.5–12.9%). There is no row of small scales on upper part of opercle as in *A. pylei* (Randall et al., 1994).

Ecology.—The series of ten types was collected from a school of about 25 individuals seen over sand with high ripple marks. Schools were fast swimming and exhibited rapid changes in direction, all fish in perfect unison. When frightened, as by a spear shot into the school, a few dove into

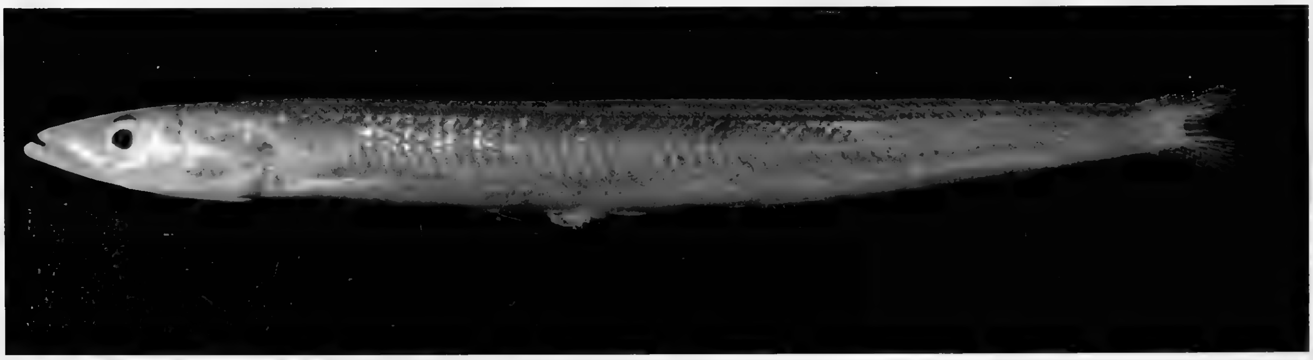

Fig. 1. *Ammodytoides leptus.* Paratype, USNM 360077, 86.9 mm SL, Pitcairn Island, off Gudgeon Point; 20 Jan 1971. Photo by J. E. Randall.

Table 2.—Morphometric comparison of four species of *Ammodytoides* expressed in percent of standard length. (Data for *A. kimurai* from Ida & Randall 1993; for *A. pylei* from Randall et al. 1993; and for *A. gilli* from Collette & Robertson 2000).

	A. leptus		*A. kimurai*		*A. pylei*		*A. gilli*	
	Min	Max	Min	Max	Min	Max	Min	Max
Standard length (mm)	75.8	96.2	99.4	121	93.2	168	51.6	84.5
Body depth	8.6	9.5	10.0	10.3	10.0	11.7	9.5	11.2
Body width	5.6	6.3	8.1	8.4	7.2	9.5	5.9	7.8
Head length	23.3	25.1	22.2	23.6	22.0	24.6	25.4	27.8
Snout length	6.7	7.3	6.7	7.5	6.4	7.0	6.9	7.9
Orbit diameter	4.1	4.5	2.8	3.3	2.9	3.7	4.1	5.1
Interorbital space	3.5	3.7	4.1	4.6	3.5	4.1	3.8	4.9
Upper jaw length	7.8	8.6	7.6	7.9	6.6	7.9	7.8	9.5
Caudal peduncle depth	4.7	5.1	4.0	5.0	4.5	5.2	4.8	5.4
Caudal peduncle length	6.6	8.3	8.4	9.8	10.6	12.0	3.6	6.0
Predorsal length	24.0	28.5	23.1	24.2	21.8	24.7	25.1	26.9
Preanal length	63.3	66.2	61.3	65.3	63.8	66.8	62.5	65.3
Caudal fin length	13.6	14.5	11.5	12.9	10.5	12.0	12.8	16.0
Caudal concavity	6.3	7.1	6.1	7.3	5.3	5.8	6.3	7.8
Pectoral fin length	9.0	10.1	9.1	9.5	8.4	9.2	9.9	11.1
N	9		6		10		10	

the sand. A larger school (about 100 individuals) was observed in 30 m around an offshore rock in the same general area. *Ammodytoides leptus* is eaten by larger pelagic fishes such as the jack, *Carangoides ferdau,* as are other species of *Ammodytoides.*

Etymology.—Named *leptus* because it is thinner than other species of *Ammodytoides.*

Distribution.—Ammodytoides leptus is presently known only from Pitcairn Island.

Discussion.—Ammodytoides leptus, as well as two additional species recently described by Ida & Randall (1993) and Randall et al. (1994), fits the definition of the genus as given by Ida et al. (1994) and differs from species of *Bleekeria* in the following characters: no teeth in jaws; infraorbital canal interrupted; lateral line ending high on caudal peduncle instead of curving downward and continuing onto caudal fin base; two predorsal bones present; olfactory rosettes absent; neural and haemal spines on four posterior caudal vertebrae expanded and flattened; dorsal-fin rays 51–53 (three more than the previously recorded range for the genus), and anal-fin rays 21–25.

In addition to *Ammodytoides leptus,* known species of the genus include the type-species, *A. vagus* (McCulloch & Waite, 1916) from Lord Howe Island and New South Wales; *A. renniei* (Smith, 1957) from South Africa, Seychelles Islands, and the Chagos Archipelago (Winterbottom et al. 1989, Winterbottom & Anderson 1999); *A. kimurai* Ida & Randall, 1993 from the Ogasawara Islands; *A. pylei* Randall et al., 1994 from the Hawaiian Islands; and *A. gilli* (Bean, 1895) from the eastern tropical Pacific (Collette & Robertson 2000).

Material examined.—23 specimens (71.4–127 mm SL) from 3 original lots from Pitcairn Island. Holotype USNM 360076 (1, 96.2), off Gudgeon Harbor, 10.5 m, rotenone; J. E. Randall and D. B. Cannoy; 20 Jan 1971. Paratypes BPBM 16949 (2, 79.8–89.1), MCZ 157036 (1, 81.3), AMS I.39856-001 (1, 82.9), NSMT-P 59154 (1, 86.4), USNM 360077 (3, 75.8–86.9), and USNM 360078 (1, 89.8, cleared and stained), same data as holotype. BPBM 16441 (1, 83.3), dredge haul 2, 48–54 fms; 16 Oct 1967. Additional material examined but not designated as types due to their poor condition: BPBM 1660 (12, 71.4–127), off W. Harbour, stomach of *Carangoides fer-*

dau, 50 ft, J. E. Randall and S. Christian; 27 Dec. 1970.

Comparative material examined: *Ammodytoides kimurai* Ida & Randall, 1993. Paratype. USNM 324610 (1, 121), Japan, Ogasawara Islands, off Minami-shima, 15 m; H. Ida & R. L. Pyle; 1 Jun 1992.

Ammodytoides pylei Randall, Ida, and Earle, 1994. Paratype. USNM 316514 (1, 137), Hawaiian Islands, Oahu, Kahe Point; R. L. Pyle, A. Y. Suzumoto, J. B. Culp; 19 May 1989.

Ammodytoides renniei (Smith, 1957). RUSI 8440 (1, 56.4), Seychelles Islands, 3°57′S, 54°32″E; 25 Jul 1978. ROM 41487 (1, 60.7), Chagos Archipelago, Peros Banhos Atoll, Isle du Coin, 5°25′21″S, 71°46′52″E; 6 Feb 1979; R. Winterbottom.

Ammodytoides vagus (McCulloch & Waite, 1916). Holotype. AMS I-9272 (143 mm SL), Lord Howe Island.

Bleekeria mitsukurii Jordan & Evermann, 1903. USNM 59599 (2, 78.5–151), Japan, Kochi; H. M. Smith. UW 21253 (2, 91.6–107), Taiwan.

Bleekeria viridianguilla (Fowler, 1931). Paratypes. ANSP 53462-5 (4, 116–137), Hong Kong; 1930; G. A. C. Herklots.

Protammodytes sarisa (Robins & Böhlke, 1970). Holotype ANSP 113091 (115 mm SL) and paratype ANSP 113092 (99.2), Windward Islands, off east coast of St. Vincent; 13°11′12″N, 61°05′18″W; 187 m; *Pillsbury* sta. 874; 6 Jul 1969.

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PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Neostrengeria binderi, a new species of pseudothelphusid crab from the eastern Andes of Colombia (Crustacea: Decapoda: Brachyura)

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Abstract.—A new species of freshwater crab of the genus *Neostrengeria* Pretzmann, 1965, *N. binderi,* is described from Alto de Cunday, Tolima Department, Colombia. The addition of this new species brings to 18 species and 2 subspecies the total number of taxa known in this genus endemic to the Eastern Andes of Colombia.

The genus *Neostrengeria* Pretzmann, 1965, comprising 18 species and 2 subspecies of pseudothelphusid crabs, is endemic to the Eastern Andes of Colombia. On the west slope, the genus was known as far south as Cundinamarca, but recent collections in the Cunday region of eastern Tolima have resulted in the discovery of a new species, which extends the range of the genus ca. 50 km further south. Additional explorations in the region have failed to locate this species west of the Magdalena river, confirming the association of the genus with the Eastern Andes.

The systematics of *Neostrengeria* were established by Rodríguez (1982) and have been recently reviewed by Campos (1992, 1994). The geographical distribution of the genus has been discussed by Campos & Rodríguez (1985), and Campos (1992, 1994). The general characteristics of the genus and a key for the identification of the species was presented by Campos & Lemaitre (1998).

The terminology used for the different processes of the male first gonopods is that established by Smalley (1964) and Rodríguez (1982). The material is deposited in Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN). The abbreviations cb and cl indicate carapace breadth and carapace length, respectively. Color nomenclature follows Smithe (1975).

Family Pseudothelphusidae Rathbun, 1893
Tribe Strengerianini Rodríguez, 1982
Genus *Neostrengeria* Pretzmann, 1965
Neostrengeria binderi, new species
Fig. 1, 2

Holotype.—Laguna Los Catorce, Vereda Alto de Cunday, Tolima Department, Colombia, 470 m alt., 22 May 1998, leg. P. Binder: 1 male, cl 20.7 mm, cb 37.8 mm (ICN-MHN-CR 1702).

Paratypes.—Same locality data as holotype: 2 females, cl 19.1, 17.9 mm, cb 33.6–31.4 mm (ICN-MHN-CR 1703).

Type locality.—Laguna Los Catorce, Vereda Alto de Cunday, Tolima Department, Colombia, 470 m alt.

Diagnosis.—Carapace with median groove deep, reaching upper border of front. First male gonopod with mesial border slightly convex with strongly subapical notch in caudal view; apex compressed cephalo-caudal, expanded mesially into subtriangular projection; mesial lobe forming acute triangle.

Description of holotype.—Carapace (Fig. 1A) with cervical groove nearly straight, deep, ending some distance from lateral margin. Anterolateral margin with shallow depression behind external orbital angle, followed by series of papillae on anterolateral half; posterior half smooth. Postfrontal lobes small, oval, delimited anteriorly by 2 depressions; median groove deep, reaching upper border of front. Surface of carapace in front of postfrontal lobes inclined anteriorly, depressed towards midline. Front bilobed, lacking distinct upper border in frontal view; lower margin visible in dorsal view, strongly sinuous in frontal view, with tubercles. Orbital margins each with row of tubercles. Dorsal surface of carapace smooth, covered by small papillae; regions distinctly marked. Third maxilliped with merus having sharp angle on distal half of external margin; exognath 0.57 length of ischium (Fig. 1D). Orifice of efferent branchial channel irregularly ovate (Fig. 1B).

First pereiopods heterochelous, left cheliped larger than the right. Merus with 3 longitudinal crests as follows: upper one with rows of tubercles, internal lower one with row of teeth, and external lower one with row of tubercles. Carpus with few tubercles on internal crest, and blunt distal spine. Palms of both chelipeds smooth and swollen; fingers elongate, each 0.58 the length of propodi, tips crossing, and surfaces with rows of small tubercles; finger of larger chelae not gaping when closed.

Walking legs (pereiopods 2–5) slender (Fig. 1A). Dactyli elongated, each 1.5 times as long as propodi, with papillae and 5 longitudinal rows of large spines diminishing in size proximally. Number of spines and papillae on each dactylus arranged as follows: 1 anterolateral row and 1 anteroventral row each with 6 spines; 1 external row with 5 spines and 4 intercalated papillae and 1 pair of proximal papillae; 1 posterolateral row with 4 spines and 1 posteroventral row with 5 spines. First gonopod wide in caudal view, mesial border (Fig. 2A, 1) slightly convex with strongly subapical notch in caudal view. Accesory lobe (Fig. 2A, 2), shorter than lateral lobe (Fig. 2A, 3), flat caudally, elongate; lateral lobe wide and semicircular (Fig. 2A–D). Apex in distal view compressed cephalo-caudally (Fig. 2E), expanded cephalically into subtriangular projection; mesial lobe (Fig. 2E, 4) forming acute triangle; mesocaudal projection of spermatic channel (Fig. 2E, 5) bifid with acute spinules.

Color.—The holotype preserved in alcohol is light brown (near 121C, Mikado Brown) with pale brown (Verona Brown, 223 B) specks on the dorsal side of the carapace. The walking legs and chelipeds are cinnamon brown (Tawny, 38) dorsally and ventrally. The ventral surface of the carapace is buffy-brown (Antique Brown, 37).

Etymology.—The species is named in honor of Dr. Philippe Binder, Colombian scientist who collected the specimens, and to recognize his efforts in stimulating a new generation of scientists at the Universidad de los Andes, Bogotá.

Remarks.—This species is most similar to *Neostrengeria aspera* Campos, 1992. Both can be distinguished by features of the first gonopod. The mesial border of the first gonopod (in caudal view) of *N. aspera* is slightly convex, similar to *N. binderi,* but this latter species has a strong subapical notch. The elongate accesory lobe of *N. binderi* is shorter than the lateral lobe, whereas in *N. aspera* this lobe is as long as the lateral lobe, with the apical portion irregular in form and densely covered with spinules on the distal half (cf., Campos & Lemaitre 1998). The lateral lobe is spatulate, rounded in its distal portion, and separated from the accesory lobe by a deep notch in *N. aspera,* while in *N. binderi* the lateral lobe is semicircular and is almost adpressed to the accesory lobe. In the apex of the gonopod, *N. binderi* is most similar and probably closely related to *N. gilberti* Campos, 1992. The differences are basically that in *N. gilberti* the apex is oval (not compressed cephalo-caudally) and there is an expansion with a conspicuous cephalic spine (cf. Campos 1992), whereas in *N. binderi* the apex consists of a subtriangular projection. The mesial lobe in *N. binderi* shows an acute subtriangular feature, while

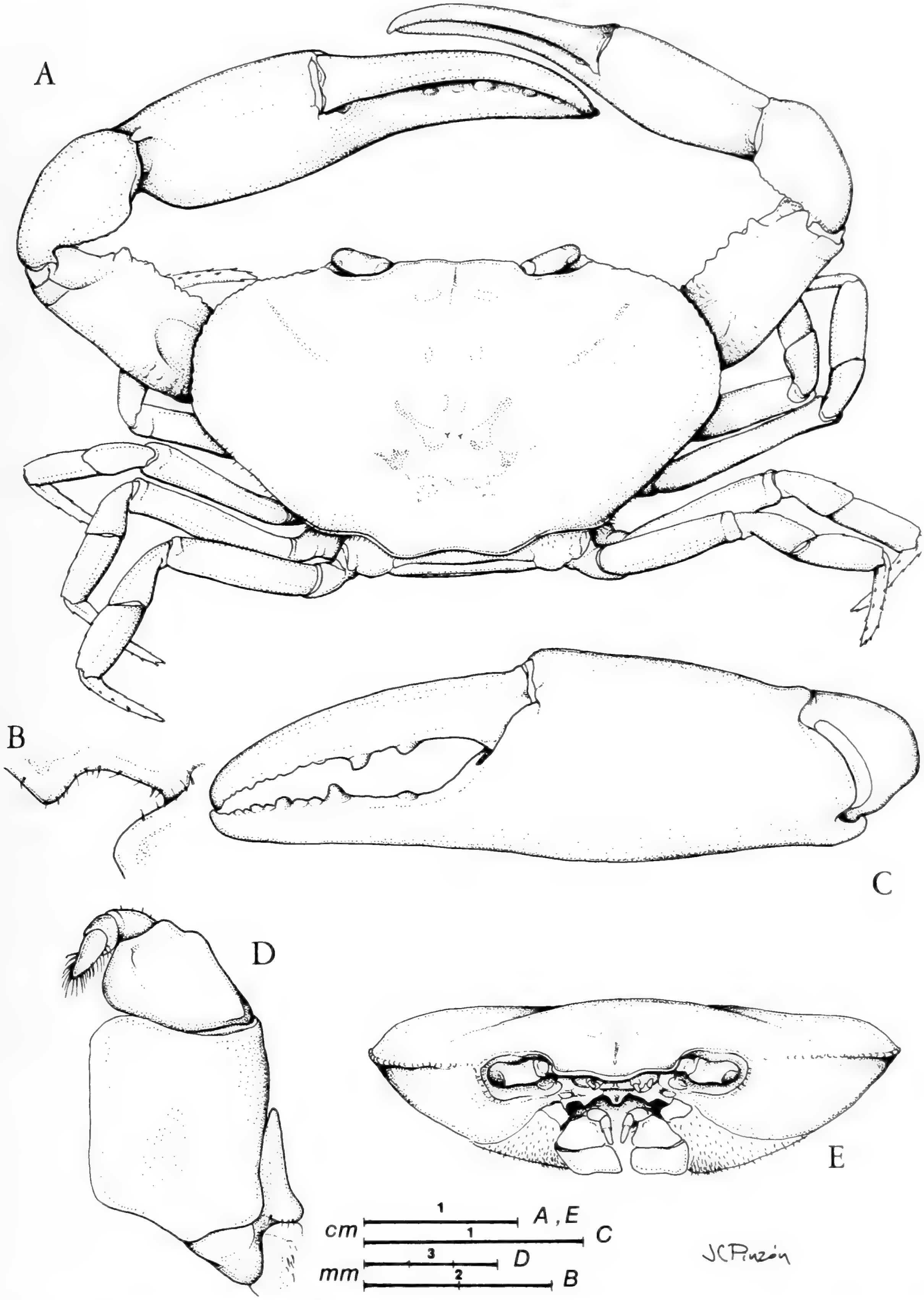

Fig. 1. *Neostrengeria binderi,* new species, male holotype, ICN-MHN-CR 1702. A, dorsal view of carapace and pereiopods; B, opening of left efferent branchial channel, external view; C, left chela, external view; D, left third maxilliped, external view; E, frontal view of carapace.

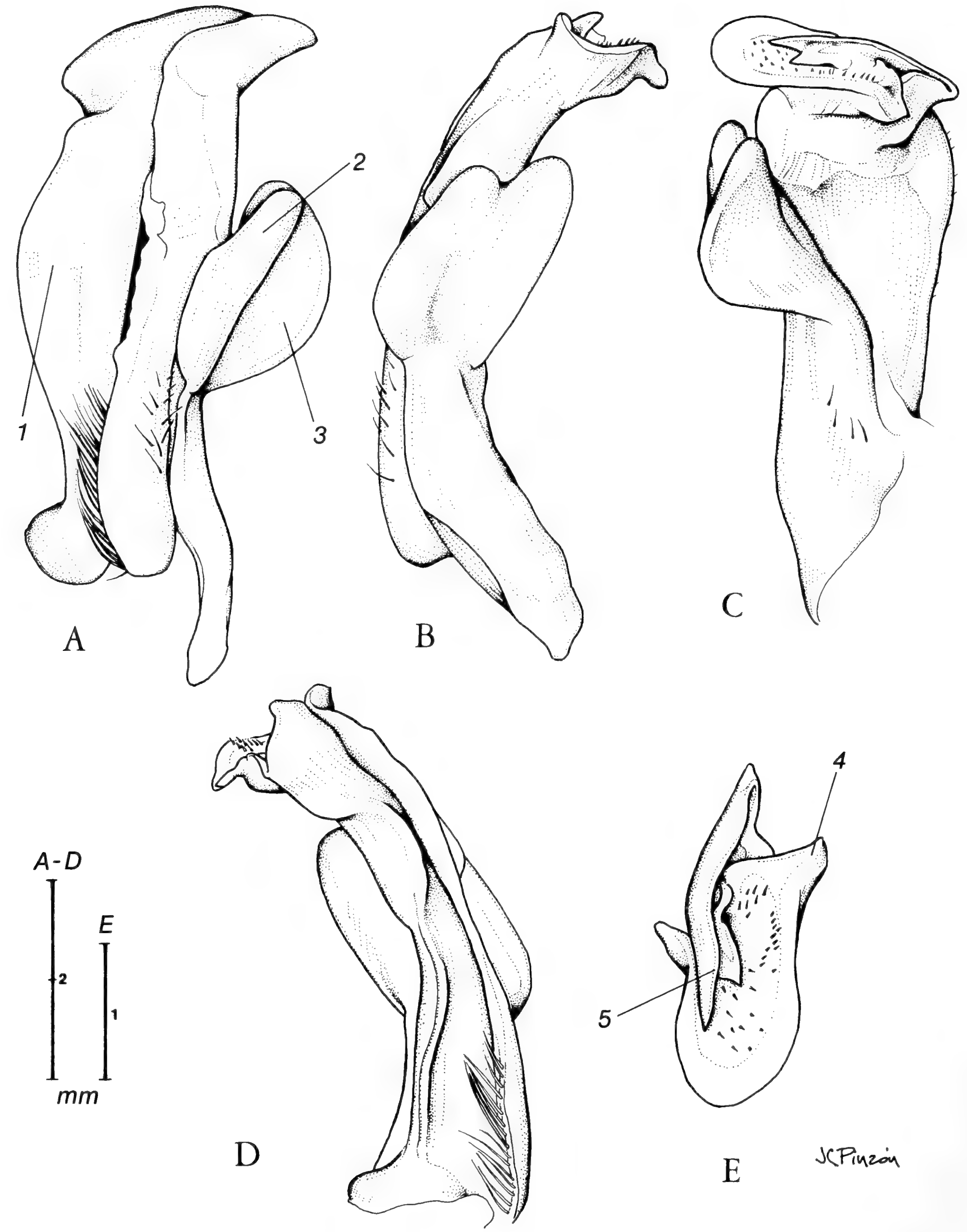

Fig. 2. *Neostrengeria binderi,* new species, male holotype, ICN-MHN-CR 1702. A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view. 1, mesial border; 2, accesory lobe; 3, lateral lobe; 4, mesial lobe; 5, mesocaudal projection of spermatic channel.

in *N. gilberti* it is smaller and subcircular with a papilla. The mesocaudal projection of the spermatic channel in *N. gilberti* is awl-shaped, with one spinule on the inner side, while in *N. binderi* it is bifid with acute spinules.

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Freshwater crabs (Brachyura: Potamoidea: Potamonautidae) from the rainforests of the Central African Republic, Central Africa

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Abstract.—A collection of freshwater crabs of the family Potamonautidae from the Central African Republic made recently by the Central African Republic Expedition of the American Museum of Natural History, New York, comprised four species in two genera. The collection included two species of *Potamonautes* MacLeay, 1838, *P. paecilei* A. Milne-Edwards, 1886, and *P. ballayi* A. Milne-Edwards, 1886 and two species of *Sudanonautes* Bott, 1955, *S. africanus* A. Milne-Edwards, 1869, and *S. sangha,* new species. Only six species of freshwater crabs have been previously reported to occur in the Central African Republic. The addition of *S. africanus* and *S. sangha* brings to eight the number of species of freshwater crabs reported from that country.

The freshwater crabs reported on here were collected during a systematic survey of the freshwater and terrestrial Mollusca of the Central African Republic made by the American Museum of Natural History. The survey aimed to document biodiversity, to catalogue introduced species, and to identify intermediate hosts that may serve as vectors of parasite larvae responsible for disease in humans and domestic animals. The freshwater crab collections were made in the vicinity of the village of Bayanga, Central African Republic, which lies on the banks of the Sangha river in a remote and largely roadless area close to southern Cameroon, the Republic Populaire du Congo (formerly French Congo), and Gabon. This region includes an area of tropical forest that supports elements of both the West African and Zaire river basin faunas, and consequently has an unusually high biodiversity.

The collection of freshwater crabs obtained included two species of *Potamonautes* MacLeay, 1838, and two species of *Sudanonautes* Bott, 1955. Both of these genera belong to the exclusively African freshwater crab family Potamonautidae Bott, 1970. The two species of *Potamonautes* are *P. ballayi* (A. Milne-Edwards, 1886) and *P. paecilei* (A. Milne-Edwards, 1886). Both are little-known species and their diagnostic characters are redescribed here. Additionally, a lectotype is herein designated for *P. paecilei.*

One of the species of *Sudanonautes* is clearly *S. africanus* (A. Milne-Edwards, 1869). This is a common and well-known species that was recently redescribed by Cumberlidge (1995a, 1999). The second species of *Sudanonautes* in the collection is superficially similar in some respects to *S. africanus, S. chavanesii* (A. Milne-Edwards, 1886), *S. faradjensis* (Rathbun, 1921), *S. floweri* (de Man, 1901), *S. granulatus* (Balss, 1929) and *S. aubryi* (H. Milne Edwards, 1853). However, the new specimen from the Central African Republic has a number of important characters that do not conform to the descriptions of any of these species (Cumberlidge 1993, 1994, 1995a, 1995b, 1995c, 1995d; 1999). Although the specimen is a subadult female, and ideally an adult male is needed to make a definitive identification, a preliminary description is provided here, based on several unique somatic characters of the specimen. This new taxon is the eleventh species of *Sudanonautes* to be described (Cumberlidge 1999). Characters of the gonopods, male abdomen, and male chelipeds will be described when more material (including an adult male) becomes available.

Only six species of freshwater crabs have been previously reported to occur in the Central African Republic (Bott 1955, Cumberlidge 1999). These are: *Potamonautes ballayi* (A. Milne-Edwards, 1886), *P. paecilei* (A. Milne-Edwards, 1886), *P. dybowski* (Rathbun, 1904), *Sudanonautes faradjensis* (Rathbun, 1921), *S. floweri* (de Man, 1901) and *S. granulatus* (Balss, 1929). The addition of *S. africanus* and *S. sangha* new species in the present work brings to eight the number of species of freshwater crab reported from the Central African Republic.

Materials and Methods

Figures were prepared by capturing an image with a digital camera and completed using the programs Adobe Photoshop™ and Adobe Illustrator™ (Harvey 1999). The specimens are deposited in the American Museum of Natural History, New York, U.S.A. (AMNH). Abbreviations: Muséum national d'Histoire naturelle, Paris, France (MNHN); Muséum royale d'Afrique central, Tervuren, Belgium (MRAC); Biology, Northern Michigan University, Marquette, Michigan, U.S.A. (NMU); Senckenberg Museum, Frankfurt, Germany (SMF); cw, distance across the carapace at the widest point; cl, carapace length measured along the median line, from the anterior to the posterior margin; ch, carapace height (the maximum height of the cephalothorax); fw, front width measured along the anterior margin; s, thoracic sternite; e, thoracic episternite; s4/s5, s4/s5, s5/s6, s6/s7, s7/s8, sternal sulci between adjacent thoracic sternites; s4/e4, s5/e5, s6/e6, s7/e7, episternal sulci between adjacent thoracic sternites and episternites; P1–P5, pereiopods 1–5.

Systematic Account

Genus *Potamonautes* MacLeay, 1838

Diagnosis.—Postfrontal crest completely crossing carapace and meeting anterolateral margins at epibranchial teeth. Anterolateral margin always lacking intermediate tooth between exorbital angle and epibranchial tooth. Mandibular palp always two-segmented. Exopod of third maxilliped always with long flagellum. Terminal article of gonopod 1 short, about one-quarter to one-third as long as subterminal segment of gonopod 1. Terminal article of gonopod 2 a long flagellum about 0.5–0.75 times as long as subterminal segment of gonopod 2.

Remarks.—Bott (1955) revised *Potamonautes* and included 38 species and 14 subspecies, and erected 15 subgenera to accommodate these taxa. Since that work, a number of other species and subspecies have been described. These are *Potamonautes triangulus* (Bott, 1959), *P. brincki* (Bott, 1960) (Cumberlidge 1994, 1999; Stewart 1997a), *P. (Isopotamonautes) anchetiae machadoi* Bott, 1964, *P. (Lirrangopotamonautes) lirrangensis adeleae* Bott, 1968, *P. (I) senegalensis* Bott, 1970, *P. dentatus* Stewart, Coke, & Cook, 1995, *P. parvispina* Stewart, 1997b, *P. granularis* Daniels, Stewart, & Gibbons, 1998, and *P. reidi* Cumberlidge, 1999.

Bott (1955) assigned *Potamonautes ballayi* and *P. paecilei* to the subgenus *Longipotamonautes* Bott, 1955, which also included a number of other species of rainforest river crabs from Central Africa in which adult males have an elongated, highly arched right cheliped and sharp teeth on the anterolateral margins of the carapace: *P. vandenbrandeni* (Balss, 1936), *P. schubotzi* (Balss, 1914), *P. punctatus* Bott, 1955, *P. ballayi acristatus* Bott, 1955, and *P. ballayi gono-*

cristatus Bott, 1955. Although Bott (1955) recognised numerous subgenera of *Potamonautes* including *Isolapotmonautes, Platypotamonautes, Lirrangopotamonautes* and *Longipotamonautes,* we prefer here to follow Cumberlidge (1999) and use *Potamonautes* sensu lato for all species, pending a revision of the entire genus.

Potamonautes ballayi (A. Milne-Edwards, 1886)

Figs. 1, 2

Thelphusa Ballayi A. Milne-Edwards, 1886: 149.—A. Milne-Edwards, 1887:132, pl. 7, figs. 2, 2a.

Potamon (*Potamon*) *ballayi:* Rathbun, 1904: 294, pl. 12, fig. 9.—Rathbun, 1921:419–422, pl. 27–28, figs. 1, 10.

Potamon (*Potamonautes*) *ballayi:* Balss, 1936:174–177, figs. 9, 12–13.

Potamon ballayi: Chace, 1942:206.—Capart, 1954:827, fig. 3.

Potamonautes (*Longipotamonautes*) *ballayi ballayi:* Bott, 1955:244–245, pl. VII, figs. 2a–d, figs. 23, 73.

Type material and type locality.—Female holotype, Ngancin (=Nganchu = Ngabé), Republic Populaire du Congo (formerly French Congo), 03°18′S, 16°6′E, on opposite bank to Kwamouth, Democratic Republic of Congo (formerly Zaire), coll. Apr 1884, MNHN.

Material examined.—Central African Republic. 1 adult male, cw 18.8 mm (AMNH 17826), about 19 km from the village of Bayanga, Yobei (Yobé) river, depth 0.1 m, sandy shore near large dam made entirely of closely interwoven branches and vines, coll. J. Cordeiro, 18 Jun 1998.

Diagnosis.—Postfrontal crest not complete, epigastric lobes significantly separated from postorbital crests, and lateral ends of postorbital crests not quite meeting anterolateral margins (Fig. 1A). Exorbital angle produced into small pointed tooth; epibranchial tooth large, sharp, and pointing forward; anterolateral margin between exorbital angle tooth and epibranchial tooth smooth, curving slightly outward, lacking intermediate tooth; anterolateral margin posterior to epibranchial tooth smooth, raised, curving inward over mesobranchial surface of carapace, and not continuous with posterolateral margin. Carapace height approximately equal to front width (ch/fw 1.07). Front very broad, measuring almost one half width of carapace (fw/cw 0.45) (Fig. 1B). Sidewall of carapace with distinct vertical sulcus, continuing downward in pterygostomial region, dividing sidewall into four parts. Exopod of third maxilliped with a long flagellum, ischium of third maxilliped smooth lacking vertical sulcus (Fig. 1D). First thoracic sternal sulcus s1/s2 absent; second sulcus s2/s3 deep, running horizontally across sternum; third sternal sulcus s3/s4 absent so that sternum in this region completely smooth (Fig. 1C). Thoracic episternal sulci s4/e4, s5/e5, s6/e6 and s7/e7 smooth, none marked by visible groove. Major cheliped of adult males distinct, with widely arched dactylus and propodus longer than carapace width (Fig. 1G). First carpal tooth of inner margin of carpus of cheliped large, slender, pointed; second carpal tooth pointed, half size of first tooth. Lateral inferior margin of merus of cheliped lined by small teeth, medial inferior margin of merus of cheliped smooth, with single large pointed distal meral tooth at distal end (Fig. 1J); superior surface of merus ridged by rows of short carinae (Fig. 1I). Terminal article of gonopod 1 short (about one-third as long as subterminal segment), longitudinal groove visible on dorsal and superior sides (but not on ventral side); entire terminal article slim, tubular, and directed outward at 45° angle to vertical, ending in wide tip forming distinct pointed process on medial side; lateral and medial folds on terminal article of gonopod 1 approximately equal (Figs. 2A–C). The adult size range of *P. ballayi* is between cw 28–30 mm.

Description.—For a detailed description and additional illustrations see Rathbun (1921) and Bott (1955). For a brief description of the type, see Capart (1954, fig. 3).

Remarks.—Rathbun (1921) recorded the

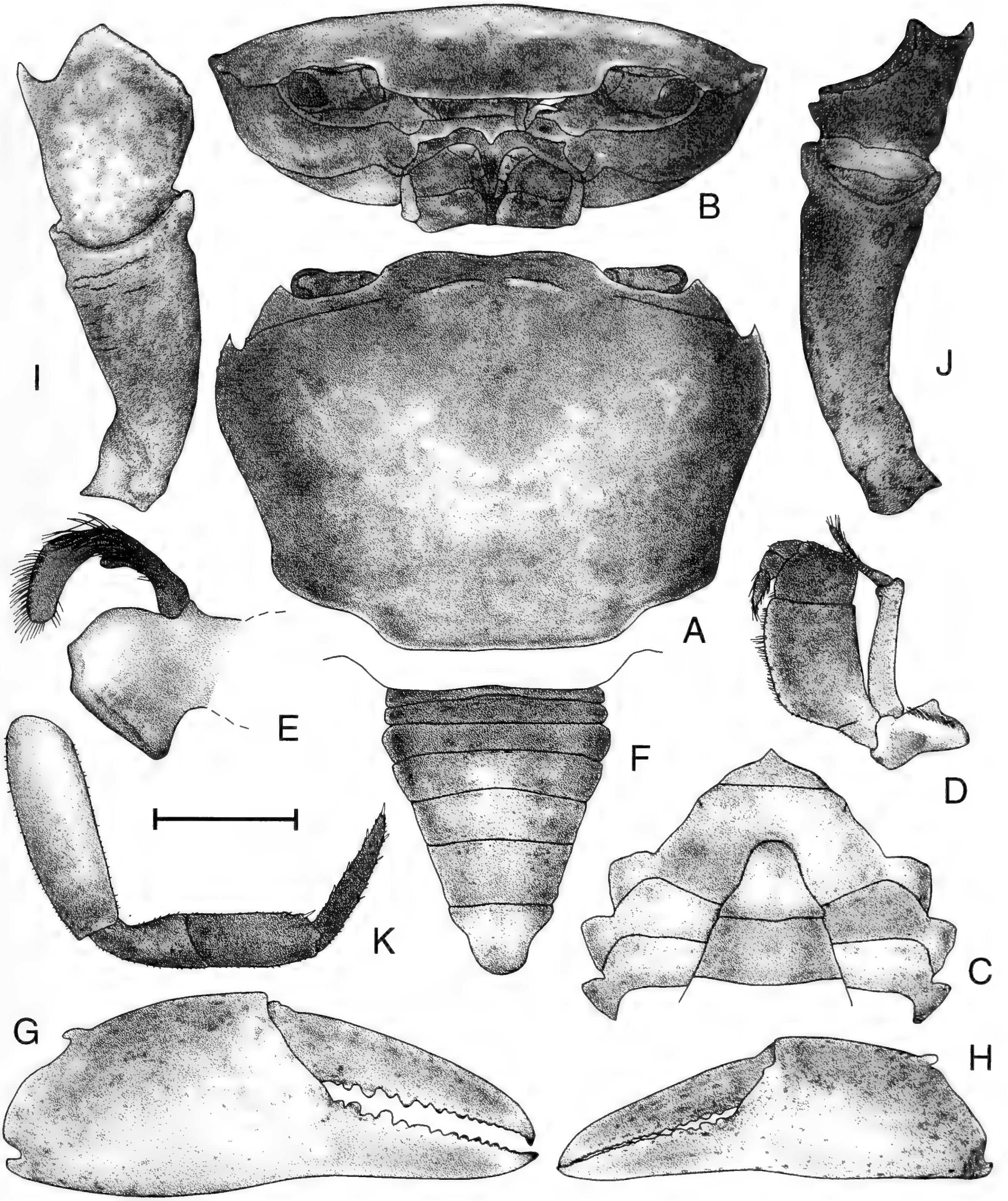

Fig. 1. *Potamonautes ballayi* (A. Milne-Edwards, 1886). Male, cw 17.3 mm, AMNH 17826. A, carapace and eyes, dorsal view; B, cephalothorax, carapace and eyes, frontal view; C, anterior sternum; D, left third maxilliped; E, left mandible; F, abdomen; G, right cheliped, frontal view; H, left cheliped, frontal view; I, carpus and merus of right cheliped, lateral view; J, carpus and merus of right cheliped, mesial view; K, left second pereiopod, lateral view. Scale = 1.6 mm (E), 3.3 mm (D, G–J), and 4.4 mm (A–C, F, K).

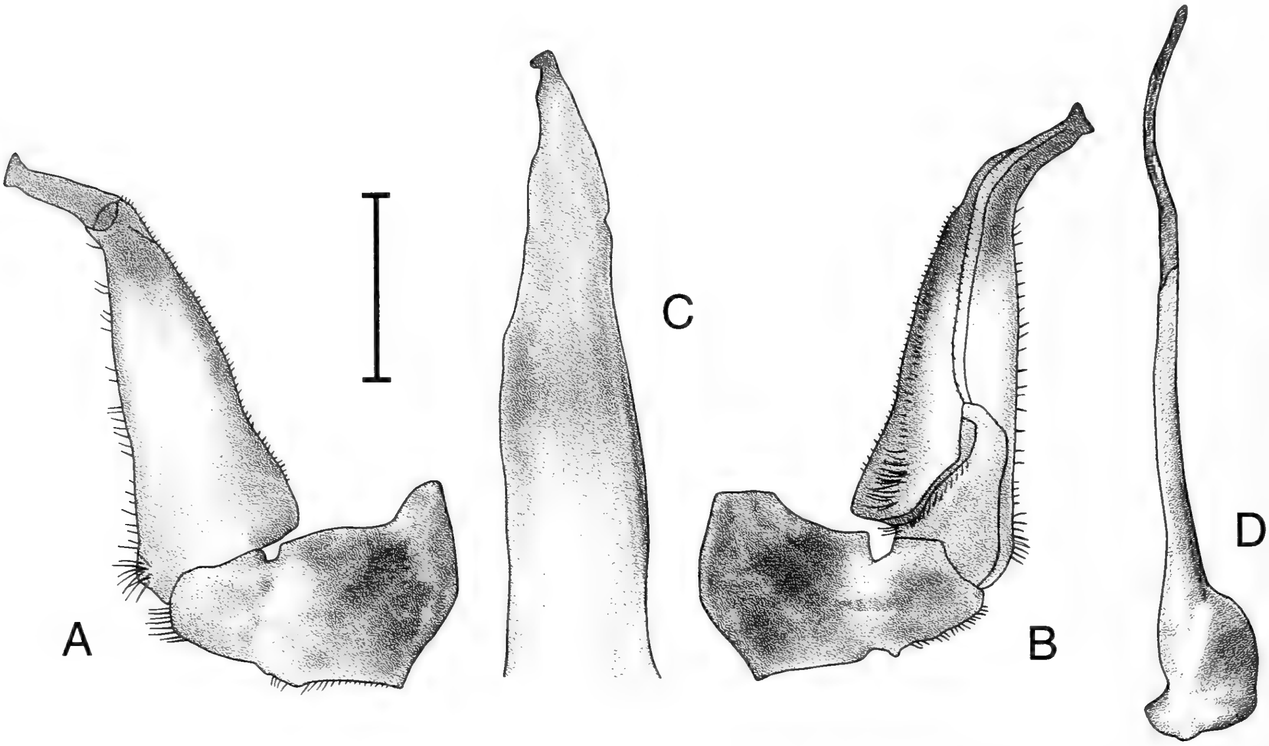

Fig. 2. *Potamonautes ballayi* (A. Milne-Edwards, 1886). Male, cw 17.3 mm, AMNH 17826. A, left gonopod 1, cephalic view; B, left gonopod 1, caudal view; C, distal portion of left gonopod 1, superior view; D, left gonopod 2. Scale = 0.80 mm (C), and 1.67 mm (A, B, D).

mandibular palp as three-segmented. This is an error, for it is clearly two-segmented (Fig. 1E), as is the case for all members of the genus, and, indeed all potamonautid African freshwater crabs (Cumberlidge 1999). Because the type of *P. ballayi* is a female, the gonopods were not illustrated in the first descriptive works on the species. Gonopod 1 of *P. ballayi* was subsequently illustrated by Rathbun (1921) who used a male (cw 26 mm, AMNH 3356) from Stanleyville (now Kisangani, Democratic Republic of Congo) and by Bott (1955), who used a male (cw 33 mm, MRAC 17413) from Karawa, Ubangi, Democratic Republic of Congo. Gonopod 1 of the male from the Central African Republic is shown here in more detail (Figs. 2A–C), and gonopod 2 of *P. ballayi* is illustrated for the first time (Fig. 2D).

Ecology.—The specimen from the Central African Republic was caught in shallow water (only 0.1 m deep) near a dam made entirely of closely interwoven branches and vines. Herbert Lang's field notes (in Rathbun 1921) record that *P. ballayi* is common in shallow forest streams around Stanleyville (now Kisangani). Lang wrote that it is probable that *P. ballayi* can live out of water and that it is only dependent on a certain amount of moisture. When disturbed, crabs were reported to instantly cover themselves with mud and secure protection beneath any object.

Distribution.—Republic Populaire du Congo (formerly French Congo), Democratic Republic of Congo, and Gabon. The type locality of *P. ballayi* at Ngabé, Republic Populaire du Congo lies on the banks of the Zaire river opposite Kwamouth, Democratic Republic of Congo. The present study showed that *P. ballayi* is present in the Yobé river, a tributary of the Sangha river which drains into the Zaire river in a broad marshy area at Mossaka, Republic Populaire du Congo. For more localities see Rathbun (1921), Balss (1936), and Bott (1955).

Potamonautes paecilei (A. Milne-Edwards, 1886)
Fig. 3

Thelphusa paecilei A. Milne-Edwards, 1886:149

Parathelphusa paecilei: A. Milne-Edwards, 1887:143, pl. 7, figs. 1, 1a; Ortmann, 1897:300.

Potamon (*Parathelphusa*) *paecilei:* Rathbun, 1905:257, fig. 167.

Potamon paecilei: Chace, 1942:208.—Capart, 1954:841–842, figs. 34, 37.

Potamonautes (*Longipotamonautes*) *paecilei:* Bott, 1955:242–243, pl. VI, figs. 2a–d, text figs. 21, 71.

Type material and type locality.—Adult male lectotype, cw 32 mm (MNHN-B263), Central Africa, Republic Populaire du Congo (formerly French Congo), Latéké (=Lékéti), Alima river (14°56′E, 1°36′S), coll. M. de Brazzae.

Material examined.—Central African Republic. 1 adult female, cw 18.6 mm, (AMNH 17827), 17.3 km from the village of Bayanga (02°45′43″N, 16°14′12″E), Lossi creek, depth 1–2 m, bottom of the fine sand and mud, caught in net in swiftly moving black water, coll. J. Sullivan, 19 Jun 1998.—1 adult male, cw 20.7 mm (AMNH 18032), 17.3 km from the village of Bayanga (02°45′43″N, 16°14′12″E), Lossi creek, depth 1–2 m, bottom of fine sand and mud, caught in net in swiftly moving black water, coll. M. Lawrence, J. Sullivan, and local residents, 30 Jun 1998.

Diagnosis.—Postfrontal crest either complete or almost complete, wherein lateral ends of postorbital crests not quite meeting anterolateral margins (Fig. 3A). Exorbital angle produced into small, pointed, sharp tooth; epibranchial tooth large, pointed, directed forward; anterolateral margin between exorbital angle tooth and epibranchial tooth smooth, curving outward, lacking intermediate tooth; anterolateral margin posterior to epibranchial tooth with two sharp, forward-pointing teeth; margin otherwise smooth, continuous with posterolateral margin. Front very broad, measuring almost one-half width of carapace (fw/cw 0.45) (Fig. 3A, B). Carapace height approximately equal to front width (ch/fw 1.07). Exopod of third maxilliped with long flagellum, ischium of third maxilliped smooth, lacking vertical sulcus (Fig. 3D). First thoracic sternal sulcus s1/s2 absent; second sulcus s2/s3 deep, running horizontally across sternum; third sternal sulcus s3/s4 absent; sternum in this region completely smooth. Episternal sulci s4/e4, s5/e5, s6/e6 and s7/e7 smooth, none marked by visible groove. Major cheliped of adult males distinct, with widely arched dactylus and a propodus longer than carapace width. First carpal tooth of inner margin of carpus of cheliped large, slender, pointed; second carpal tooth half size of first. Lateral and medial inferior margins of merus of cheliped lined by small teeth; single large pointed distal meral tooth at distal end (Fig. 3J); superior surface of merus ridged by rows of short carinae (Fig. 3I). Terminal article of gonopod 1 short (about one-third as long as subterminal segment), longitudinal groove visible on superior side, but not on dorsal and ventral sides; entire terminal article slim, tubular, curved; directed outward at an approximately 45° angle to vertical; ending in broadened upcurved tip; lateral and medial folds on terminal article of gonopod 1 approximately equal size. The adult size range of *P. paecilei* is between cw 28–30 mm.

Description.—See Bott (1955), and Capart (1954).

Remarks.—One of us (NC) has examined an adult male syntype (cw 32 mm) of *P. paecilei* (MNHN-B 263) from the Alima river, Latéké French Congo collected by M. de Brazzae. We designate this specimen here as the lectotype. A different male syntype (now paralectotype) of *P. paecilei* (cw 22.7 mm) was figured by Capart (1954). The characters of this species (Fig. 3) include a large forward-pointing epibranchial tooth; a large tooth (or two teeth) behind the epibranchial tooth on the anterolateral margin; an enlarged major cheliped in adult males with a widely arched dactylus and a propodus that is longer than the carapace width; a long sharp distal meral spine on the merus of the cheliped; and the ischium of the third max-

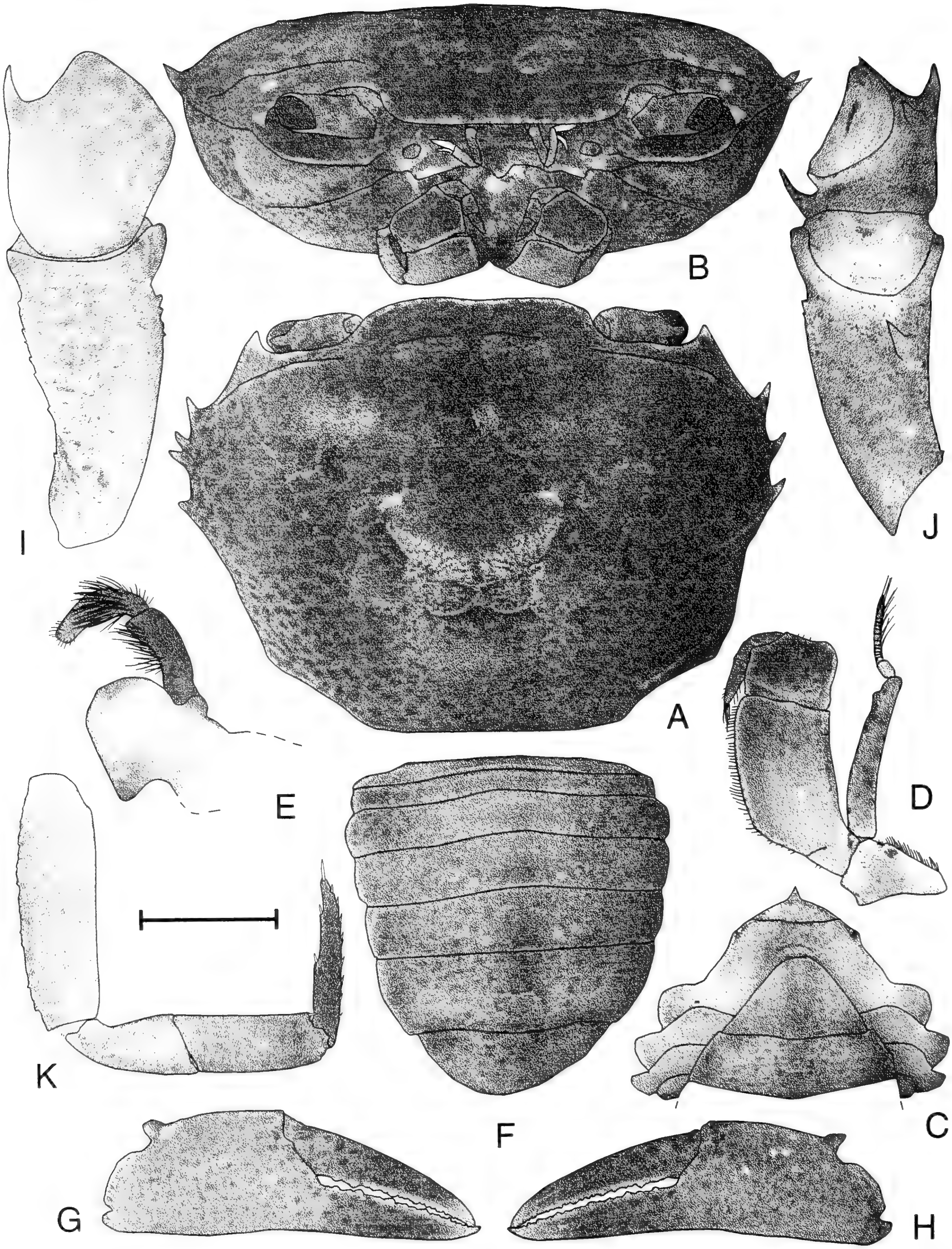

Fig. 3. *Potamonautes paecilei* (A. Milne-Edwards, 1886). Female, cw 18.6 mm, AMNH 17827. A, carapace and eyes, dorsal view; B, cephalothorax, carapace and eyes, frontal view; C, anterior sternum; D, left third maxilliped; E, left mandible; F, abdomen; G, right cheliped, frontal view; H, left cheliped, frontal view; I, carpus and merus of right cheliped, lateral view; J, carpus and merus of right cheliped, mesial view; K, left second pereiopod, lateral view. Scale = 2.2 mm (E), 3.3 mm (D, I, J), 4.4 mm (A, B, F–H, K), and 5.9 (C).

illiped is smooth and a vertical sulcus is lacking.

The sidewall of the carapace of the specimens from the Central African Republic has a distinct vertical sulcus which continues downward across the pterygostomial region, dividing the carapace sidewall into four parts. This contrasts with the type from the Republic Populaire du Congo where the sidewall of the carapace is divided into only three parts.

Ecology.—The specimens from the Central African Republic were netted in a small stream (1–2 m deep), with swiftly moving black water flowing over fine sand and mud.

Distribution.—Republic Populaire du Congo, and Democratic Republic of Congo. The Yobé river is a tributary of the Sangha river which drains southwestern Central African Republic and forms part of the border between the Central African Republic and Cameroon, and then between Cameroon and Republic Populaire du Congo, before joining the Zaire river in a broad marshy area at Mossaka, Republic Populaire du Congo. The type locality lies on the Alima river which flows into the Zaire river just to the south of Mossaka and contributes to the same expanse of marsh and wetlands as the Sangha river.

Sudanonautes Bott, 1955

Sudanonautes Bott, 1955:295.—Cumberlidge, 1999:172–176.

Diagnosis.—Intermediate tooth on anterolateral margin between epibranchial tooth and exorbital angle. Postfrontal crest prominent, almost horizontal, complete, with lateral ends meeting anterolateral margins. Carapace sidewall divided by two sulci into three parts. Mandibular palp two-segmented; terminal segment consisting of large oval posterior lobe (in three species there a small but distinct anterior process at junction between segments). Long, plumose flagellum on exopod of third maxilliped in all species. Sternal sulcus s3/s4 represented only by two short notches at sides of sternum. Terminal article of gonopod 1 very long (at least two-thirds as long as subterminal segment). Terminal article of gonopod 1 either slim and needle-like (where longitudinal groove not visible) or broadened in middle (the result of a higher medial fold) with longitudinal groove visible at least for part of length. Terminal article of gonopod 2 very short, one-fifteenth length of subterminal segment.

Distribution.—The genus is present in Côte-d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Gabon, Bioko (Fernando Po), Central African Republic, Congo, Zaire, northern Angola, and southwest Sudan. The eleven species of *Sudanonautes* are found in the inland waters of West and Central Africa in a region bounded by Côte-d'Ivoire, southwest Sudan, and northern Angola. This area includes the Upper Guinea rainforests, the Lower Guinea forest together with the savannas of the eastern part of West Africa, and the offshore island of Bioko. In Central Africa seven species of *Sudanonautes* (*S. africanus, S. aubryi, S. floweri, S. granulatus, S. chavanesii, S. faradjensis,* and *S. sangha*) share the rivers and forests with species of *Potamonautes* and *Erimetopus* A. Milne-Edwards, 1886 (Bott 1955, Cumberlidge 1999).

Sudanonautes africanus (A. Milne-Edwards, 1869)

Thelphusa africana A. Milne-Edwards, 1869:186, pl. XI, figs. 2, 2a,b.—A. Milne-Edwards, 1887:124–126, pl. IV, fig. 8.

Potamon (*Potamonautes*) *africanus:* de Man, 1903:41, pl. IX, figs. 7–9.—Rathbun, 1904, pl. 16, fig. 6.—Rathbun, 1905: 188–190, fig. 47.—Balss, 1929:124–125, figs. 5–7.—Balss, 1936:166.

Potamon (*Potamonautes*) *africanum:* Colosi, 1920:34.—Colosi, 1924:21, fig. 16.—Roux, 1927:237.

Potamon africanus: Chace, 1942:204.—Capart, 1954:824, figs. 1, 6.

Sudanonautes (*Sudanonautes*) *africanus africanus:* Bott, 1955:295–298, figs. 61, 93–95, 103 a–d, pl. 24, figs. 2a–c, 3.—Bott, 1959:1004–1005.—Monod, 1977:1216 (not figs. 93–95, 102).—Monod, 1980: 384, pl. V, fig. 27.

Sudanonautes africanus: Cumberlidge, 1995a:588–598, figs. 1–3, table 1.—Cumberlidge, 1999:181–184, figs. 30B, 32B, 33B, 34B, 35C, 36E, 37C, 53P, 54–57, 60B, 67A, table IX.

Type material.—The holotype used by A. Milne-Edwards (1869) to describe *Thelphusa africana* was a small juvenile (MNHN) (cw 17 mm) collected from Gabon by M. Aubry-Lecomte. A more detailed description by A. Milne-Edwards (1887) was based on a larger, but still subadult female (MNHN) (cw 53 mm) collected from the river Ogoué, Congo (=Gabon). Because neither of these specimens was suitable to redescribe the species (one is a juvenile and the other a subadult female), and because no topotypes were available, the species was redescribed by Cumberlidge (1995a) from an adult male (cw 83 mm) from Cross River State, Nigeria (NMU 9.IV.1983), and an adult female (cw 108 mm) from a tributary of the Ikpan river, Cross River State, Nigeria (NMU 5.IV.1983).

Material examined.—Central African Republic. Ten specimens, sub-adults and juveniles (no adults) (AMNH 18033), 19.5 km from the village of Bayanga (03°05′27″N, 16°16′40″E), Mapoyo (Mboyé) creek, depth 1–1.5 m, either on muddy bottom, or in burrows in overhanging banks, coll. M. Lawrence, J. Sullivan, and local residents, 17 Jun 1998. Four specimens, 1 adult male and 3 juveniles (AMNH 18034), about 5 km from the village of Bayanga, Mobeya [Moubia?] creek, upstream of mouth, depth 0.5–1 m, sandy, gravely and muddy pools, in burrows in overhanging banks, among roots, under logs, coll. M. Lawrence and local residents, 26 Jun 1998. One subadult male (AMNH 18035), 19.5 km from the village of Bayanga (03°05′27″N, 16°16′40″E), Mapoyo (Mboyé) creek, depth 1–1.5 m, on muddy bottom, or in burrows in overhanging banks, coll. M. Lawrence, J. Sullivan, and local residents, 17 Jun 1998. Four specimens, all juveniles (AMNH 18036), about 5 km from the village of Bayanga, Mobeya [Moubia?] creek, upstream of mouth, depth 0.5–1 m, sandy, gravely and muddy pools, in burrows in overhanging banks, among roots, under logs, coll. M. Lawrence, J. Sullivan, and J. B. Kindimoungo, 28 Jun 1998.

Type locality.—Gabon.

Diagnosis.—Carapace relatively flat (ch/fw 1.06). Postfrontal crest smooth almost straight; spanning entire carapace, meeting anterolateral margins at epibranchial teeth; posterior surface of carapace in cardiac and branchial regions with patches of raised circular blisters, lateral parts with fields of raised short lines (carinae); semi-circular, cardiac, urogastric grooves very deep. Proximal region of pollex of propodus of major cheliped of adult with large, conspicuously flattened tooth. Exorbital angle tooth large, triangular; intermediate tooth large, triangular blunt, as big as exorbital angle tooth. Epibranchial tooth small, about half size of intermediate tooth and exorbital angle tooth. Anterolateral margin behind epibranchial tooth smooth. Terminal article of gonopod 1 thin, needle-like, subterminal segment of gonopod 1 slim. This is the largest species of freshwater crab in Africa. Adult sizes range from the size at the pubertal molt (cw 70–75 mm) to largest the known specimen (cw 113 mm).

Description.—For a detailed description see Cumberlidge (1995a, 1999). For a brief description of the type see Capart (1954, figs. 1, 6).

Remarks.—*Sudanonautes africanus* is a common and well-known species that was recently redescribed (Cumberlidge 1995a, 1999).

Ecology.—This species is restricted to the more humid areas of the coastal rainforest belt from south-east Nigeria to the mouth of the Zaire river. *Sudanonautes africanus* occurs in a range of permanent aquatic habitats from large rivers and small streams (with both fast and slow flowing water) to ponds. In the Central African Republic *S. africanus* is found in creeks up to 1.5 m deep with a sand, gravel or mud bottom. Specimens were also taken from burrows in overhanging banks, among roots and under logs. Elsewhere in its range, this species is also common in streams and rivers draining mature forest, and has been reported to dig burrows near waterways. This crab also occurs in temporary water sources such as drainage culverts and ditches. For more details see Cumberlidge (1995a, 1999).

Distribution.—*Sudanonautes africanus* occurs in the coastal rainforest regions of Nigeria and Central Africa. In Central Africa *S. africanus* occurs in south Cameroon, the Republic Populaire du Congo, and Gabon (in the San Benito, Ogoué and Alima rivers), and in the lower reaches of the Zaire River basin. For more details see Cumberlidge (1995a, 1999). The present record is the first report of the presence of *S. africanus* in the Central African Republic.

Sudanonautes sangha, new species
Fig. 4

Type material and type locality.—Central African Republic. Holotype: 1 subadult female, cw 40.5, cl 29.7, ch 12.5, fw 10.7 mm (AMNH 17825), a few km upstream from the village of Bayanga (02°45′43″N, 16°14′12″E), Sangha river, depth 1–2 m, in fish trap, eating worm, coll. J. Sullivan and J. B. Kindimoungo, 18 Jun 1998.

Diagnosis.—Exorbital tooth large, pointed; intermediate tooth small, low; epibranchial tooth small, low, not directed outward, set back behind mid-point of postfrontal crest. Postfrontal crest spanning entire carapace, crest curving backward before meeting epibranchial tooth, anterolateral margin posterior to epibranchial tooth raised, lined by small granules. Semi-circular, urogastric, transverse branchial grooves very deep. Vertical suture on carapace sidewall meeting intermediate tooth. Carapace medium height (ch/fw = 1.16). Mandibular palp two-segmented; terminal segment single, undivided, with hair at junction between segments. First carpal tooth on carpus of cheliped large, pointed; second carpal tooth reduced to small granule.

Description.—Carapace (Figs. 4A, B).—Ovoid, widest in anterior third (cw/fw 3.79), medium height (ch/fw = 1.16), semi-circular, urogastric, transverse branchial grooves very deep, regions smooth; cardiac region weakly marked, cervical grooves present but weak. Front slightly bilobed, anterior margin indented, relatively narrow, about one-quarter carapace width (fw/cw = 0.26) (Fig. 4B). Postfrontal crest smooth, spanning entire carapace, straight part consisting of fused epigastric, postorbital crests, then curving backward behind intermediate teeth to meet anterolateral margins at epibranchial teeth. Anterolateral margin smooth posterior to epibranchial tooth. Exorbital tooth large, sharp, pointed forward. Epibranchial tooth low, small, set back behind mid-point of postfrontal crest.

Carapace sidewalls mostly smooth, with faint granules in suborbital regions. Each sidewall with two sutures, one longitudinal, one vertical, dividing sidewall into three parts. Longitudinal (epimeral) suture dividing suborbital, subhepatic regions from pterygostomial region, beginning medially at lower margin of orbit, curving backward across flank. Short vertical suture dividing suborbital region from subhepatic region; vertical suture meeting intermediate tooth. First transverse groove on sternum, between sternal segments s2 and s3, complete; second groove, between sternal segments s3 and s4, consisting of two small notches at sides of sternum. Third maxillipeds filling entire oral field, except for transversely oval efferent respiratory openings at superior lateral corners; long flagellum on exopod of third maxilliped; ischium of third maxilliped smooth, with clear vertical groove (Fig. 4C). Mandibular palp two-segmented; terminal segment single, undivided, with hair but no hard flap at junction between segments (Fig. 4D). Segments 1–6 of female abdomen four-sided, last segment a broad rounded triangle, sides forming a smooth curved, rounded margin; segments 5–6 broadest (Fig. 4E).

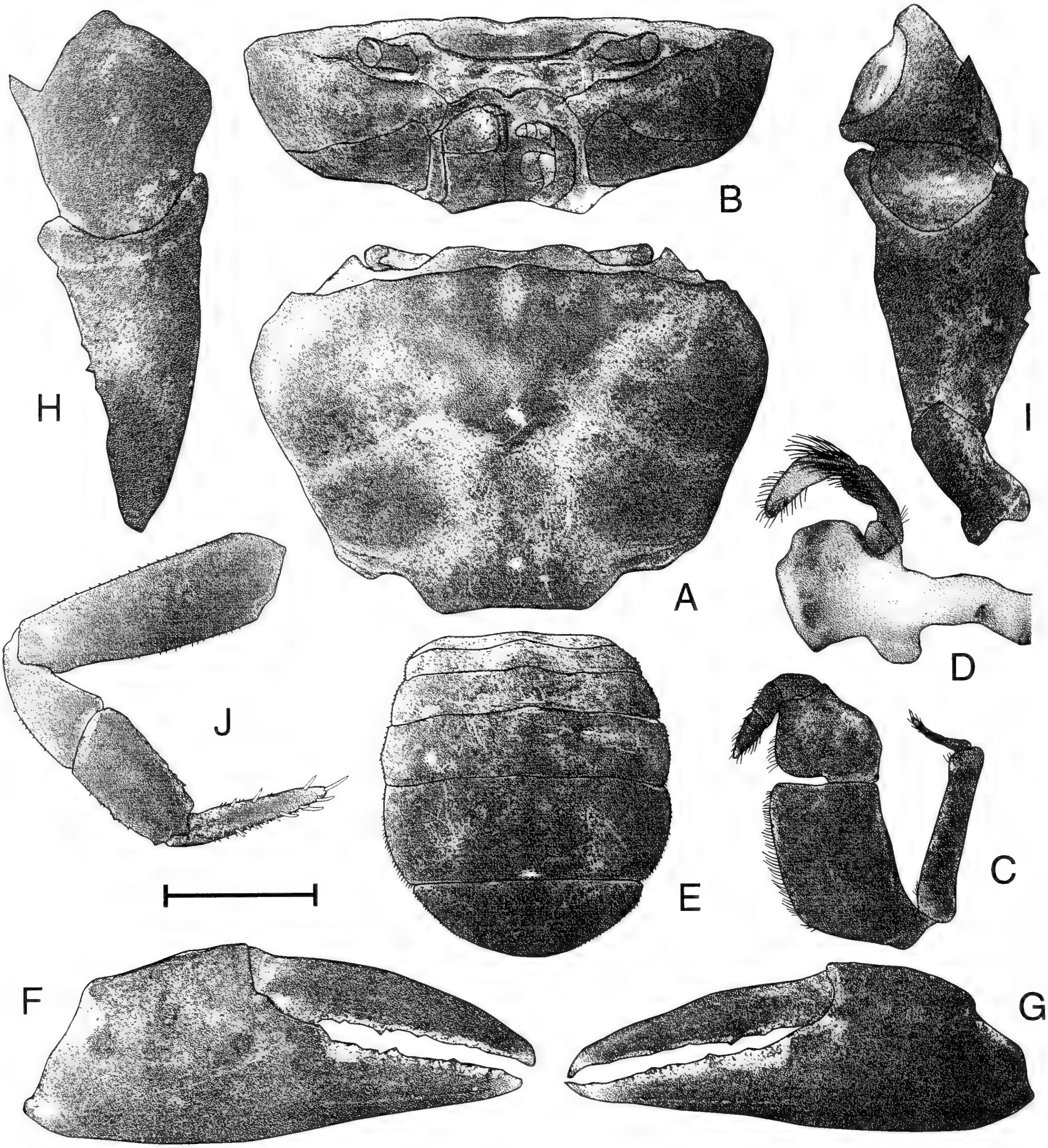

Fig. 4. *Sudanonautes sangha,* new species. Holotype subadult female, cw 40.5 mm, AMNH 17825. A, carapace and eyes, dorsal view; B, cephalothorax, carapace and eyes, frontal view; C, left third maxilliped; D, left mandible; E, abdomen; F, right cheliped, frontal view; G, left cheliped, frontal view; H, carpus and merus of right cheliped, lateral view; I, carpus and merus of right cheliped, mesial view; J, left second pereiopod, lateral view. Scale = 4.4 mm (D), 6.2 mm (I), 6.7 mm (C), 7.2 mm (H), 8.6 mm (F, G, J), and 12.7 mm (A, B, E).

Dactylus of right cheliped long, slim, straight; palm of propodus swollen; fingers of digits of chelipeds with small even teeth, forming long slim interspace when closed, fingers almost meeting when shut (Fig. 4F). Inferior margins of merus with rows of small granules, cluster of granules surrounding larger pointed distal meral tooth at distal end (Fig. 4I). Inner margin of carpus of cheliped with large, slender, pointed tooth (first carpal tooth), second carpal tooth reduced to a granule (Fig. 4I). Pereiopods P2–P5 slender

(Fig. 4J), P4 longest, P5 shortest. Propodus of P2–P5 broad, posterior margin of propodus of P2–P5 serrated, dactyli of P2–P5 tapering to point, each bearing four rows of downward-pointing sharp bristles; dactylus of P5 shortest.

Etymology.—The species is named for the Sangha river where it was collected. The Sangha river drains a large region of the Central African Republic, and is a dominant natural feature of the area. The species name *sangha* is a noun in apposition.

Remarks.—It is not normally good practice to describe a new species from a subadult female. However, we have decided to establish this taxon in light of the distinct nature of the available morphological characters, and because of the isolated nature of the study area which may mean that further specimens are unlikely to become available for some time. *Sudanonautes sangha* is the eleventh species of this West and Central African genus. Characters of the gonopods, adult male chelipeds, abdomen and sternum are not available because the only specimen of *S. sangha* is a subadult female. Nevertheless, there are a number of unique characters that distinguish *S. sangha* from other species in the genus.

Sudanonautes sangha is most likely to be confused with other large species of freshwater crabs occurring in the rain forests of Central Africa such as *S. chavanesii, S. faradjensis, S. africanus, S. aubryi* and *S. floweri.*

Sudanonautes sangha and *S. africanus* are similar in that both species have a small epibranchial tooth, and both lack large teeth on the anterolateral margins of the carapace. However, there are a number of characters which distinguish *S. sangha* from *S. africanus.* The carapace of *S. sangha* is not as flattened as that of *S. africanus* (ch/fw *S. sangha* = 1.16, *S. africanus* = 1.06), and the posterior region of the carapace of *S. sangha* is smooth, whereas that of *S. africanus* is rough with warty patches and ridges in the posterior region. The cardiac regions of *S. sangha* are flattened and are neither rounded nor well marked, whereas these regions in *S. africanus* appear as a pair of distinct raised rounded structures that are clearly outlined by deep cardiac grooves. The intermediate tooth on the anterolateral margin between the exorbital tooth and the epibranchial tooth of *S. sangha* is small and low, whereas that of *S. africanus* is large and triangular. The second carpal tooth on the cheliped of *S. sangha* is very small, only the size of a granule, whereas the second carpal tooth of *S. africanus,* while smaller than the first carpal tooth, is distinct, pointed, and is a tooth rather than a granule. The vertical groove on the carapace sidewall of *S. sangha* meets the anterolateral margin at the base of the intermediate tooth, whereas the vertical groove of *S. africanus* meets the anterolateral margin at the base of the epibranchial tooth.

Sudanonautes sangha can be distinguished from *S. chavanesii* by the position of the postfrontal crest and by the shape of the epibranchial teeth. In *S. sangha* the lateral ends of the postfrontal crest curve forward to meet the epibranchial teeth in line with the mid groove of the crest, whereas in *S. chavanesii* the lateral ends of the postfrontal crest curve sharply backward before meeting the epibranchial teeth which are set back posterior to the mid groove of the crest. In *S. sangha,* the epibranchial tooth is small, blunt, pointed forward, and positioned in line with the mid groove of the crest, whereas in *S. chavanesii,* the epibranchial tooth is large, sharp, pointed outward, and positioned well behind the mid-groove of the postfrontal crest. Further, in *S. sangha* the vertical suture on the carapace sidewall is simple, whereas in *S. chavanesii* the vertical suture on the carapace sidewall forms a Y-shaped depression beneath the intermediate tooth. Finally, in *S. sangha* the junction between the two segments of the mandibular palp is simple, whereas in *S. chavanesii* there is a small hard flap on the mandibular palp at the junction between the two segments.

Sudanonautes sangha can be distinguished from *S. faradjensis* by the form of the anterolateral margin behind the epibranchial tooth: that of *S. sangha* is raised and lined by small granules, whereas in *S. faradjensis,* there is a row of sharp teeth. *Sudanonautes sangha* can be distinguished from *S. granulatus* as follows: the exorbital tooth of *S. sangha* is wide and triangular, whereas that of *S. granulatus* is narrow and low, and the anterolateral margin of *S. sangha* is raised and lined by granules, whereas that of *S. granulatus* is completely smooth.

Sudanonautes sangha can be distinguished from *S. aubryi* by differences in the postfrontal crest: that of *S. sangha* meets the anterolateral margin at the epibranchial tooth, whereas that of *S. aubryi* meets the anterolateral margin behind the epibranchial tooth. In addition, the carapace of *S. sangha* is distinctly flatter than that of *S. aubryi* (ch/fw *S. sangha* = 1.16, *S. aubryi* = 1.29).

Finally, *S. sangha* can be distinguished from *S. floweri* by differences in the mandibular palp: in *S. sangha* the junction between the two segments of the mandibular palp is simple, whereas in *S. floweri* there is a small hard flap on the mandibular palp at the junction between the two segments. In addition, the carapace of *S. sangha* is distinctly flatter than that of *S. floweri* (ch/fw *S. sangha* = 1.16, *S. floweri* = 1.68).

Ecology.—Collected in a large river (as opposed to a small stream), and caught in a baited trap.

Distribution.—Central African Republic, a few kilometers upstream from the village of Bayanga (02°45′43″N, 16°14′12″E), Sangha river.

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The freshwater crabs of the Barbilla National Park, Costa Rica (Crustacea: Brachyura: Pseudothelphusidae), with notes on the evolution of structures for spermatophore retention

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Abstract.—The Barbilla National Park, a natural area of high biodiversity on the Caribbean slope of Costa Rica, possesses two species of freshwater crabs that share the same biotope in different localities of the Park. The first species, *Potamocarcinus magnus* (Rathbun, 1896), one of the largest species of the family Pseudothelphusidae, is widely distributed in Middle America, from Costa Rica to Southern Mexico. The other species is a new species, *Ptychophallus barbillaensis.* This is a species of small crabs, possibly restricted to the National Park and neighboring areas. It can be distinguished from all other species in the genus by the form of the receptacle formed in the apex of the male gonopod, possibly for the retention of spermatophora during copulation. The species of *Ptychophallus* Smalley, can be arranged in a morphocline according to the relative development of this receptacle, with the present new species midway between the ancestral condition and the closed channel found in *P. goldmanni* Pretzmann, 1965.

The Barbilla National Park covers 12,830 hectares of humid tropical forest on the Caribbean watershed of the Sierra de Talamanca, Costa Rica. This stretch of mostly primary vegetation is located between the valleys of the Pacuare and Chirripó rivers, between 200 and 1600 m above sea level. The area is noted for its high biodiversity.

During recent surveys carried out by the Mid Sweden University several samples of freshwater organisms have been collected in the ravines that surround the Nairi Field Station, close to the northwestern border of the Park. Two species of freshwater crabs were discovered among the materials in these collections. One of them, a new species belonging to the genus *Ptychophallus* Smalley, 1964a, is described in the present contribution. The materials recorded are deposited in the Reference Collection of the Instituto Venezolano de Investigaciones Científicas, Caracas (IVIC); the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the Museum of Natural History of Tulane University, New Orleans (TU). Other abbreviations used are cl, carapace length, and cb, carapace breadth.

Systematics

Family Pseudothelphusidae Rathbun, 1893

Genus *Potamocarcinus* H. Milne Edwards, 1853

Potamocarcinus magnus (Rathbun, 1896)

Material.—Costa Rica: Río Caño Seco (10°00′N, 83°26′W), affluent of Río Dantas, Barbilla National Park, 7 Jan 1999, leg. I. Hedström, 300 m above sea level, 1 immature female, cl 17.3 mm, cb 25.0 mm

(IVIC 1070); Casas Negras, Río Dantas, Barbilla National Park, 8 Jan 1999, leg. I. Hedström, 200 m above sea level, 1 immature male, cl 19.8 mm, cb 28.3 mm (IVIC 1071); Río Barbilla, Barbilla National Park, 28 Jan 1999, leg. I. Hedström, 100 m above sea level, 2 immature males, cl 17.0 and 12.4 mm, cb 23.7 and 18.5 mm, 1 immature female, cl 10.0 mm, cb 15.7 mm (IVIC 1072).

Remarks.—Although our specimens are immature, they can be referred with certainty to this species. *Potamocarcinus magnus* is widely distributed in Central America, but Rodríguez (1982) distinguish three different morphological groups from (a) Costa Rica, (b) El Salvador, Guatemala and southern Mexico, and (c) Guatemala. The characters of the carapace in our specimens agree with those given for the Costarican form. However, the typical flat tubercles present over the surface of the carapace cover a greater area, a characteristic possibly due to the juvenile condition of the specimens. The right cheliped has the typical long and narrow tubercle over the palm, at the base of the fingers, although it is relatively little developed. In the first male gonopods there is not an abnormal intrusion of the marginal process into the distal lobe, as was the case in the specimen from Costa Rica illustrated by Rodríguez (1982, fig. 72b). *Potamocarcinus magnus* is the largest of all species of Pseudothelphusidae, with a cb of 135 mm reported by Rathbun (1896).

Genus *Ptychophallus* Smalley, 1964a

Ptychophallus barbillaensis, new species

Fig. 1, 2C, H

Material.—Costa Rica: Río Caño Seco (10°00′N; 83°26′W), affluent of Río Dantas, Barbilla National Park, 7 Jan 1999, leg. I. Hedström, 300 m above sea level, 1 male holotype, cl 16.9 mm, cb 27.7 mm (IVIC 1073), 1 male paratype, cl 13.4 mm, cb 20.7 mm (IVIC 1074); Nairi Field Station (09°59′N; 83°27′W), 3 km north of the border of Barbilla National Park, 7 Jan 1999, leg. I. Hedström, 2 ovigerous females, cl 15.6 and 13.9 mm, cb 25.0 and 21.1 mm (IVIC 1075); Casas Negras, Río Dantas, Barbilla National Park, 8 Jan 1999, leg. I. Hedström, 200 m above sea level, 2 males, cl 12.2 and 11.9 mm, cb 18.9 and 18.7 mm (IVIC 1076); Las Cuevas, Río Dantas, Barbilla National Park, 11 Jan 1999, leg. I. Hedström, 150 m above sea level, 2 males, cl 14.2 and 11.7 mm, cb 22.5 and 18.6 mm, 1 mature female, cl 14.1 mm, cb 21.5 mm (IVIC 1077); El Recodo, Río Dantas, Barbilla National Park, 6 Jan 1999, leg. I. Hedström, 300 m above sea level, 1 male, cl 15.2 mm, cb 23.3 mm, 1 immature male, cl 9.9 mm, cb 15.0 mm, 1 male juvenile, cl 5.8 mm, cb 13.5 mm (IVIC 1078).

Diagnosis.—First gonopods with large lateral lobe divided in 2 subequal rounded segments by median notch; proximal segment smaller, subcircular; distal segment projected anteriorly and bent caudally to form cup-shaped receptacle; apex strongly bent laterally forming, with distal segment of lateral lobe, characteristic sinus; field of spines directed toward latero-cephalic side, oblong, with deep notch on mesial side; cephalic end of apex with 2 expansions, distal subtriangular in lateral and caudal views, with notch on lateral side, proximal rounded in cephalic view, beak-like in mesial view.

Description of holotype.—Carapace 1.6 times as wide as long, surface smooth and polished, except for few granules on posterior branchial regions, near margins; cervical grooves recurved backwards, narrow and deep, not reaching margins of carapace; anterolateral margins with shallow and wide postorbital notch bordered by 5 papillae, rest of borders with small papillae that becomes dentiform behind level of cervical grooves. Postfrontal lobes low, delimited anteriorly by transverse depressions; median groove narrow, deep, making incision on upper margin of front. Surface of carapace between postfrontal lobes and front flat, slightly inclined forward and towards mid-

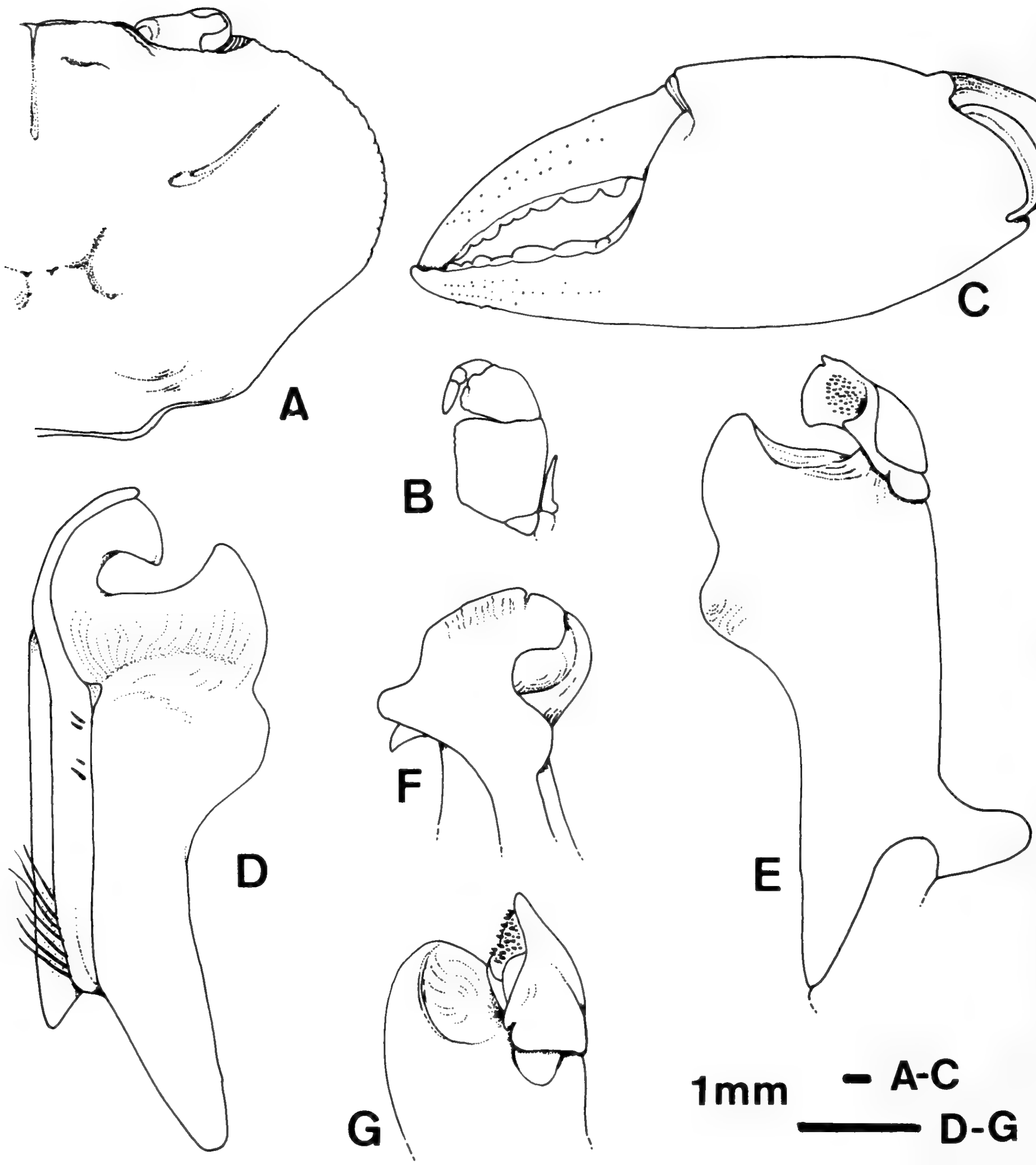

Fig. 1. *Ptychophallus barbillaensis,* new species, holotype from Río Caño Seco, Costa Rica (IVIC 1073): A, dorsal view of right side of carapace; B, third maxilliped, left; C, chela of largest cheliped (left), external view; D, first left gonopod, caudal view; E, same, cephalic view; F, same, apex, mesial view; G, same, apex, cephalic view.

dle line. Upper margin of front in dorsal view slightly convex and divided into two halves by median notch, thin, well marked, with small tubercles; lower margin thin, moderately sinuous, advanced in front of upper margin; both margins subparallel.

Exognath of third maxilliped 0.65 length of ischium of endognath. Palm of largest cheliped moderately swollen, with lower and upper margins convex; fingers gaping, with rows of small black-brown points on external surface.

First gonopods wide in latero-mesial direction, narrow in caudo-cephalic direction; large lateral lobe divided in 2 subequal rounded segments by median notch; proximal segment smaller, subcircular; distal segment projected anteriorly and bent caudally to form cup-shaped receptacle semi-enclosed by apex of gonopod; apex strongly bent laterally, forming with distal segment of lateral lobe characteristic sinus; field of spines directed toward latero-cephalic side, oblong, with deep notch on mesial side; cephalic end of apex forming two expansions; distal expansion continuous with margin of gonopod, subtriangular, in lateral and caudal views, with notch on lateral side; proximal expansion rounded in cephalic view, beak-like in mesial view.

Remarks.—This species can be distinguished from all others in the genus by the cupshaped expansion of the distal segment of the lateral lobe of the first gonopods and by the strong recurvation of the apical peduncle of gonopod over this expansion.

Etymology.—The species is named after the Barbilla National Park, Costa Rica, where the species was collected.

Evolution of Structures for Spermatophore Retention in *Ptychophallus*

Although the morphology of the first male gonopods are essential for the discrimination of the species of Pseudothelphusidae, very little is known of the function of the different processes of these appendages during copulation. In all species, the apex is provided with a field of minute spines (Smalley 1964b) which surround the opening of the spermatic channel and serve to hold the spermatophore once it is extruded by the piston-like pumping action of the second gonopod.

In the species of *Ptychophallus* a trend can be observed towards a reaccomodation of the lateral lobe and the various components of the apex of the gonopod, to form a structure that possibly serves to receive and keep the spermatophore once it is extruded. This is fully developed in *Ptychophallus goldmanni* Pretzmann, 1965, but the other species can be arranged in a morphocline comprising several stages of development of this structure, as follows.

Stage I (Fig. 2A, F).—In the primitive condition there is a wide lateral lobe, which is foliose, with a shallow depression or deeply notched, with the distal portion advanced and transverse. The field of spines is located distant from the lateral lobe, facing caudo-laterally, its long axis forming an angle of approximately 60° with the longitudinal axis of the appendage. Species at this stage are *P. colombianus* (Rathbun, 1893), *P. exillipes* (Rathbun, 1898), *P. kuna* Campos & Lemaitre, 1999, and *P. tristani* (Rathbun, 1896).

Stage II (Fig. 2B, G).—Lateral lobe deeply notched as in some species of stage I, but he distal portion is more advanced and joins the caudal side of the apical peduncle. The field of spines approaches the lateral lobe and is directed laterally, with its long axis forming an angle of approximately 180° with the longitudinal axis of the appendage. Species at this stage are *P. micracanthus* Rodríguez, 1994, *P. montanus* (Rathbun, 1898), and *P. tumimanus* (Rathbun, 1898).

Stage III (Fig. 2C, H).—Lateral lobe as in stage II, but the distal portion is cupped, and its border is continuous with the caudal margin of the apical peduncle. The field of spines faces the lateral side, and its long axis forms an angle of approximately 230° with the longitudinal axis of the appendage. The only species at this stage is *P. barbillaensis.*

Stage IV (Fig. 2D, I).—The lateral lobe has the proximal segment strongly reduced, the distal one very advanced and forms, together with the border of the field of spines, a channel-like receptacle which is wide open. The field of spines is directed laterally, its long axis forming an angle of approximately 180° with the longitudinal axis of the appendage. The only species at this stage is *P. cocleensis* Pretzmann, 1965.

Stage V (Fig. 2E, J).—The lateral lobe is reduced to a distal segment, very advanced and forms, together with the border of the field of spines, an almost closed channel-like receptacle. The field of spines is directed laterally, its long axis forming an angle of approximately 180° with the longitudinal axis of appendage. The only species

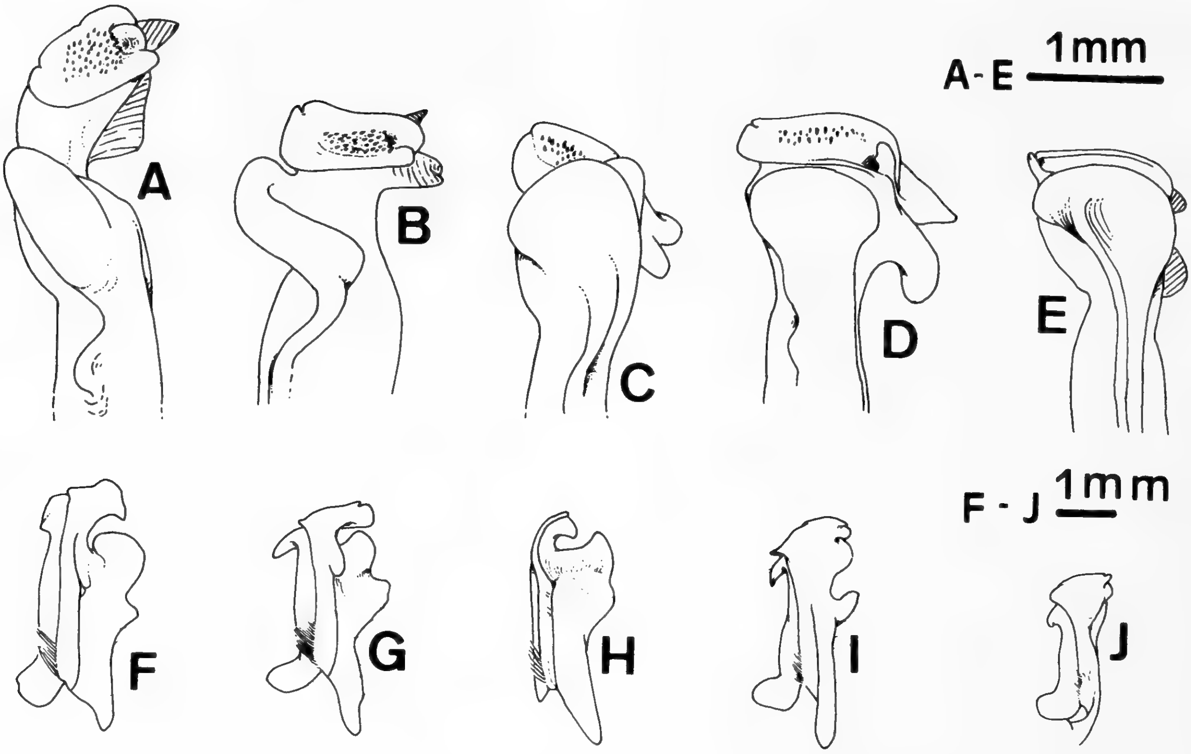

Fig. 2. First left gonopod of *Ptychophallus* species: A, F, *P. tristani* (Rathbun, 1896), male from ~1.8 km E Atenas, San José Province, Costa Rica (TU 4436); B, G, *P. montanus* (Rathbun, 1898), male from ~3 km N San Jerónimo de Moravia, San José Province, Costa Rica (TU 4442); C, H, *P. barbillaensis,* new species, holotype from Río Caño Seco, Costa Rica (IVIC 1073); D, I, *P. cocleensis* Pretzmann, 1965, holotype from Rio Coclé del Norte, Panama (USNM 119869); E, J, *P. goldmanni* Pretzmann, 1965, holotype from Cana, Panama (USNM 54044); A–E, detail of apex, lateral view: F–J, total view, caudal.

at this stage is *P. goldmanni* Pretzmann, 1965.

A similar morphocline, although not leading to the formation of a structure for the retention of the spermatophore, has been observed in the lateral lobe of species of the genera *Pseudothelphusa* Saussure, 1857, and *Tehuana* Rodríguez & Smalley, 1969, in southern Mexico (Rodríguez 1986). In this case the morphocline follows a general westward direction, suggesting an allopatric speciation of primitive demes, encompassing a migration along the same geographical axis. In the case of *Ptychophallus* the pattern is more complex. Species of stages I and II overlap their areas of distribution in Costa Rica, and the areas of *P. kuna* (stage I) and *P. micracanthus* (stage II) are relatively close in Central Panama (see map in Campos & Lemaitre 1999). The area of *P. barbillaensis* (stage III) is nested among the species of stages I and II. *P. cocleensis* (Stage IV) is found in Central Panama, and *P. goldmanni* (Stage IV) further East, near the Colombian border. Notwithstanding this complex pattern, the general trend of the morphocline is eastward. This direction contrasts with the supposed radiation of the family, that proceeded westward from an ancestral area in northern Colombia (Rodríguez 1986).

Two species of *Ptychophallus* cannot be placed in this morphocline. *P. lavallensis* Pretzmann, 1978, has a field of spines strongly upturned cephalically and a very wide undivided lateral lobe that does not approach the field of spines. *P. paraxanthusi* Bott, 1968, has a field of spines bent mesially and a wide, shallow-notched, lateral lobe that displays distally several ridges but does not form a receptacle. These species possibly represent phyletic lines that differ both among themselves, as with those species in the morphocline described above.

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Acanthilia, a new genus of leucosioid crabs (Crustacea: Brachyura) from the Atlantic coast of the Americas

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Abstract.—A new monotypic leucosioid genus, *Acanthilia,* is established from the Atlantic coast of the Americas, for one species of the genus *Iliacantha* Stimpson, *I. intermedia* Miers. The new genus differs from *Iliacantha* in its tridentate anterior margin of the efferent branchial channel, the shorter cheliped fingers, the glabrous pereiopodal dactyls, the convex margins of the sixth abdominal segment in the male, and the claw-tipped first male pleopod.

As part of an on-going study of leucosioidean crabs, the leucosioids of the Atlantic coast of the Americas at the National Museum of Natural History, Smithsonian Institution (USNM), were examined. An investigation of *Iliacantha* Stimpson, 1871, showed that *I. intermedia* Miers, 1886, differs from the five other members of the genus in its tridentate anterior margin of the efferent channel, the shorter cheliped fingers, the glabrous pereiopodal dactyls, the convex margins of the sixth abdominal segment in the male, and the claw-tipped male pleopod. *I. intermedia* was removed from the genus *Iliacantha* and placed in a new genus herein established.

Acanthilia, new genus

Diagnosis.—Carapace subovate, globose; regions indistinct. Front narrow, prominent, bilobed. Basal antennular segment forming an operculum, partially sealing antennular aperture. Antennular fossa not separated from orbit. Orbital margin with 3 sutures, basal antennal segment inserted in orbital hiatus proximally on ventral margin. Postorbital region concave. Third maxillipeds fitting closely, sealing buccal cavity, efferent branchial channel. Inner surface of 3 maxilliped exognath glabrous. Anterior margin of efferent branchial channel produced, tridentate, contiguous with lower orbital margin.

Anterolateral margin of carapace medially concave, posterolateral margin uniformly curved. Posterior margin of carapace bidentate. Spine on posterior intestinal region upcurved, projecting beyond posterior denticles. Abdominal sulcus in male deep, nearly reaching buccal cavity.

Chelipeds long; merus subcylindrical; propodus swollen basally; fingers half as long as propodus, opening vertically. Pereiopods short, dactyls triqueterous, longer than propodi, glabrous.

Male abdomen with segments 3–5 fused, tapering distally, basio-lateral regions of fused segments somewhat inflated; lateral margins of segment 6 convex. Female abdomen with segments 4–6 fused, greatly swollen.

Male first pleopod stout, tip claw-shaped; second pleopod short, distally scoop-like.

Type species.—*Iliacantha intermedia* Miers, 1886.

Etymology.—*Acanthilia* is an anagram of *Iliacantha* Stimpson, 1871.

Remarks.—Stimpson (1871) erected the genus *Iliacantha* for two species, *I. subglobosa* and *I. sparsa,* collected off Florida, and characterized by three posterior spines,

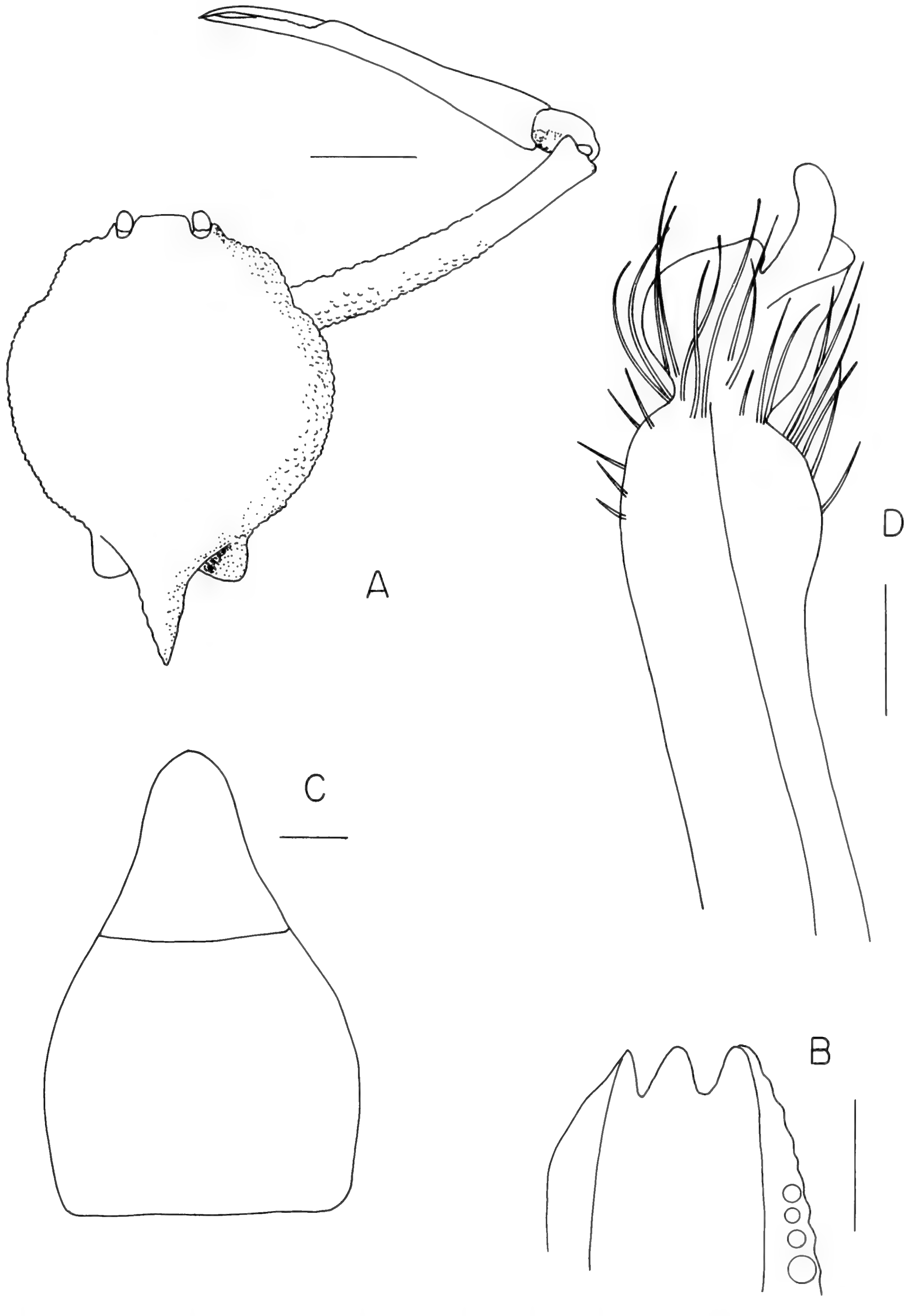

Fig. 1. *Acanthilia intermedia* (Miers, 1886).—♂ (USNM 274840). A, carapace and right cheliped, dorsal view; B, anterior margin of efferent branchial channel; C, sixth abdominal segment and telson, ventral view; D, tip of first pleopod, ventral view. A, 5 mm; B,C,D, 0.1 mm.

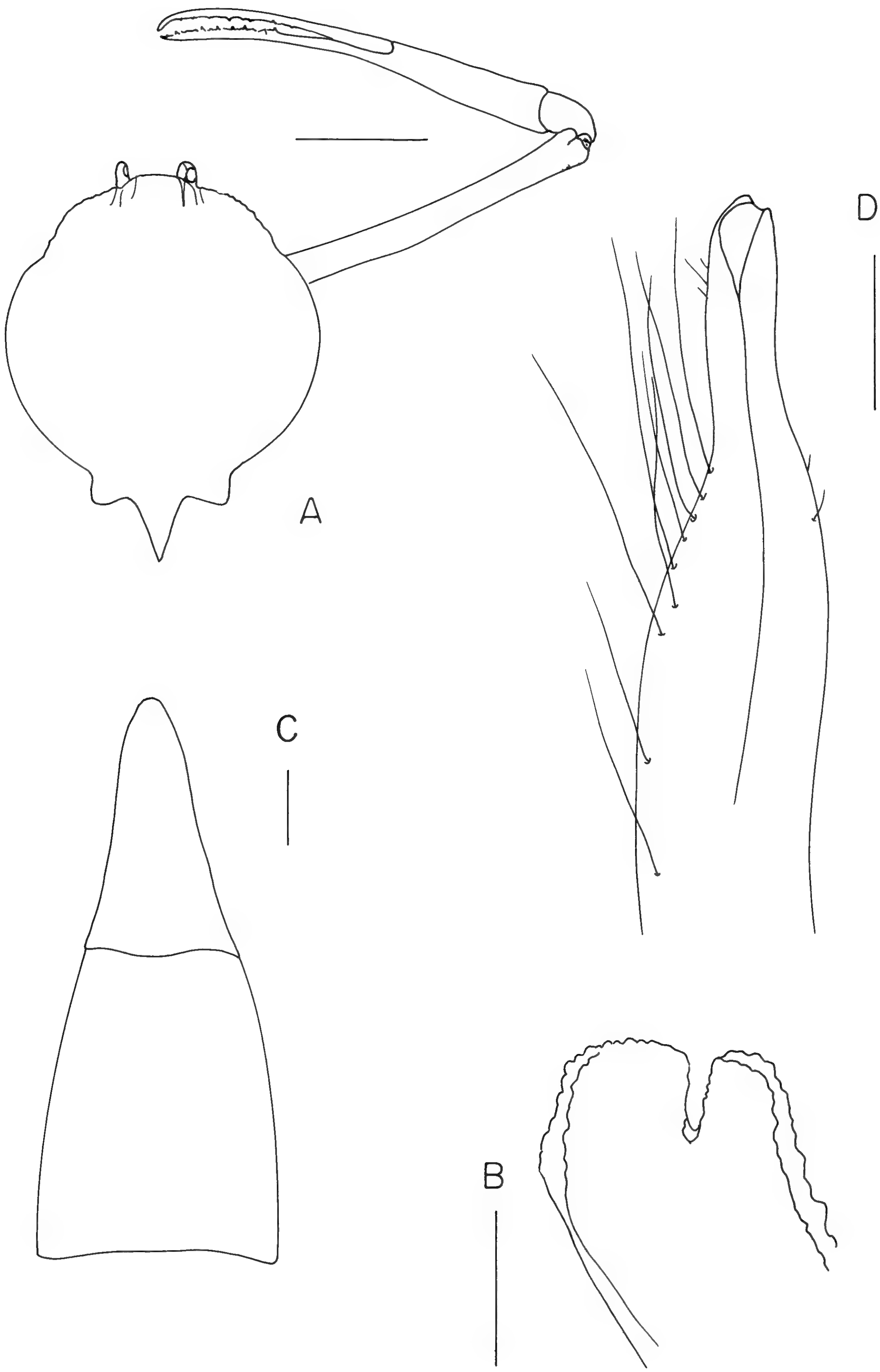

Fig. 2. *Iliacantha subglobosa.*—♂ (USNM 274724). A, carapace and right cheliped, dorsal view; B, anterior margin of efferent branchial channel, ventral view; C, sixth abdominal segment and telson, ventral view; D, tip of first pleopod, ventral view. A, 5 mm; B,C,D, 0.1 mm.

cheliped fingers opening vertically, and projecting pterygostomian channels. When describing *I. intermedia,* Miers (1886:302) noted it differed from Stimpson's species in the "length of the dactyli of the chelipeds".

Acanthilia, new genus, is easily distinguished from *Iliacantha* by the tridentate margin of the efferent branchial channel (Fig. 1B), the cheliped fingers half as long as the propodus (Fig. 1A), the glabrous pereiopodal dactyls, the convex margins of the male abdominal segment 6 (Fig. 1C), and the claw-tipped first male pleopod (Fig. 1D); whereas in *Iliacantha* the margin of efferent channel is bilobate (Fig. 2B), the cheliped fingers are longer than the propodus (Fig. 2A), pereiopodal dactyls are setose, margins of the male abdominal segment 6 are straight (Fig. 2C), and the first male pleopod is distally tapering, simple (Fig. 2D).

Acanthilia intermedia (Miers, 1886)
Fig. 1

Iliacantha intermedia Miers, 1886:302, pl. 26, fig. 3.—Hay & Shore, 1918:424, pl. 32, figs. 3, 3a.—Rathbun, 1937:186, pl. 54, figs. 1, 2.—Williams, 1965:151, fig. 129; 1984:290, fig. 225.—Coelho, 1970: 234.—Coelho & Ramos, 1972:184.—Fausto-Filho, 1975:81; 1979:51.—Gómez & Ortiz, 1976:8.—Powers, 1977: 37.—Coelho & Torres, 1980:72.—Rodrigues, 1980:259.—Takeda, 1983: 118.—Keith, 1985:254, fig. 2f.—Abele & Kim, 1986:42, fig. 485 b.—Taissoun, 1988:126.—Werding & Müller, 1990: 412, figs. 7a–c.—de Melo, 1996:159, fig.—de Melo et al., 1998:450.

Iliacantha liodactylus Takeda, 1983:119, fig.

Material examined.—United States. North Carolina, 33°20'N, 77°46'W, 25 m, 16 Aug 1977, 2 ♂♂ 15.8, 20.0 mm, ♀ juv. 12.2 mm (USNM 174250).—Georgia, 31°41.12'N, 80°20.48'W, 28 m, 30 Jan 1980, ♂ 21.6 mm (USNM 214909).—Sapelo Is., 22 m, 5 Mar 1963, coll. M. Gray, ♂ 22.5 mm (USNM 155484).—Florida, 25°45.56'N, 82°09.21'W, 19.6 m, 28 Apr 1981, coll. R. Lemaitre, ovigerous ♀ 25.1 mm (USNM 242750).

Redescription.—Dorsal surface of carapace granulate, front minutely shagreened. Fronto-orbital margin half as wide as posterior margin, slightly concave. Anterolateral margin set with prominent pearliform granules, subhepatic margin somewhat inflated. Posterior margin bearing pair of dorso-ventrally flattened triangular denticles laterally, pearliform granules medially. Intestinal spine prominent, granulate, upcurved.

Anterior margin of efferent branchial channel prominently tridentate, advanced beyond orbital margin. Third maxilliped bearing fungiform granules, crowded anteriorly, female ischium longitudinally traversed by row of setae.

Cheliped merus granulose, granules larger proximally; carpus and propodus smooth, fingers costate. Pereiopodal meri minutely granulate, upper margin of propodi prominently costate, dactyli styliform.

Thoracic sternites closely granulate. Male abdomen minutely granulate, fused segments of female abdomen smooth except for granulate basal margin. Male first pleopod slightly sinuous, dorso-ventrally flattened, subapically setose; cornute tip bearing subquadrate plate proximally, claw-like appendix distally.

Color.—"gray, without markings of any kind" (Hay & Shore 1918:424), "Amarillo crema o gris con puntos pequeños dispersos de color marrón claro" (Taissoun 1988: 126).

Remarks.—The color plates of *I. intermedia* and *I. liodactylus* (Takeda, 1983:118, 119) were erroneously exchanged.

Distribution.—North Carolina to Brazil; 10–329 m.

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Cambarus (*Cambarus*) *davidi*, a new species of crayfish (Decapoda: Cambaridae) from North Carolina

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Abstract.—*Cambarus* (*Cambarus*) *davidi* is a new species of crayfish from the eastern Piedmont Plateau of North Carolina, where it is restricted to intermittent streams, seepage areas, springs, and burrows. Although the ranges of the two species appear to be broadly disjunct, *C.* (*C.*) *davidi* is most closely related to the ecologically more tolerant *Cambarus* (*C.*) *bartonii* (s.l.), and especially resembles some members of the controversial subspecies *C.* (*C.*) *b. cavatus*. *Cambarus* (*C.*) *davidi* is distinguished by a suite of characters that includes a vaulted carapace; a deeply excavate, ladlelike rostrum; a very narrow, sparsely punctate areola; and an obtuse to nearly obsolete suborbital angle that almost always bears a small tubercle.

On 18 August 1993, David G. Cooper collected several specimens of a *Cambarus* from under large rocks in a shallow, intermittent tributary of the Neuse River, Wake County, North Carolina. In the field they appeared to be aberrant individuals of the burrowing species, *Cambarus* (*Depressicambarus*) *reduncus* Hobbs, 1956, which is not uncommon in such habitats in the upper Neuse River watershed. In the laboratory, however, I was surprised to discover that the specimens belonged to the subgenus *Cambarus,* and to some species previously unknown from the Neuse River basin, whose crayfish fauna is well documented (Cooper & Ashton 1985, Cooper & Braswell 1995, Cooper & Cooper 1995). Since that time, many additional specimens from the Neuse and Cape Fear river basins have either been collected or have been recognized in prior collections. They belong to an undescribed species of *Cambarus* that seems to have its closest affinities with congeners that occur in the Tennessee and Ohio river drainages.

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

Cambarus (*Cambarus*) *davidi,*
new species
Fig. 1, Table 1

Diagnosis.—Body and eyes pigmented, eye small ($\bar{X}$ adult diam 1.7 mm, $n = 30$). Carapace vaulted, thoracic section averaging 1.3 times wider than deep ($n = 52$). Rostrum acarinate; margins elevated, subparallel, caudally thickened, strongly to moderately constricted at base of acumen, lacking marginal spines or tubercles; floor (dorsal surface) of rostrum deeply concave, ladlelike; acumen 24.5 to 49.1% ($\bar{X} = 33.6\%$, $n = 52$) length of rostrum, latter 13.0 to 19.3% ($\bar{X} = 16.2\%$, $n = 52$) of TCL. Areola 5.2 to 14.5 ($\bar{X} = 8.1$, $n = 76$) times longer than wide, constituting 35.4 to

41.8% ($\bar{X}$ = 37.6%, *n* = 76) of TCL and 42.2 to 47.3% ($\bar{X}$ = 44.1%, *n* = 45) of PCL; areola sparsely punctate, with 2 (*n* = 22) to 3 (*n* = 64) punctations across narrowest part. Cervical spines reduced to multiple tubercles. Branchiostegal spine reduced to small tubercle; hepatic and surrounding regions of carapace crowded with tubercles. Suborbital angle obtuse to nearly obsolete, almost always bearing small tubercle; postorbital ridge short, cephalic margin rounded and usually devoid of tubercle. Antennal scale 2.0 to 3.6 ($\bar{X}$ = 2.5, *n* = 50) times as long as broad, widest just distal to midlength, lateral margin thickened and with long distal spine.

Palm of chela of cheliped 1.5 to 1.8 ($\bar{X}$ = 1.6, *n* = 51) times wider than deep, width 1.3 to 1.7 ($\bar{X}$ = 1.5, *n* = 51) times length of mesial margin; dorsolateral margin costate distally, without impression; mesial margin of palm with 2, rarely 3, rows of tubercles: mesial row of 6 to 8 (usually 7) large, generally adpressed tubercles, subtended dorsally by row of 1 to 5 (usually 4 or 5) smaller tubercles. Fixed finger of chela costate laterally, with well defined longitudinal ridges dorsally and ventrally; opposable surface of finger with row of 4 to 11 (usually 5 or 6) tubercles in addition to subconical tubercle; dactyl 1.7 to 2.6 ($\bar{X}$ = 2.0, *n* = 51) times as long as mesial margin of palm, with strong longitudinal ridge dorsally, weaker ridge ventrally; mesial margin with prominent tubercles; opposable surface with row of 6 to 14 (usually 7 to 9) tubercles. Carpus of cheliped generally lacking dorsomesial tubercles; merus with prominent multiple dorsodistal tubercles and often row of small squamous tubercles along dorsal ridge.

Hook on ischium of third pereiopod of males, that of form I male (Fig. 1K) uniramous, overreaching basioischial articulation and opposed by tubercle on basis; coxa of fourth pereiopod of males with vertically disposed, caudomesial boss.

In situ gonopods (Fig. 1G) symmetrical, with abutted or slightly separated, tubercle-like proximomesial apophyses; proximolateral portion of gonopod set off from rest of shaft by weak groove; in lateral aspect (Fig. 1B), central projection curved over 90° to plane of shaft, untapered, with proximally directed subapical notch; mesial process inflated, symmetrically tapered, slightly constricted at base of caudal third, with subacute, caudally directed apex extending slightly farther caudally than apex of central projection; caudal process reduced to swelling at caudodistal margin of shaft; in mesial aspect (Fig. 1C), distal portion of gonopod with essentially flat surface, few setae at midlength.

Annulus ventralis of allotypic female (Fig. 1H) 1.3 times broader than long, generally symmetrical and subrhomboidal; cephalic margin convex and fused to sternum, caudal margin subangular, free and capable of slight movement; cephalic half of annulus depressed, sloping, with narrow median trough, flanked each side by low, poorly defined ridge; ridges diverging caudally, sinistral ridge continuing obliquely and terminating before joining caudosinistral wall, dextral ridge curving caudodextrally to merge with upper arm of heavy, C-shaped caudodextral wall; transverse tongue prominent, originating from sinistral wall near caudal midline, continuing cephalically and slightly obliquely before turning dextrally and plunging into fossa beneath dextral wall; sinus dissecting caudal wall near midline.

Measurements of type specimens provided in Table 1.

Description of holotypic male, form I.—Body and eyes pigmented, eye 1.8 mm diam. Cephalothorax (Fig. 1A, D) subcylindrical, thoracic section 1.2 times wider than deep. Areola 9.2 times longer than wide, constituting 39.3% of TCL (45.1% of PCL), sparsely punctate, with 3 punctations across narrowest part. Rostrum acarinate, with slightly thickened caudal margins moderately converging to base of acumen, where moderately constricted; margins of acumen slightly concave and converging to

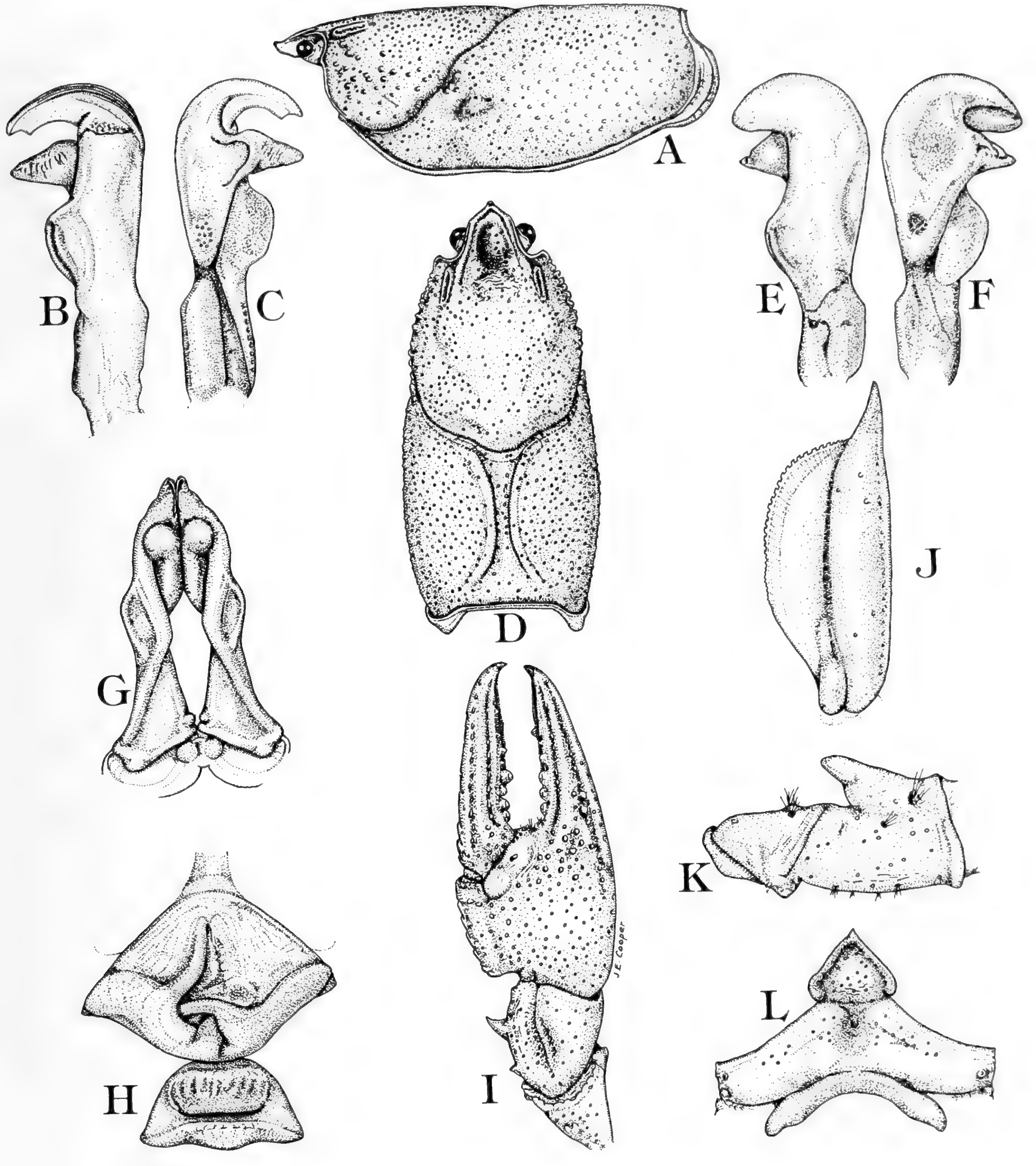

Fig. 1. *Cambarus* (*Cambarus*) *davidi,* new species (all from holotypic male, form I, except E, F, from morphotypic male, form II, and H, from allotypic female): A, lateral aspect of carapace; B, E, lateral aspect of gonopod (first pleopod); C, F, mesial aspect of gonopod; D, dorsal aspect of carapace; G, caudal aspect of in situ gonopods; H, annulus ventralis and postannular sclerite; I, dorsal aspect of distal podomeres of right cheliped; J, antennal scale; K, hook on ischium of third pereiopod; L, epistome.

dorsally directed apical tubercle, which reaching just beyond midlength of penultimate podomere of antennular peduncle; acumen comprising 30.2% of rostrum length, latter constituting 14.2% of TCL; floor of rostrum excavate, ladlelike, moderately punctate, and ascending caudally into broad dorsomedian depression of carapace; subrostral ridge strong, visible to base of acumen in dorsal aspect.

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

	Holotypic male	Allotypic female	Morphotypic male
Carapace			
Total length	30.3	36.5	30.7
Postorbital length	26.4	31.6	26.6
Length cephalic section	18.4	22.4	19.0
Width	15.7	18.4	15.3
Depth	12.6	15.1	12.2
Length rostrum	4.3	5.6	4.9
Length acumen	1.3	2.2	1.2
Length areola	11.9	14.1	11.7
Width areola	1.3	2.1	1.9
Antennal scale			
Length	4.5	5.4	5.2
Width	1.8	2.1	1.8
Abdomen			
Length	29.6	37.7	30.6
Width	13.6	16.4	12.2
Cheliped			
Length lateral margin chela	24.4	26.7	23.8
Length mesial margin palm	7.3	8.8	7.5
Width palm	11.5	13.4	11.1
Depth palm	6.8	7.8	6.7
Length dactyl	15.5	16.3	15.2
Length carpus	10.0	11.1	9.5
Width carpus	7.2	8.0	6.7
Length dorsal margin merus	12.0	13.8	12.2
Depth merus	7.1	8.5	6.9
Gondopod length	8.4	N/A	8.0

Postorbital ridge strong, groove essentially lateral, cephalic margin with vestigial tubercle. Branchiostegal spine reduced to tubercle; suborbital angle obtuse, without tubercle. Thoracic section of carapace dorsally and dorsolaterally punctate, laterally with large, scattered granules; cephalic section 1.5 times longer than areola and constituting 60.7% of TCL, laterally crowded with large tubercles and with row of small tubercles along ventral margin of cephalic section of cervical groove; gastric region mostly glabrous. Cervical spine region on right with 4 large and 3 smaller tubercles (2 large and 2 smaller on left). Abdomen slightly narrower and shorter than cephalothorax. Proximal podomere of uropod without spine or tubercle on lateral lobe, with prominent caudomedian spine on mesial lobe; mesial ramus of uropod with median keel bearing strong caudal spine, tip of which reaching caudal margin of ramus, caudolateral margin with small spine; lateral ramus with submedian keel bearing terminal spine at transverse flexure, latter with total of 17 fixed spines along margin and 1 long, movable sublateral spine. Telson with 1 long stationary and 1 long articulated spine in each caudolateral corner of cephalic section; caudal margin domelike.

Epistome (Fig. 1L) with symmetrical, subtriangular cephalic lobe bearing short cephalomedian projection; margins of lobe uninterrupted, moderately thickened, lateral apices thicker than rest; floor (ventral surface) of lobe punctate and slightly convex, concave along lateral margins; transverse basal sulcus complete; central depression of body broad, moderately deep, with cephalomedian fovea; lamellae punctate, lateral margins subtruncate, with 2 large subacute tubercles and 1 small rounded tubercle in right caudolateral corner (1 large subacute and 1 small rounded tubercle on left); zygoma moderately arched, pits elongate. Antennal peduncle with small cephalolateral tubercle on basis, small ventral tubercle on ischium; antennular peduncle with small, laterally displaced subdistal spine on ventral surface of basal podomere. Antennal scale (Fig. 1J) 2.5 times longer than wide, broadest just distal to midlength; lateral margin thickened, terminating in long distal spine, tip of which reaching distal margin of penultimate podomere of antennular peduncle; lamella ca. 1.3 times as wide as thickened lateral margin; distal margin of lamella subtransverse for most of width, then sloping to widest point; mesial margin subparallel to lateral margin for most of length.

Third maxilliped with tip of endopodite reaching about midlength of penultimate podomere of antennal peduncle; exopodite hirsute, tip reaching base of distal two-thirds of merus of endopodite; cephalolateral corner of ischium slightly produced, not spinelike; ventrolateral ridge flanked mesially by row of punctations bearing moderately long setae; lateral half of ischium with punctations bearing short setae, punctations most abundant on proximal third; mesial half with long stiff setae largely obscuring mesial margin, latter with 27 denticles on right. Right mandible with incisor ridge bearing 7 denticles (6 on left).

Right chela (Fig. 1I) 2.1 times longer than wide; palm 1.7 times broader than deep, width 1.6 times length of mesial margin; latter 29.9% of chela length, 47.1% of dactyl length. Dorsal surface of palm punctate; distolateral margin of palm and lateral margin of fixed finger costate, area at juncture of palm and finger with aggregation of large punctations creating slight impression; lateral margin of palm rounded and with row of large punctations. Ventral surface of palm less punctate than dorsal, distolateral area with moderate depression and aggregation of large punctations; lateral eminence of articular ridge with distal tubercle, none proximal to ridge. Mesial margin of right palm with mesial row of 7 adpressed tubercles, proximal 3 of which with elevated distal margins (same on left), mesial row subtended dorsally by row of 4 smaller tubercles (5 on left) and ventrally by 1 small, squamous distal tubercle (3 on left).

Fingers gaping in proximal three-fourths of length, greatest width of gape about four-fifths width of base of fixed finger; opposable base of fixed finger with tuft of short setae; both fingers slightly curved distoventrally in lateral aspect, dactyl very slightly bowed in dorsal aspect. Mesial margin of right dactyl bearing row of 4 prominent and 4 weaker tubercles on proximal half, distal half of margin punctate; dorsal surface of dactyl with low, rounded longitudinal ridge, flanked mesially by punctate groove, laterally by row of large, spaced punctations; ventral surface with similar longitudinal ridge; opposable surface with 8 tubercles, fourth from base very large and slightly displaced ventrally (7 tubercles on left, third from base largest); denticles in 2 or 3 rows from near tip of finger to sixth tubercle from base, single row from there. Fixed finger with very strong dorsomedian ridge flanked mesially by deep punctate groove and second narrower ridge, laterally by deep punctate groove; lateral margin with irregular row of large punctations; ventral surface with very strong longitudinal ridge, flanked both sides by row of large punctations; opposable margin with subconical tubercle ventral to denticles at base of distal third of finger, and 5 tubercles proximal to subconical one, third from base more prominent than others (4 tubercles on left finger, third from base very large); denticles in 2 or 3 rows from tip of finger to subconical tubercle, single row from there.

Carpus (Fig. 1I) 1.4 times as long as wide, 1.4 times as long as mesial margin of palm; carpus dorsally with long, deep, slightly oblique sulcus, lateral and mesial to which surface punctate; mesial margin with large distal spine and prominent proximal tubercle; ventral surface with stout, rounded tubercle at lateral articular condyle, similar distomedian tubercle, and 1 small tubercle proximomesial to latter. Right merus 1.7 times longer than deep; dorsal surface with 3 prominent and 2 smaller subdistal tubercles (2 prominent and 1 smaller on left), and small squamous tubercles along much of dorsomedian ridge; ventrolateral ridge with 2 small acute tubercles and 1 minuscule tubercle near articular condyle (1 small acute tubercle and minuscule distal tubercle on left); ventromesial ridge with 10 spiniform tubercles, distalmost one somewhat larger than others; ischium with 3 small ventral tubercles (4 on left).

Palm and fingers of chela of second pereiopod hirsute. Ventral margins of pleura subtruncate or slightly rounded, caudoventral corners slightly angular, caudal margins rounded; terga very punctate, except articular cephalic portions glabrous. Sternites between third and fourth coxae with very dense, matted setae, covering distal ends of in situ gonopods.

Gonopods (Fig. 1B, C, G) as described in "Diagnosis." Length of gonopod 27.7% of TCL (31.8% of PCL).

Description of allotypic female.—Except for secondary sexual characters, differing from holotypic male in following respects: Areola 6.7 times wider than long, constituting 38.6% of TCL (44.6% of PCL). Acumen comprising 39.3% of rostrum length, latter constituting 15.3% of TCL. Suborbital angle nearly obsolete, with small tubercle. Cervical spine region on both sides of carapace with 3 prominent tubercles, largest of those on right side subacute. Caudolateral corner of cephalic section of telson with 2 spines on right, 3 on left. Cephalic lobe of epistome subcordiform; lamellae with single tubercle each caudolateral corner; zygoma strongly arched. Antennal peduncle lacking tubercle on basis; antennal scale 2.6 times longer than wide, lamella about 1.5 times as wide as thickened lateral margin. Incisor ridge of right mandible bearing 8 denticles. Right chela 2.0 times longer than wide, palm length 33.0% of chela length, 54.0% of dactyl length. Opposable surface of right dactyl with 10 tubercles (9 on left); opposable surface of both fixed fingers with 6 tubercles in addition to subconical one, fourth from base largest. Carpus of cheliped 1.3 times as long as mesial margin of palm; merus 1.6 times longer than deep, dorsal surface with 2 prominent and 2 smaller subdistal tubercles (same on left); ventrolateral ridge with 5 small tubercles (same on left), ventromesial ridge with 8 spiniform tubercles (9 on left).

Annulus ventralis (Fig. 1H) as described in "Diagnosis." In addition, first pleopods short, reaching caudal margin of annulus when abdomen flexed; annulus about 3 times wider than postannular sclerite, which elongate, ventrally domed, punctate.

Description of morphotypic male, form II.—Differing from holotypic male in following respects: Thoracic section of carapace 1.3 times wider than deep. Areola 6.2 times as long as wide, constituting 38.1% of TCL (44.0% of PCL). Margins of rostrum less constricted at base of acumen, converging at ca. 45°, acumen comprising 24.5% of rostrum length, latter constituting 16.0% of TCL. Suborbital angle obtuse and with very small tubercle. Cephalic section of carapace 1.6 times longer than areola and constituting 61.9% of TCL. Cervical region on both sides of carapace with 3 prominent and 1 moderate tubercle, ventralmost of which on right side subacute. Transverse flexure of lateral ramus of right uropod with 16 spines in addition to sublateral one. Lateral corners of lamellae of epistome with 1 moderate tubercle on right, 2 on left; zygoma strongly arched. Antennal scale 2.9 times wider than long, lamella ca. 1.5 times width of thickened lateral margin, distal margin moderately declivous. Length of palm of cheliped 31.5% of chela length, 49.3% of dactyl length. Mesial margin of palm with mesial row of 6 adpressed tubercles, subtended dorsally on right palm by row of 3 moderate tubercles (4 on left) and ventrally by 4 small squamous tubercles (2 on left). Opposable surface of dactyl with 9 tubercles on right, 8 on left, basalmost largest. Opposable surface of fixed finger with 6 tubercles on right in addition to subconical one, 7 on left, third from base largest. Carpus 1.3 times as long as palm. Merus 1.8 times longer than deep; dorsal surface of right merus with patch of 5 prominent subdistal tubercles and 5 smaller tubercles proximal to them (2 moderate and 6 smaller on left); ventrolateral ridge on right with 2 subacute and 2 other tubercles (2 small, and 1 minuscule articular tubercle, on left); ventromesial ridge on right with 10 small tubercles (9 on left).

Hook on ischium of third pereiopod weak, not overreaching basioischial articulation, opposed by tubercle on basis; boss on coxa of fourth pereiopod moderately developed.

Gonopod (Fig. 1E, F) length 26.1% of TCL. In situ gonopods with weak, separated proximomesial apophyses; mesial process noncorneous, bulbous, distal surface creased near extruded tip; in lateral aspect, gonopod with weak juvenile suture; central projection noncorneous, curved 90° to shaft, tapered to subacute tip; mesial process tapered, triangular in outline, tip directed caudally and inclined slightly distolaterally. Setae on sternites between third and fourth coxae not dense.

Color notes.—Adult ground color usually dark olivaceous, sometimes light brown with orange or tan overtones. Cephalic section of carapace often lighter in color than thoracic section. Hepatic region with orangish midlateral streak just cephalic to cervical groove. Margins of rostrum outlined in tan; antennal scale pale orangish-tan with dark lateral margin, antennal flagellae green. Most tubercles, spines, and granules of carapace and chelipeds tan to orangish. Dorsal surface of cheliped greenish or olivaceous; articular ridges of chela pinkish or orangish, ventral surface of chela pale grayish-tan. Lateral surface of entire propodus (palm and fixed finger) strikingly colored, varying from pinkish-tan to creamy orange or yellow. Tips of fingers of chelipeds pale orange or orangish-tan, color not subtended by black band. Proximal podomeres of other pereiopods pale tan to light brown with darker mottling, distal podomeres greenish or bluish, fingers of chelae of second and third pereiopods pale blue. Cephaloventral structures bluish-gray, except epistomal zygoma almost white. Annulus ventralis usually pale, mottled with orange in one female.

Cephalicmost tergite of abdomen with transverse dark brown or black rectangular band. Lighter colored adults and all juveniles with dark, diagonal blotch each side of caudal margin of thoracic section of carapace, blotches extending onto dorsolateral surfaces of two adjacent tergites as short, curved markings. Series of short, dark bars producing interrupted dorsolateral stripe each side of abdomen. Other dorsal surfaces of abdomen with scattered dark spotting. Ventrolateral pleura of abdomen with pale pink cephalic area and narrow oblique or V-shaped black bar dorsal to it, series of these bars producing zigzag lateral stripe each side of abdomen. Juveniles generally paler than adults, color patterns in most respects similar but more vivid.

Type locality.—North Carolina, Wake County, small intermittent stream entering cove along western shore of Falls Lake (impoundment of Neuse River), ca. 1.4 air km NW of western end of NC 98 bridge & ca. 2.6 air km W of Stony Hill (Bayleaf 7.5′ USGS quadrangle, UTM zone 17, 3984850/712190).

The shallow stream, which lies at the bottom of a steep ravine in a hardwood forest, is seasonally intermittent and has a maximum width of about 1.2 m. All specimens from this locality were found in the mud of shallow residual pools under large rocks when water levels were very low.

Disposition of types.—The holotypic male, allotypic female, and morphotypic male are in the crustacean collection of the NCSM (catalogue numbers NCSM C-4413, C-4414, and C-2656, respectively), as are paratypes consisting of 2 ♂ I, 15 ♂ II, 6 j ♂, 18 ♀, and 5 j ♀.

Range and specimens examined.—Apparently limited to the upper Neuse and Cape Fear river basins in the eastern Piedmont Plateau of North Carolina. Voucher specimens (*n* = 107), all in the crustacean collection at NCSM (catalogue numbers in parentheses), have been collected at the following localities.

Neuse River Basin: Durham Co.; upper trib Little R near Durham, 1 ♂ II (C-4742), 13 Feb 1995, coll. T. Cuffney. Orange Co.; small intermittent stream in headwaters West Fork Eno R at SR 1358, 2.4 air km E of Carr, 3 j♀ (C-3425), 25 Jul 1995, coll. M.A. Hartman, M.E. Savacool. Wake Co.; seep entering small trib New Light Crk along SR 1918, 0.3 km SW of jct SR 1909, ca. 7.4 air km NNE of Bayleaf, 2 j♂ (C-44), 18 Feb 1976, coll. A.L. Braswell (ALB), N. Murdock; type locality, 1 ♂ II (C-2656), 1 j♂ (C-2657), 4 Jul 1994, coll. D.G. Cooper (DGC), JEC, 1 j♂, 3 ♀ (C-2779), 1 j♀ (C-2780), 3 j♂ (C-2781), 18

Aug 1993, coll. DGC, JEC, 1 ♂ I (C-4413), 8 ♂ II, 6 j♂, 6 ♀, 7 j♀ (C-3795), 14 Jun 1997, coll. DGC, 1 ♀ (C-4553), 20 Jun 1998, coll. DGC; spring on small trib Lower Barton Crk between SR 1005 & SR 1844, SW of Bayleaf, 2 j♀ (C-3055), 6 Apr 1996, coll. S. Yirka, DGC, 1 j♂, 1 ♀, 2 j♀ (C-3293), 4 Jul 1996, coll. D. DeOliveira (DD), DGC; spring on S shore Lower Barton Crk, W of SR 1005, ca. 1.6 km NNW of center of Bayleaf, 1 ♂ II (C-3333), 11 Aug 1996, coll. DGC; small spring entering Falls Lake, ca. 0.8 km N of entrance of Lower Barton Crk into lake, 2 ♂ II, 1 ♀, 3 j♀ (C-5151), 11 Apr 1999, coll. DGC; "Raleigh," 2 ♀ (C-3143), 28 Nov 1924, coll. C.S. Brimley, W.B. Mabee; small intermittent stream entering lake at Schenck Forest, Raleigh, 1 ♂ II (C-3471), 25 Oct 1996, coll. DGC, 1 ♀ (C-3603), 4 Apr 1997, coll. DGC; small trib to Richland Crk near SW side of Reedy Creek Rd, Schenck Forest, Raleigh, 2 ♀ (C-5077), 10 Apr 1999, coll. DGC; small stream E of Jeffrey Dr off Lake Wheeler Rd, SE of Lake Wheeler, Raleigh, 3 ♀, 5 j♀ (C-3717), 20 May 1997, coll. DD, DGC, 1 ♂ II, 5 j♂, 4 j♀ (C-3766), 1 ♀ (C-4414), 24 May 1997, coll. DGC; Crabtree Crk below Duraleigh Rd, Raleigh, 1 j♀ (C-4591), 30 Aug 1998, coll. D.A. Jackan.

Cape Fear River Basin: Alamance Co.; spring on trib Toms Crk, Scott farm off SR 1612, 0.8 km NW of Union Ridge, 1 ♂ I, 1 ♀ in amplexus (C-45), 2 Mar 1976, coll. F.D. Scott (FDS); burrow at 403 Glen Raven Rd, Burlington, 1 ♂ II (C-3618), 25 Jun 1993, coll. C. McGrath (CM). Caswell Co.; Benton Branch between SR 1103 and 1105, S of SR 1100, ca. 1.9 air km SW of town of Stoneycreek, 1 ♂ II, 1 j♂, 1 ♀ (C-789), 14 May 1975, coll. FDS, JEC. Chatham Co.; small, intermittent upper trib New Hope Crk at SR 1716, 6.6 km NNE of jct US 64, ca. 10.4 air km ENE of center of Bynum, 1 j♂ (C-3026), 1 Apr 1986, coll. D.R. Lenat (DRL), T. MacPherson, 1 j♀ (C-3106), 15 Oct 1992, coll. CM, 1 j♀ (C-3748), 1 Feb 1993, coll. CM, 1 ♂ I (C-4464), 13 Feb 1998, coll. DRL, D. Penrose (DP); upper trib Robeson Crk at US 64, Pittsboro, 1 ♀ (C-4316), 6 Mar 1997, coll. DP. Harnett Co.; upper trib Kenneth Crk at SR 1447, NE of Rawls, 2 ♂ II, 1 j♂ (C-2963), 28 Aug 1991, coll. N. Medlin (NM), DP. Rockingham Co.; spring on small trib Benaja Crk, ca. 0.3 air km ESE of jct SR 2426 and 2427, 1 ♂ II, 1 j♂, 2 ♀, 2 j♀ (C-3104), 1 ♂ II (C-3105), 3 Jun 1976, coll. M.R. Cooper, JEC; drainage ditch in floodplain Haw R, Camp Guilrock, ca. 19.2 air km SE of Monroeton, 1 ♀ (C-4843), Mar 1998, coll. A.B. Somers & students; Little Troublesome Crk at SR 2600, ca. 1.1 air km W of Williamsburg, 1 ♀ (C-4912), 6 Apr 1998, coll. B. Tracy, NM, L. Eaton, DP.

Variations.—In addition to those addressed in the "Diagnosis," the following variations have been recorded. The margins of the rostrum are usually abruptly or at least moderately constricted at the base of the acumen, but in seven specimens the margins, while increasing in convergence, are not notably constricted. The number of prominent cervical tubercles varies from one to six (usually three to five), and in some specimens at least one of these tubercles is spiniform. In three individuals, the usual small tubercle on the suborbital angle is absent, and in several the angle itself is subacute. Nearly all specimens have a minuscule tubercle or very weak spine on both the basis and ischium of the antennal peduncle, but five lack a tubercle on the ischium and two lack a tubercle on the basis. The width of the lamella of the antennal scale ranges from approximately 1.1 to 2.0 ($\bar{X}$ = 1.4) times the width of the thickened lateral margin. The distal margin of the lamella is usually either subtransverse or moderately sloping for much of its width, but in three females it is strongly declivous from the base of the distolateral spine to the mesial margin.

Most individuals have two spines in each caudolateral corner of the cephalic section of the telson, but seven of them have two spines in one corner and three in the other, and two have two spines in one corner and one in the other. The lateral lobe of the proximal podomere of the uropod normally lacks a spine or tubercle, but 12 specimens have a very small spine or acute tubercle on this lobe. The spine on the mesial lobe of this podomere varies in size from very small to moderate, and is absent in one animal.

The chela of form I males is longer than that of mature form II males and females, averaging 81% of TCL. In form II males the average is 71.6% and in females it is 70.8%. The largest tubercle on the opposable surface of the fixed finger varies from the third to the fifth from the base, but in most specimens the fourth tubercle is much larger than the others. The largest tubercle on the comparable surface of the dactyl varies from the first to the fifth, but in most it is the fourth, and the largest tubercle is almost always offset toward the ventral surface. The dorsal surface of the merus bears from one to eight prominent subdistal tubercles, with the usual number being three or four. Most specimens have from two to four weaker tubercles just proximal to the more prominent ones, and many have squamous to subsquamous tubercles along at least part of the dorsal ridge. The number of tubercles on the ventrolateral ridge of the merus ranges from two to five (usually three), and the distalmost is very small or vestigial. The number of tubercles on the ventromesial ridge ranges from six to eleven (usually nine or ten), and the distalmost is seldom much larger than the largest of the others.

In 17 adult females the width of the annulus ranges from 1.2 to 1.8 ($\bar{X} = 1.5$) times its length, and the cephalomedian trough varies from moderately wide to nearly obliterated. The thick, C-shaped wall of the annulus, beneath which lies the deepest part of the fossa, is dextral in 22 females, sinistral in eight others.

The floor (dorsal surface) of the rostrum of juveniles and some subadults, while notably excavate, is often less ladlelike than it is in larger, mature animals. Also in these smaller individuals, the setae on the opposable surface of the fixed finger of the cheliped are far longer and more dense than they are in adults, often filling the space between the fingers and obscuring the tubercles on both.

Size.—The largest specimens collected are two females measuring 50.7 and 50.0 mm TCL (44.4 and 44.5 mm PCL), both from the Haw River subdrainage of the Cape Fear River basin. The next largest specimen is a form I male, which measures 42.5 mm TCL (37.3 mm PCL). The largest form II male measures 33.4 mm TCL (28.7 mm PCL).

Life history notes.—A form I male was collected at the type locality on 14 June 1997, one was taken in Chatham County on 13 February 1998, and one was found in amplexus with a female in Alamance County on 2 March 1976. No females with attached ova or young have yet been seen, but one measuring 32.5 mm TCL, taken on 4 April 1997, had all cement glands highly developed.

Crayfish associates.—Seldom have other crayfishes been found in the same habitats with *C.* (*C.*) *davidi.* At a few localities, however, a number of specimens of *Cambarus* (*Depressicambarus*) *latimanus* (LeConte, 1856), and of at least one of the species in the complex subsumed under *Cambarus* (*Puncticambarus*) *acuminatus* Faxon, 1884, have been found. At two sites, juvenile *C.* (*D.*) *reduncus* were collected. While juvenile *Cambarus* (*Lacunicambarus*) *diogenes* Girard, 1852, have been taken from under cover near the mouth of the stream at the type locality, and chimneyed burrows of this species may be seasonally abundant along the nearby shoreline of Falls Lake, this burrowing species has not been found with *C.* (*C.*) *davidi.*

Relationships.—It appears to me that *C.* (*C.*) *davidi* has its strongest affinities with *Cambarus* (*Cambarus*) *bartonii* (Fabricius, 1798). Students of American crayfishes, however, have long been cognizant of the taxonomic perplexities presented by the broadly distributed and highly variable populations currently assigned to this species. Two subspecies have been described, *Cambarus* (*Cambarus*) *bartonii cavatus* Hay, 1902, and *Cambarus* (*Cambarus*) *bartonii carinirostris* Hay, 1914, but opinions anent their validity have for years fluctuated (see Faxon 1914, Ortmann 1931, Hobbs 1972, 1989, Bouchard 1976, Thoma & Jezerinac 1982, Jezerinac 1985, Fitzpatrick 1983, Jezerinac & Thoma 1984, Jezerinac et al. 1995, Cooper 2000). The status of *C.* (*C.*) *b. cavatus* remains controversial, but *C.* (*C.*) *b. carinirostris* has been elevated to species status (Thoma & Jezerinac 1999). Although it is still difficult at this time to establish precise diagnostic parameters for these taxa throughout their ranges (whatever those ranges might be), current diagnoses must be used in assessing the relationships of *C.* (*C.*) *davidi.*

In his brief description of *C. b. cavatus,* whose type locality is the Powell River (Tennessee-Ohio river drainage) near Tazewell, Claiborne County, Tennessee, Hay (1902:435) emphasized its "deeply excavated rostrum," an areola that is "narrower and more thickly punctate than in *C. bartoni bartoni,*" and a carapace that is "more nearly cylindrical." Except for the "more thickly punctate" areola, a number of the characters displayed by *C.* (*C.*) *davidi* indicate a possible relationship with the progenitors of "topotypic" *C.* (*C.*) *b. cavatus,* although their similarities could just as well be a result of convergence. In Ohio and West Virginia, this putative subspecies apparently lacks the deeply excavate rostrum, and displays other characters that differ from those of the "typical" form (Jezerinac 1985, Jezerinac et al. 1995).

The combination of a narrow (but not obliterated), sparsely punctate areola, a ladlelike rostrum, and a vaulted, unflattened carapace will serve to separate *C.* (*C.*) *davidi* from all other members of the subgenus except some *C.* (*C.*) *b. cavatus,* and some upland southern populations currently assigned to *C.* (*C.*) *b. bartonii* (s.l.). *Cambarus* (*C.*) *davidi* differs from *C.* (*C.*) *b. cavatus* and most populations of *C.* (*C.*) *b. bartonii* (s.l.) in its obtuse to nearly obsolete suborbital angle, the shape of its antennal scale, and the presence of multiple tubercles on the dorsal surface of the merus of the cheliped. In some montane populations of *C.* (*C.*) *b. bartonii* (s.l.) the carapace is relatively vaulted and the rostrum is deeply excavate and somewhat ladlelike. These populations, however, characteristically have areolae that are broader and have more punctations across the narrowest part than does the areola of *C.* (*C.*) *davidi.* Also, in nearly all *C.* (*C.*) *bartonii* (s.l.) the lamella of the antennal scale is much narrower than it is in *C.* (*C.*) *davidi,* and its distal margin is usually quite declivous from the base of the lateral spine to the mesial margin. In addition, *C.* (*C.*) *bartonii* (s.l.) seldom displays prominent multiple tubercles on the dorsal surface of the merus.

Roger F. Thoma, whose knowledge of subgenus *Cambarus* is extensive, has suggested that a comparison of *C.* (*C.*) *davidi* with the burrower, *Cambarus* (*Cambarus*) *ortmanni* Williamson, 1907, would be useful. That species differs from *C.* (*C.*) *davidi* in many ways, including the following: Areola of *C.* (*C.*) *ortmanni* generally obliterated or nearly so, constituting 41.0 to 44.0% of TCL; suborbital angle obsolete and lacking tubercle; cephalothorax markedly longer than abdomen; subdistal spine on mesial margin of carpus of cheliped thick and knoblike rather than long and acute; cervical region of carapace lacking strong, multiple tubercles; ventrolateral ridge of merus of cheliped usually lacking tubercles; and annulus ventralis and form I male gonopod quite different in configuration.

Remarks.—Current evidence indicates that the range of *C.* (*C.*) *davidi,* limited to parts of the eastern Piedmont Plateau in two endemic North Carolina river basins, is disjunct from that of other members of the subgenus. The nearest known North Carolina populations of *C.* (*C.*) *bartonii* (s.l.) are in the mountains and eastern foothills. Whether or not *C.* (*C.*) *davidi* is indeed allopatric, however, will only be revealed by more extensive field work throughout the Piedmont Plateau. Specimens of subgenus *Cambarus* from seeps and burrows in the Dan River subdrainage of the Roanoke River basin resemble *C.* (*C.*) *davidi* in many respects, differ in others. The sample size of available adult specimens is far too small for accurate assignment of the Roanoke material at this time.

Cambarus (*C.*) *davidi* has yet to be found in the Tar-Pamlico River basin, whose crayfish fauna is as well known as that of the Neuse and is nearly identical (Cooper & Braswell 1995). Unfortunately, almost no sampling has been done in appropriate habitats within the Tar-Pamlico basin.

Etymology.—I take great pleasure in naming this species for my son, David George Cooper, an avid naturalist who brought the species to my attention and who spent many hours tromping in mud and muck to collect quite a few of the existing specimens.

Suggested vernacular name: Carolina ladle crayfish.

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Two new species of *Hyalella* (Crustacea: Amphipoda: Hyalellidae) from Death Valley National Park, California, U.S.A.

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Abstract.—Two new species *Hyalella* (*Hyalella*) *muerta* and *Hyalella* (*Hyalella*) *sandra* are described from Death Valley National Park, California. *Hyalella* (*H.*) *muerta,* the first North American hypogean hyalellid, is blind, lacks dorsal mucronations and antenna 1 is longer than antenna 2. *Hyalella* (*H.*) *sandra* collected from nearby epigean waters, also lacks dorsal mucronations, but has normal eye pigmentation and antenna 1 is shorter than antenna 2. Populations of both species rarely, if ever, coexist together in Death Valley National Park.

Five species in the genus *Hyalella* occur in the continental United States. These are *Hyalella* (*Hyalella*) *azteca* (Saussure, 1858); *Hyalella* (*Hyalella*) *inermis* Smith, 1874; *Hyalella* (*Hyalella*) *montezuma* Cole & Watkins, 1977; *Hyalella* (*Hyalella*) *texana* Stevenson & Peden, 1973; *Hyalella* (*Hyalella*) *longicornis* Bousfield, 1996. All are epigean species, have normal eye pigmentation and have antenna 1 shorter than antenna 2. Only *H.* (*H.*) *inermis* and *H.* (*H.*) *longicornis* lack dorsal mucronations.

Examination of recently collected material from Death Valley National Park, California clearly shows the presence of two new species of *Hyalella,* both of which are newly described in this paper.

In the figures, body parts are marked by the following abbreviations: A, antenna; Gn, gnathopod; LL, lower lip; UL, upper lip; Md, mandible; Mx, maxilla; Mxpd, maxilliped; P, pereopod; T, telson; U, uropod; Pl, pleopod; R, right; L, left. Type material is deposited in the Departments of Invertebrate Zoology at the following museums: National Museum of Natural History (USNM); Museum of Comparative Zoology, Harvard University (MCZ) and California Academy of Sciences (CASIZ).

Hyalella (*Hyalella*) *muerta,* new species
Figs. 1–5

Diagnosis.—Eyes absent. Antenna 1 longer than antenna 2. Accessory flagellum absent. Pereon lacking dorsal mucronations or spines. Sternal gills reduced in size and present on pereonites 3–7. Maxilla 1, inner plate narrow with 2 terminal plumose setae. Male gnathopod 2, carpus with strong posterior lobe with 4 submarginal setae; propodus robust and much larger than male gnathopod 1, palm with rectangular tooth near hinge of dactylus. Telson rounded, with 4 distal marginal setae.

Description of male.—Body lacking dorsal mucronations or spines. Eyes absent. Head cuboidal, equal to pereonites 1 and 2 in length. Coxae 1–4 enlarged, subquadrate with distomarginal setae, coxae 5–6 with distinct anterior and posterior lobes. Sternal gills small, present on pereonites 3–7.

Antenna 1, 57% of total body length, peduncular ratio 1:0.7:0.6, flagellum 9 articulate; accessory flagellum absent. Antenna 2 shorter than antenna 1, 49% of body length, peduncle nearly equal in length to head, articles 4 and 5 equal in length, flagellum 8 articulate.

Upper lip rounded, anterior margin with fine setae. Mandibles lacking palp; left incisor and lacina with 4 teeth, molar normal. Right incisor with 5 teeth, outer the largest and bifid, lacina with 3 teeth, spine row with 2 plumose setae, molar normal, with accessory plumose seta. Lower lip large, lacking inner lobes. Maxilla 1, inner plate narrow with 2 terminal plumose setae, inner margin finely setose; outer plate with 8 strong apical serrate spines; palp vestigial, 1 articulate. Maxilla 2, plates subequal in width; inner plate with 1 marginal and 12 apical plumose setae, outer margin with fine setae distally; outer plate with 10 apical plumose setae, both margins with fine setae. Maxilliped, inner plate with 3 strong apical teeth, inner margin with 3 plumose setae distally; outer plate with 7 apical plumose setae, with marginal and submarginal plumose setae; palp 4 articulate, nearly 3× length of outer plate, inner margin of article 2 with distal plumose setae, article 3 with distal setae, dactylus triangular with 3 distal setae.

Gnathopod 1, basis elongate broadening distally, posterior lobe of carpus with 6 marginal setae; propodus rectangular, wider and longer than carpus; palm and hind margin equal in length, palm with marginal and submarginal setae. Gnathopod 2, basis elongate; posterior lobe of carpus strong with 4 submarginal setae; propodus robust and much larger than that of gnathopod 1, distal anterior margin with triangular projection; palm with rectangular tooth near hinge of dactylus, with marginal and submarginal setae. Pereopods 3 and 4 similar in shape and size; carpus of both with distal anterior lobe and 2 setae. Pereopod 5, approximately 70% length of pereopod 6. Pereopod 7 slightly larger that pereopod 6. Pereopods 5–7 bases expanded posteriorly, stronger in pereopod 7; carpus with distal posterior lobe, with 3–4 spines.

Pleopods 1–3 long and slender, peduncles with 2 coupling hooks, rami with plumose setae. Uropod 1, peduncle outer margin with 4 bifurcate spines, inner margin with distal marginal seta; inner ramus with 4 apical spines; outer ramus with 5 apical and 2 marginal spines. Uropod 2, 60% the length of uropod 1, peduncle with 2 marginal spines and 1 marginal seta; inner ramus with 6 apical spines; outer ramus with 5 apical spines. Uropod 3, peduncle with 3 distal marginal spines; ramus with 2 apical spines and 1 apical seta. Telson rounded with 4 distal marginal setae.

Female.—All features same as male except as noted below. Antenna 1, 43% of total body length; flagellum 9 articulate. Antenna 2, 34% of total body length; flagellum 9 articulate. Gnathopod 2 and pereopods 3–5 with oostegites. Gnathopod 1 resembling male, posterior lobe of carpus with 8 marginal setae. Gnathopod 2, basis elongate; posterior lobe of carpus with 6 submarginal setae; propodus longer than wide, palm and hind margin distinct.

Etymology.—The specific epithet is derived from the Spanish muerta as a noun in apposition for the word death referring to Death Valley.

Material examined.—Male holotype, 3.28 mm, USNM 230433, Texas Spring, just uphill of the Texas Spring Campground, Death Valley National Park, Inyo County, California, William D. Shepard, 20 Jul 1994. Female (ovigerous) allotype, 3.28 mm, USNM 230434, same data as holotype. Male paratype, 3.28 mm, USNM 230435, same data as holotype. Female (ovigerous) paratype, 3.24 mm, USNM 230436, same data as holotype. 6 males, 8 females (4 ovigerous) paratypes, USNM 230437, same data as holotype. Male (4.00 mm) and female (3.60 mm), paratypes, USNM 230438, Texas Spring tunnel, Death Valley National Park, Inyo County, California, 36°27′27.54″N, 116°50′14.44″W,

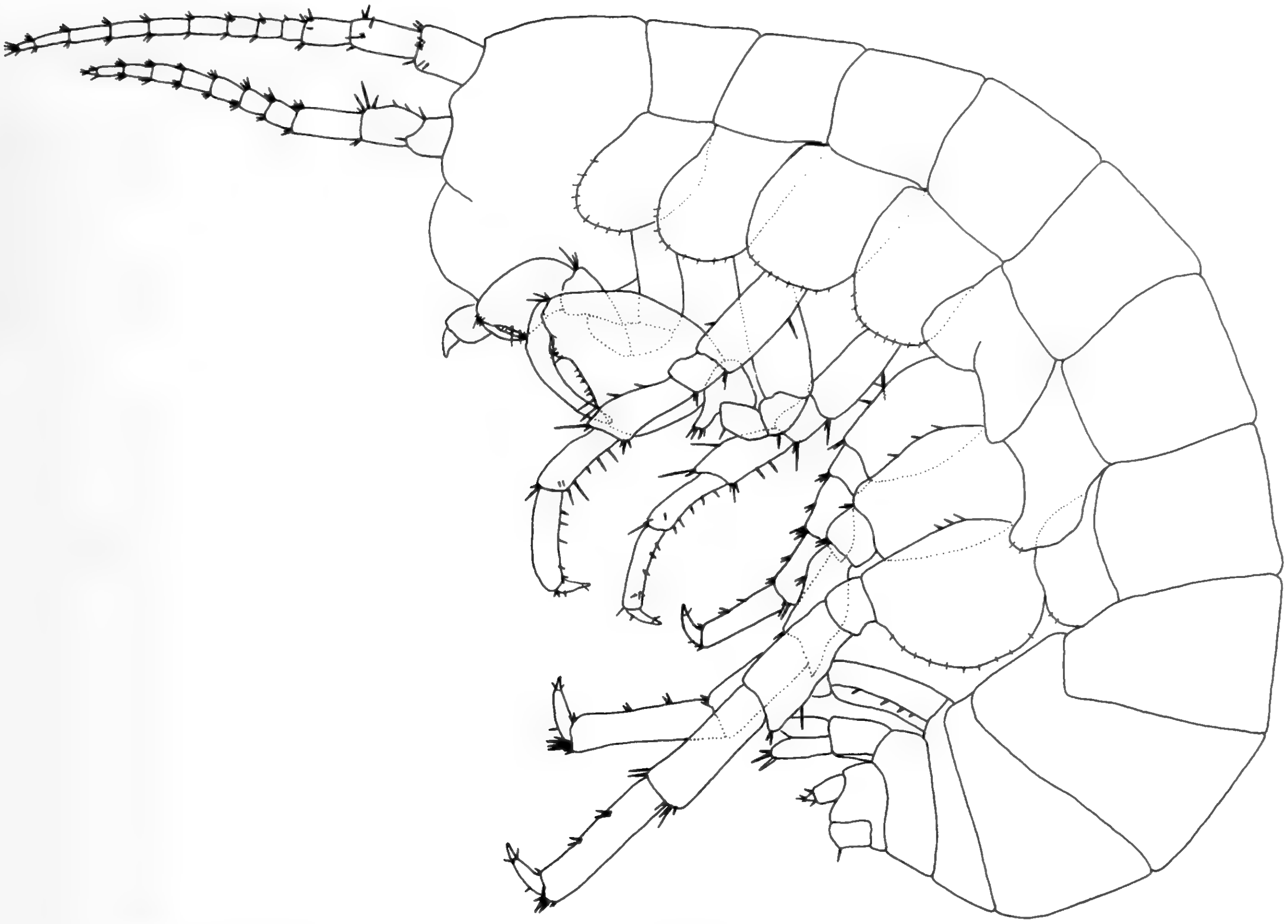

Fig. 1. *Hyalella* (*Hyalella*) *muerta*, male, 3.28 mm, USNM 230435.

Doug L. Threloff, 19 Dec 1997. Paratypes, MCZ 25390, CASIZ 121603, Texas Spring tunnel, Death Valley National Park, Inyo County, California, 36°27′27.54″N, 116°50′14.44″W, D. L. Threloff, 7 Dec 1997. Paratypes, MCZ 25391, CASIZ 121604, Texas Spring tunnel, at discharge point, Death Valley National Park, Inyo County, California, 36°27′26.18″N, 116°50′16.93″W, D. L, Threloff, 19 Dec 1997.

Remarks.—*Hyalella* (*H.*) *muerta* is morphologically similar to *Hyalella* (*Mesohyalella*) *anophthalma* Ruffo, 1957 and *Hyalella* (*Mesohyalella*?) *caeca* Pereira, 1989; the former is known from a cave in Venezuela and the latter from Brazil. Both species have sternal gills on pereonites 2–7 and antenna 2 is longer than antenna 1. In contrast, *H.* (*H.*) *muerta* has sternal gills on pereonites 3–7 and antenna 1 is longer than antenna 2.

Hyalella (*Hyalella*) *sandra*, new species

Figs. 6–10

Diagnosis.—Eyes present. Antenna 1 shorter than 2, flagellum 10–11 articulate; accessory flagellum absent. Antenna 2 elongate, flagellum 20–24 articulate. Pereon lacking dorsal mucronations or spines. Sternal gills on pereonites 3–7, approximately ⅓ the size of coxal gills. Maxilla 1, inner plate narrow with 2 terminal plumose setae. Male gnathopod 2, carpus with strong posterior conical lobe with marginal setae. Uropod 3, ramus with 7 distal spines. Telson, rounded with 2 distal submarginal spines.

Description of male.—Body lacking dorsal mucronations or spines. Eyes pigmented. Head cuboidal, subequal to pereonites 1 and 2 in length. Coxae 1–3 enlarged, quadrate with distomarginal setae, coxae 5–6 with distinct anterior and posterior lobes.

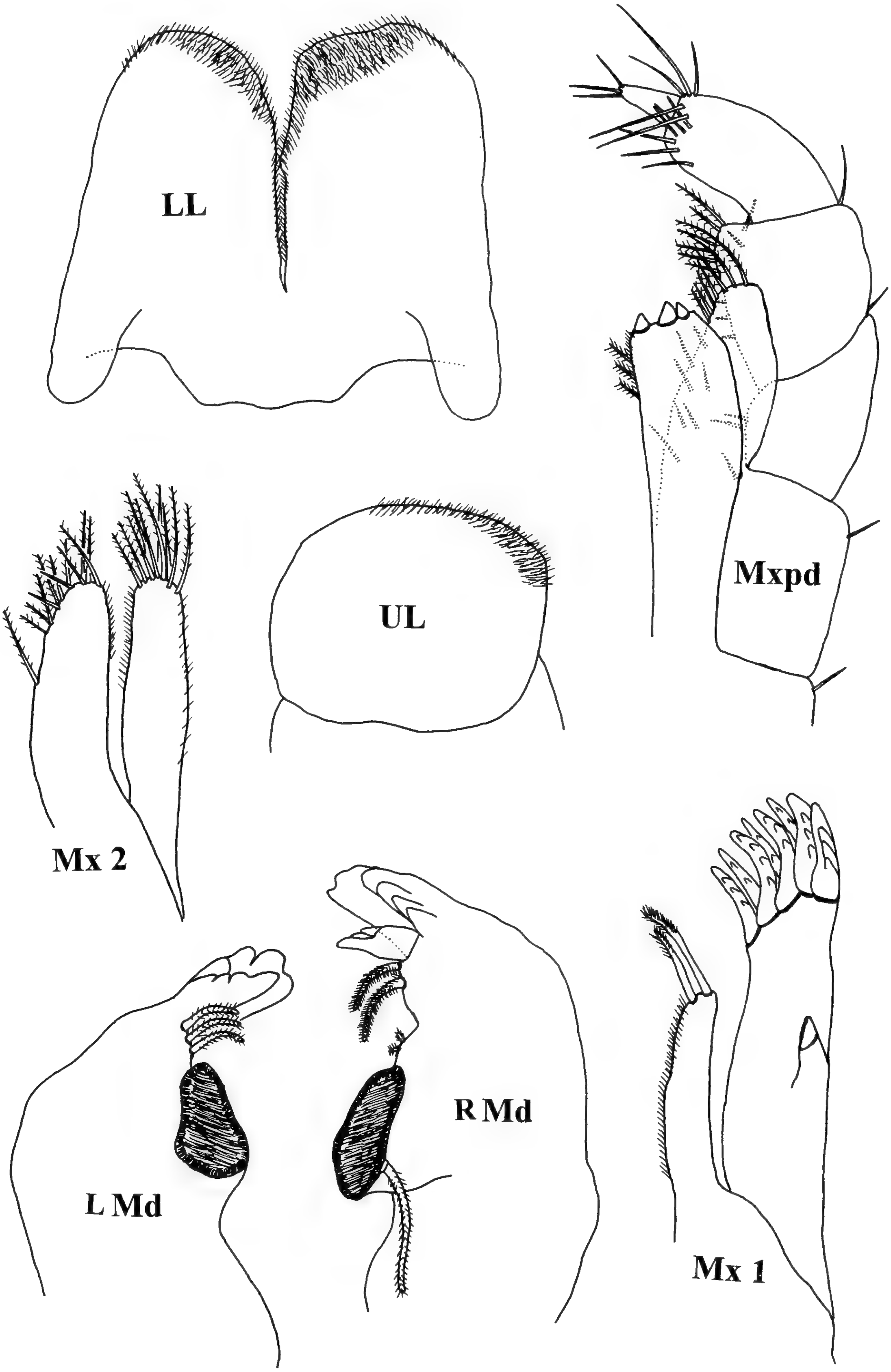

Fig. 2. *Hyalella* (*Hyalella*) *muerta*, male, 3.28 mm, USNM 230435.

Sternal gills on pereonites 3–7, approximately ⅓ the size of coxal gills.

Antenna 1, 25% of total body length, peduncular ratio 1:1:0.8, flagellum 11 articulate each with small aesthetasc-like spines; accessory flagellum absent. Antenna 2 much longer than antenna 1, 50% of body length, peduncle articles 3 and 4 equal in length to 5, flagellum 20 articulate.

Upper lip rounded, anterior margin with fine setae. Mandibles lacking palp, molars normal with accessory plumose seta; left incisor and lacina with 5 teeth, spine row with 3 plumose setae. Right incisor with 5 teeth, lacina with 3 teeth. Lower lip large, setose and lacking inner lobes. Maxilla 1, inner plate narrow, with 2 terminal plumose setae; outer plate with 9 strong apical serrate comb-like spines; palp vestigial, 1 articulate. Maxilla 2, plates subequal in width; inner plate with 2 submarginal spines and apical plumose setae; outer plate with apical plumose setae. Maxilliped, left inner plate with 2 strong apical teeth, right plate with 3; left outer plate with submarginal and apical plumose setae; palp 4 articulate, dactylus with two apical spines.

Gnathopod 1, basis elongate; posterior lobe of carpus with 8 marginal setae; propodus equal in length to carpus; palm with submarginal setae, proximoposterior corner with distinct spine. Gnathopod 2, basis elongate; carpus with strong posterior conical lobe with marginal setae; propodus robust and much larger than that of gnathopod 1; palm with marginal spines and setae, proximoposterior corner with tooth like spine. Pereopods 3 and 4 similar in shape and size; coxal plate of pereopod 4 subquadrate and much larger than that of pereopod 3; merus on both with distal anterior lobe with 3 and 2 spines respectively. Pereopod 5, approximately 75% the length of pereopod 6; basis expanded posteriorly with marginal and submarginal setae. Pereopod 7 slightly smaller than pereopod 6. Pereopods 5–7 bases, anterior margins spinose, posterior margins expanded posteriorly, much stronger in pereopod 7; merus and carpus of each distal posterior lobe spinose.

Pleopods 1–3 long and slender, peduncles with 3 coupling hooks, except pleopod 3 with 2, rami with plumose setae. Uropod 1, peduncle with outer marginal with 4 bifurcate spines, both margins with distal spine; inner ramus, with 2 marginal and 4 apical spines; outer ramus with 3 marginal and 5 apical spines. Uropod 2, 75% the length of uropod 1, peduncle outer margin with 4 marginal spines, inner margin with a strong distal spine; inner and outer rami with 3 marginal and 4 apical spines. Uropod 3, peduncle with 3 distal marginal and 1 submarginal spines; ramus with 7 apical spines. Telson rounded, with 2 distal submarginal spines and 5 small submarginal setae.

Female (*ovigerous*).—All features same as male except as noted below. Antenna 1, 27% of total body length; flagellum 7 articulate. Antenna 2, 63% of total body length flagellum 14 articulate. Gnathopod 2 and pereopods 3–5 with oostegites. Gnathopod 2, basis elongate; carpus longer than wide, lacking posterior conical lobe and with 9 submarginal setae; palm and hind margin distinct.

Etymology.—The specific epithet is a name in apposition in reference to the first author's wife Sandra, for her support and encouragement towards his research endeavors.

Material examined.—Male holotype, 4.80 mm, MCZ 25392, Travertine Spring, approximately 1.9 km southeast of Texas Spring, Death Valley National Park, Inyo County, California, 36°26′28.40″N, 116°49′57.01″W, D. L. Threloff, 21 Dec 1997. Female (ovigerous) allotype, 3.36 mm, MCZ 25393, same data as holotype. Male paratype, MCZ 25394, same data as holotype, 4.88 mm. Female (ovigerous) paratype, 3.36 mm, MCZ 25395, same data as holotype. Male paratype, 4.80 mm, MCZ 25435, same data as holotype. Male paratype, 4.72 mm, MCZ 25396, Texas Spring outflow, 34 m downstream of discharge

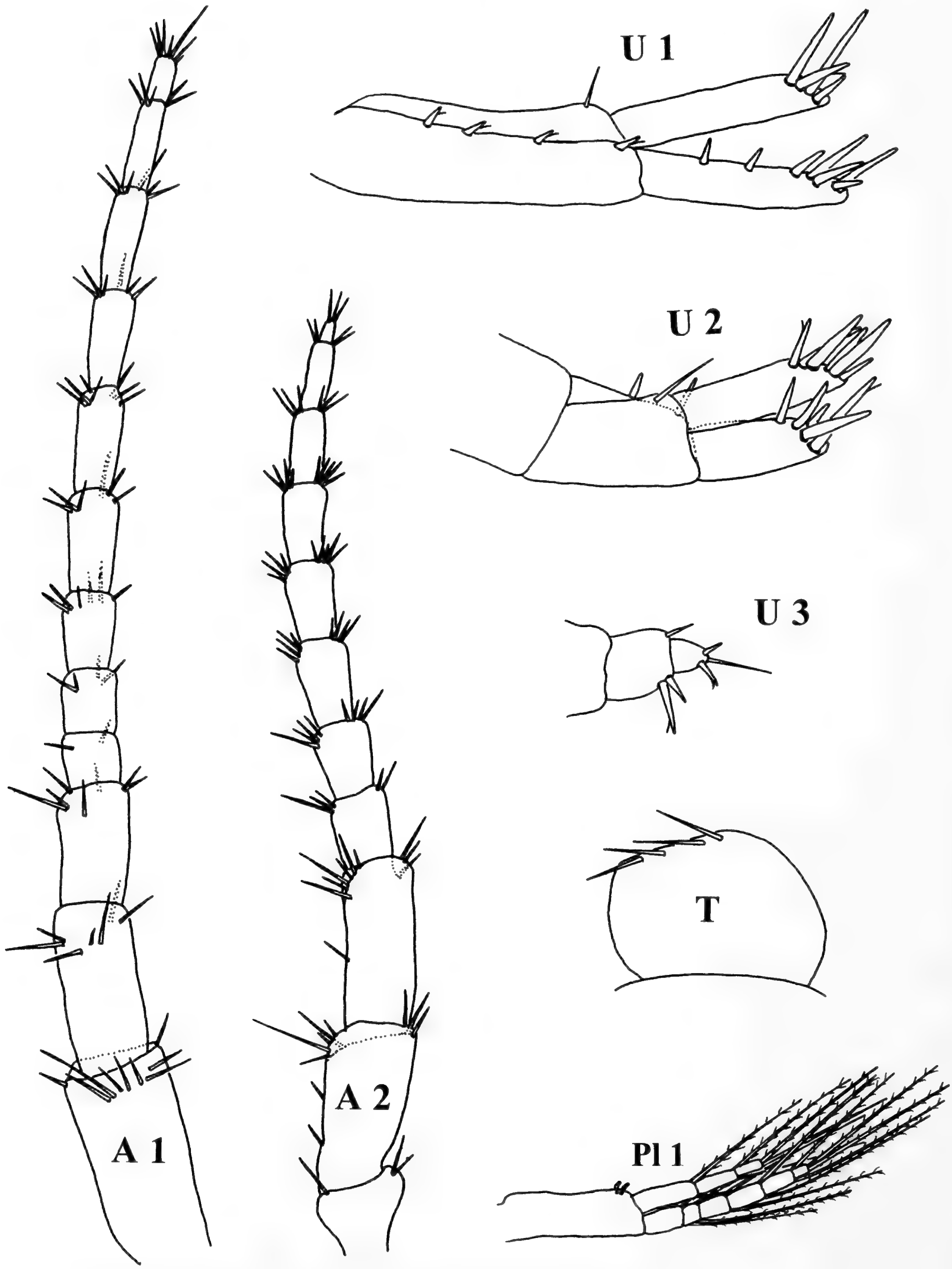

Fig. 3. *Hyalella (Hyalella) muerta,* male, 3.28 mm, USNM 230435.

point, Death Valley National Park, Inyo County, California, 36°27′25.44″N, 116°50′18.01″W, D. L. Threloff, 19 Dec 1997. Male paratype, 5.20 mm, MCZ 25397, Texas Spring outflow, 13 m downstream of discharge point, Death Valley National Park, Inyo County, California, 36°27′25.86″N, 116°50′17.20″W, D. L.

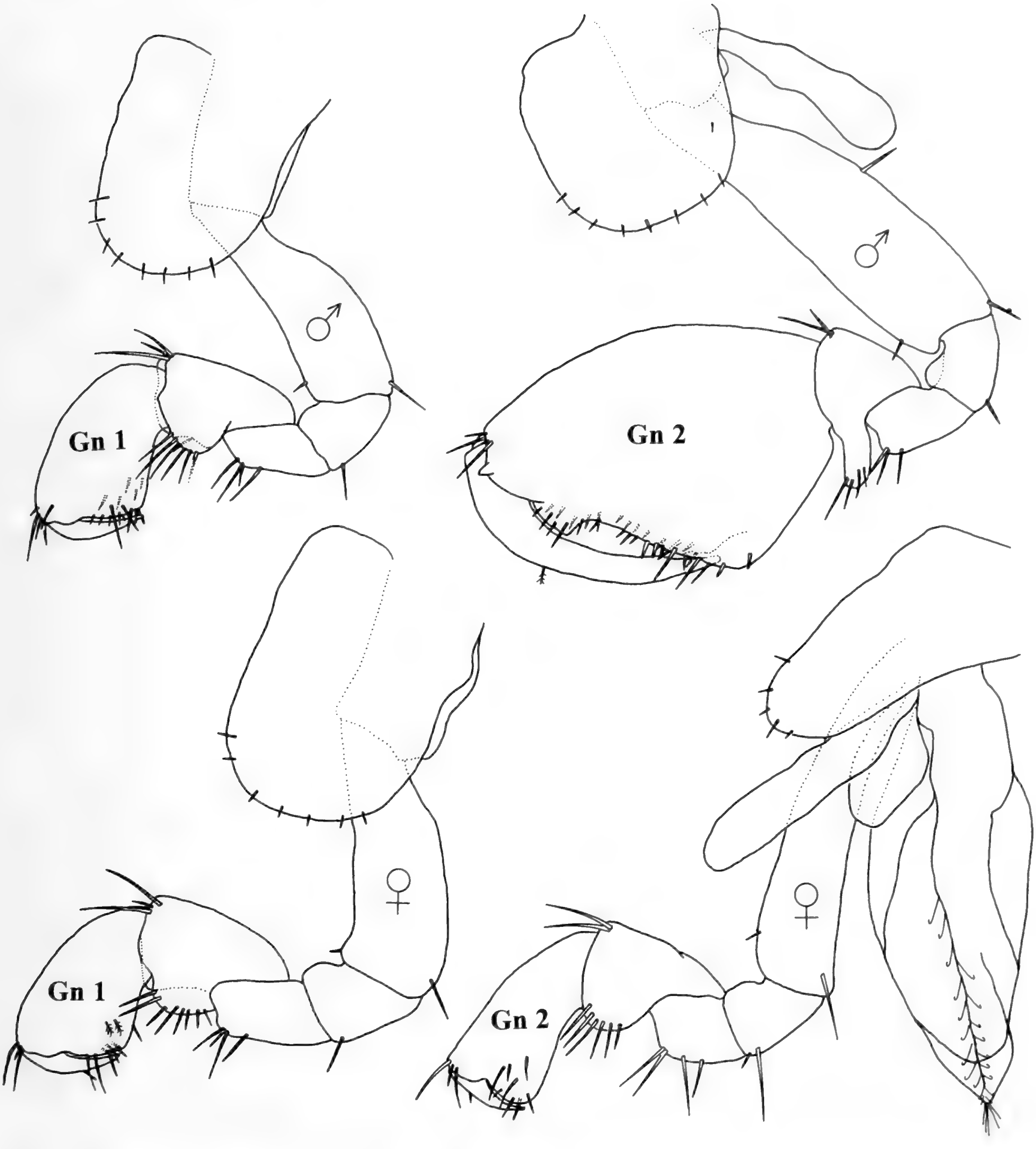

Fig. 4. *Hyalella* (*Hyalella*) *muerta,* male, 3.28 mm, USNM 230435: Gn1, Gn2. Female, 3.24 mm, USNM 230436: Gn1, Gn2.

Threloff, 21 Dec 1997. Paratypes, USNM 230439, CASIZ 121605, same data as holotype. Paratypes, MCZ 25398, USNM 230411, CASIZ 121606, Texas Spring outflow, 34 m downstream of discharge point, Death Valley National Park, Inyo County, California, 36°27′25.44″N, 116°50′18.01″W, D. L. Threloff, 19 Dec 1997. Paratypes, MCZ 25399, USNM 230440, CASIZ 121607, Texas Spring outflow, 13 m downstream of discharge point, Death Valley National Park, Inyo County, California, 36°27′25.86″N, 116°50′17.20″W, D. L. Threloff, 21 Dec 1997.

Remarks.—*Hyalella* (*H.*) *sandra* is morphologically similar to *H.* (*H.*) *longicornis,* which is larger in size and is known from only the type locality in Utah. Examination

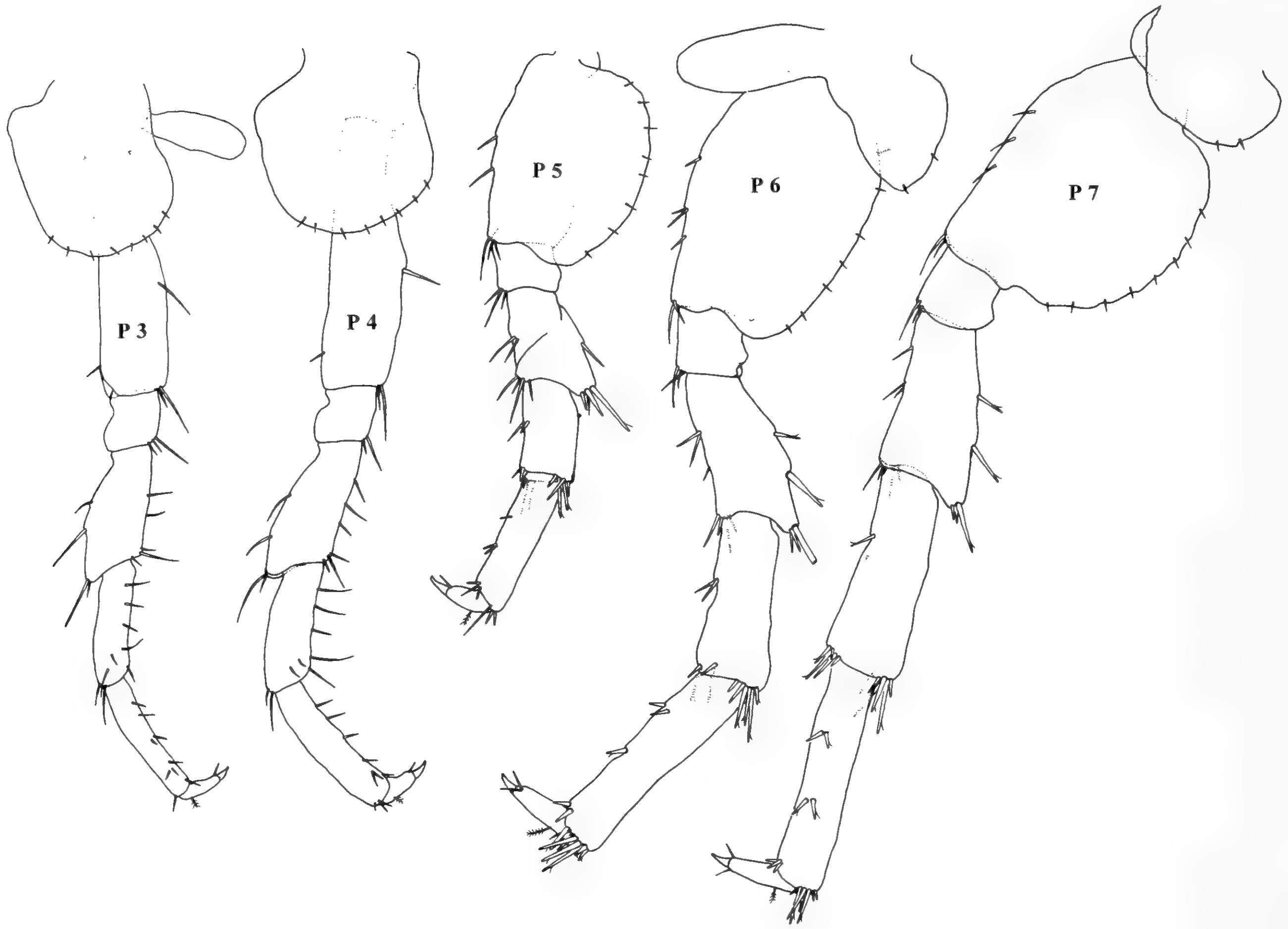

Fig. 5. *Hyalella* (*Hyalella*) *muerta,* male, 3.28 mm, USNM 230435.

of the type specimens of *H.* (*H.*) *longicornis* showed that the most significant differences between *H.* (*H.*) *sandra* and *H.* (*H.*) *longicornis* are: the ramus of uropod 3, *H.* (*H.*) *sandra* robust, with 7 apical spines and *H.* (*H.*) *longicornis* slender, with 4–5 apical setae; the telson, *H.* (*H.*) *sandra* with 2 submarginal spines and *H.* (*H.*) *longicornis* with 2 long slender apical setae; the flagellar articles of the male antenna 2, *H.* (*H.*) *sandra* with 20–24 and *H.* (*H.*) *longicornis* with 16; the palp of maxilla 1, *H.* (*H.*) *sandra* vestigial, 1 articulate and *H.* (*H.*) *longicornis* tall, length >2× the width; basis of gnathopod 2 posterior margin, *H.* (*H.*) *sandra* with 1–3 marginal setae and *H.* (*H.*) *longicornis* with 9 marginal setae.

Discussion.—In 1874, Smith established the genus *Hyalella,* describing *Hyalella dentata* and *Hyalella inermis,* both from Colorado. Faxon (1876), working on South American hyalellids, regarded the genus *Allorchestes* as the senior synonym of *Hyalella* and determined *H. inermis* was a variety of *H. dentata,* calling it *Allorchestes dentata* var. *inermis.* Nearly 30 years later, Stebbing (1903) resurrected *Hyalella* and established *H. inermis* as a valid species, noting differences in the antennae, mouthparts, gnathopods and pereopods. Weckel (1907), in re-examining the North American hyalellid species, concluded that *H. inermis, H. dentata* and *Hyalella faxoni* Stebbing, 1903 were all junior synonyms of *Hyalella knickerbockeri* Bate, 1862 and mentioned that only *H. azteca* var. *inermis* lacked dorsal mucronations. Later, Barnard (1958) provided a list of the *Hyalella* species and listed *H. faxoni* and *H. knickerbockeri* as junior synonyms of *H. azteca* and considered *H. inermis* a valid species. However, Bousfield (1958, 1973) concluded that *H. azteca* is a single morphologically variable species with the number of dorsal micronations varying from 1–3, that specimens totally lacking dorsal mycrona-

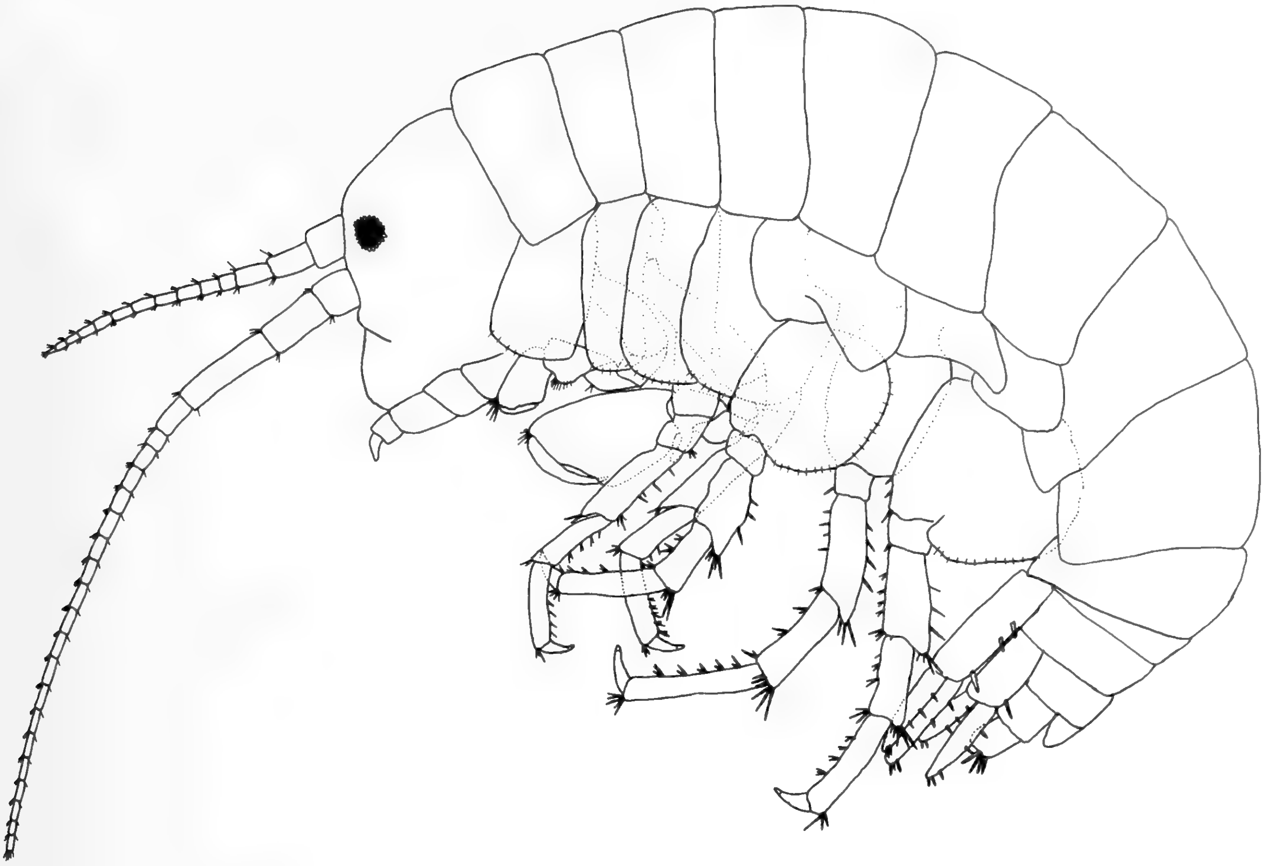

Fig. 6. *Hyalella* (*Hyalella*) *sandra,* male, 4.88 mm, MCZ 25394.

tions were *H. azteca* forma *inermis,* and that both taxa occurred throughout the United States. Stevenson & Peden (1973) then described *Hyalella texana* from Texas, a species that coexisted with *H. azteca.* Shortly thereafter, Cole & Watkins (1977) described *Hyalella montezuma* from the Montezuma Well system in Arizona, but this species coexisted with *H. azteca* forma *inermis.* Holsinger (1981) provided a list of the 32 species of *Hyalella* and mentioned that most workers agreed that *H. dentata, H. inermis* and *H. knickerbockeri* are synonyms of *H. azteca.* Lastly, Bousfield (1996) described *Hyalella* (*Hyalella*) *longicornis* that lacked dorsal mucronations and was known only from Utah [although table 1 of Bousfield (1996) gives distribution as "Texas"].

Bousfield (1996) divided *Hyalella* into three subgeneric groups (*Hyalella, Austrohyalella,* and *Mesohyalella*) based on geographical distributions and morphological characters (i.e., body mucronations, the propodus of gnathopods 1 and 2, rami of uropods 1 and 3, ornamentation of the telson). The plesiomorphic subgenera *Austrohyalella* and *Mesohyalella* are confined to continental South America while the more apomorphic subgenus *Hyalella* is endemic to the West Indies, Central and North America (Bousfield 1996). However, Bousfield (1996) mentions that northern distributed species of *Mesohyalella* show morphological similarities to species in the North American subgenus *Hyalella.*

Both species described here exhibit some morphological characters similar to species in the subgenus *Mesohyalella* [*H.* (*H.*) *muerta,* smooth body, 1 plumose seta on the inner plate of maxilla 2; *H.* (*H.*) *sandra,* smooth body, 1 submarginal spine on the inner plate of maxilla 2, spines on the telson]. However, the presence of 5 sternal gills, the morphology of male gnathopod 1 [*H.* (*H.*) *muerta,* propodus with 5 week and short facial setae, palm margin convex and short; *H.* (*H.*) *sandra* propodus with 5 week

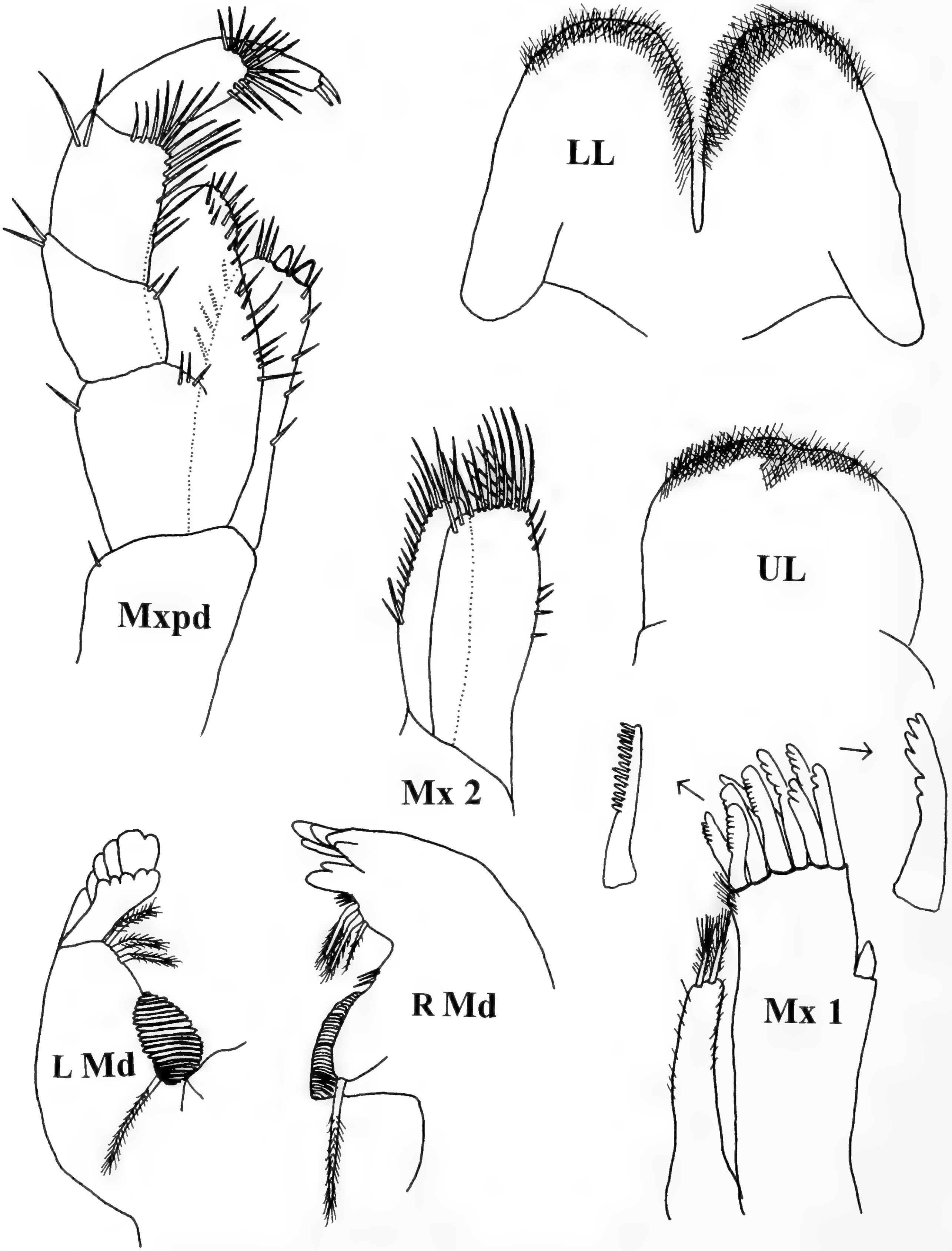

Fig. 7. *Hyalella* (*Hyalella*) *sandra,* male, 4.88 mm, MCZ 25394.

and short facial setae, palm margin convex and short, palmer angle with 1 short spine] and the morphology of the female gnathopod 2 of both species (propodus long and slender) would place them in the subgenus *Hyalella.* In addition, as both new species lack copulatory spines on uropod 1, have a peduncle and ramus of uropod 3 subequal

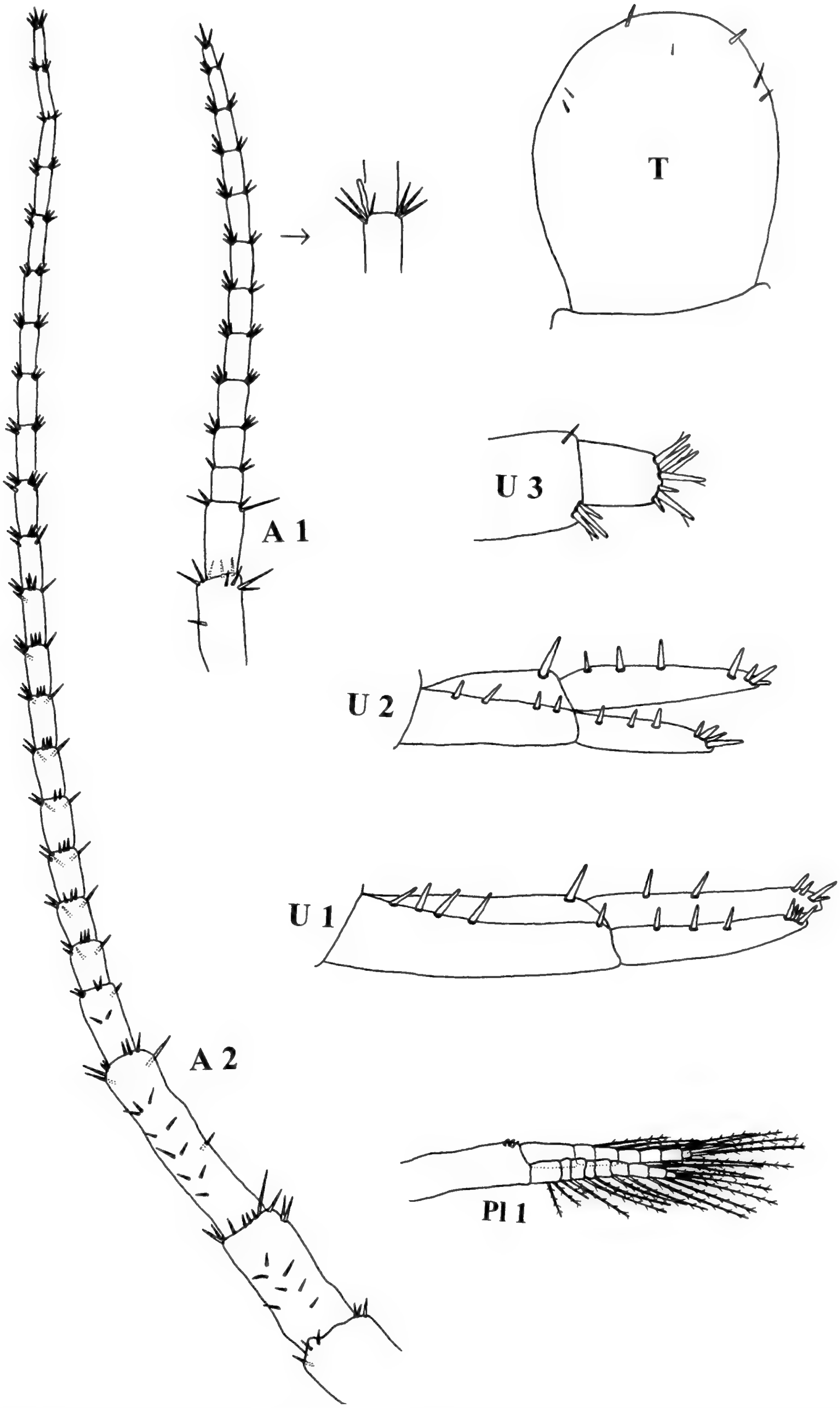

Fig. 8. *Hyalella* (*Hyalella*) *sandra,* male, 4.88 mm, MCZ 25394: A1, A2, U3, T, Pl1. Male, 4.80 mm, MCZ 25435: U1, U2.

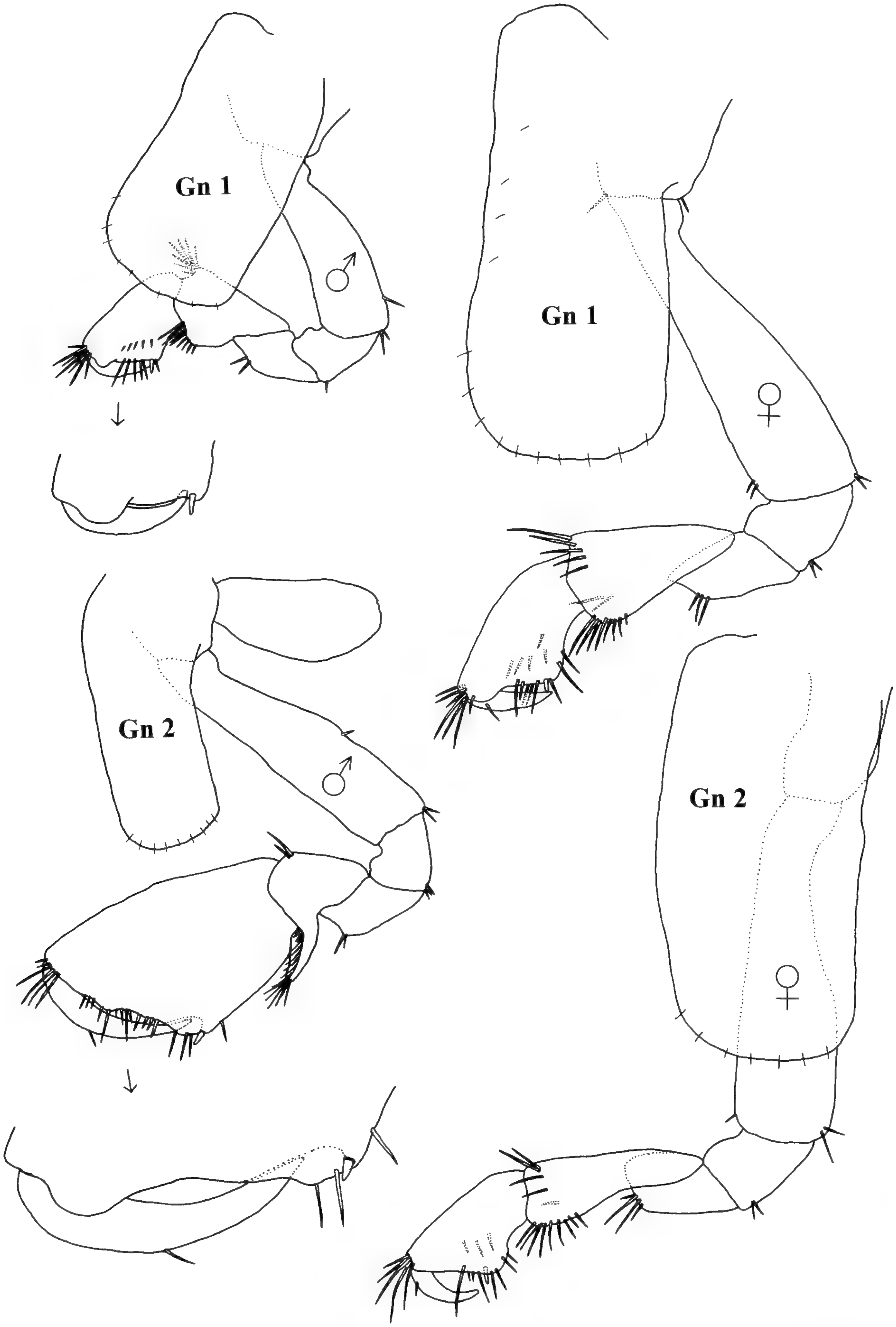

Fig. 9. *Hyalella* (*Hyalella*) *sandra,* male, 4.88 mm, MCZ 25394: Gn1, Gn2. Female (ovigerous), 3.36 mm, MCZ 25395: Gn1, Gn2.

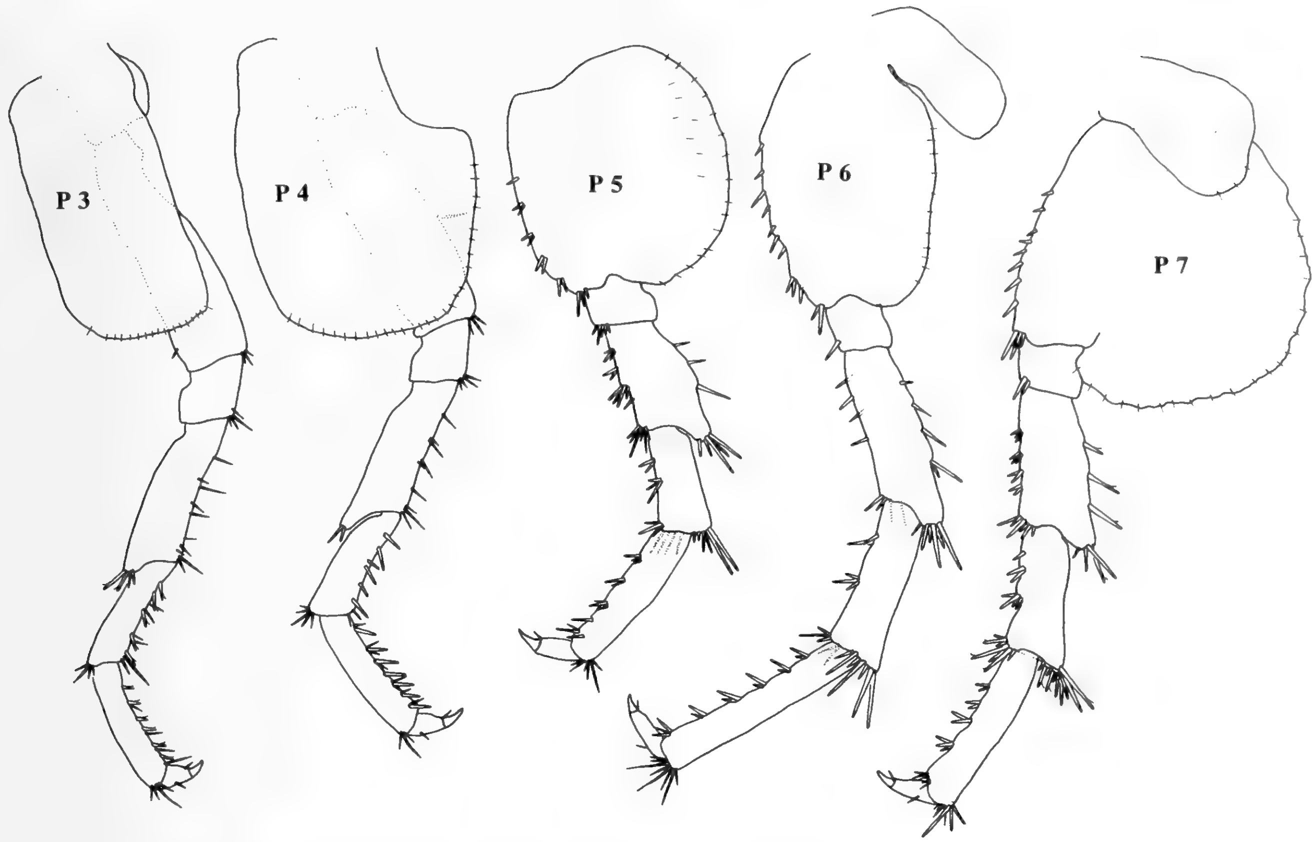

Fig. 10. *Hyalella* (*Hyalella*) *sandra*, male, 4.88 mm, MCZ 25394.

in length, and have setae on their telson support their subgeneric placement. Lastly, the North American distribution that defines the subgenus *Hyalella* as suggested by Bousfield (1996) are consistent with the known distribution of the two new species described here.

Hyalella (*H.*) *muerta* and *H.* (*H.*) *sandra* occur in Death Valley National Park, California but rarely if ever coexist together. *Hyalella* (*H.*) *muerta*, the first North American hypogean hyalellid, is blind, lacks dorsal mucronations and antenna 1 is longer than antenna 2. *Hyalella* (*H.*) *sandra*, collected from epigean waters near Texas Spring, also lacks dorsal mucronations but has normal eye pigmentation and antenna 1 is shorter than antenna 2, as in the other North American *Hyalella* species. These two new species bring the total number of North American *Hyalella* taxa to seven.

Specimens of *H.* (*H.*) *muerta* were collected in an artificial tunnel that was excavated in the 1930's. The tunnel was most likely excavated in an effort to increase the volume of water that was being diverted as a potable water supply. Prior to the development of the tunnel, Texas Spring is believed to have issued water directly from the local hillside. The interior of the tunnel is typically 1.5 m wide by 1.5–2.0 m high and is approximately 70 m in length. Flow into the upstream portion of the tunnel develops as water exits a fractured rock zone. The water runs along the floor of the tunnel in a stream that is 60–150 cm wide and 3–30 cm deep. Overburden above the tunnel consists of soft silt, 1–10 m thick. Collapse of the tunnel has been prevented through the installation of thick wooden cross members that support the ceiling and side wall surfaces of the tunnel. Specimens of *H.* (*H.*) *muerta* were found among the submerged roots originating from surface-inhabiting, riparian plants. In 1995, a one meter portion of the wooden tunnel structure collapsed. It is not known if the concurrent sediment input had any impact on the amphipod population.

At Texas Spring the water emerges from

local exposures of gravel and sand (Pistrang & Kunkel 1958). The rate of flow has always been low, ranging from 0.2–0.5 cfs. Because Texas Spring provides water for human consumption, the water quality has been regularly tested. Miller (1977) provided the following water chemistry analysis for Texas Spring water: temperature: 31°C; silica: 25–40 mg/l; calcium 30 mg/l; sodium: 150 mg/l; bicarbonate 330 mg/l; dissolved solids: 600–700 mg/l; pH: 7.5–8.5.

Specimens of *H.* (*H.*) *sandra* were collected from Travertine Spring approximately 1.9 km southeast of Texas Spring and 13–34 m down stream from the Texas Spring discharge. In mid to late 1970's, the potable water collection system at Texas Spring was replaced, and the entire spring flow was placed in a PVC pipe in an effort to eliminate the percolation of water into the ground. Between 1989 and 1994, Death Valley National Park maintenance personnel diverted some of the piped water back onto the ground in an effort to re-establish a stream habitat. Maintenance personnel then transplanted benthic sediment and vegetation from Travertine Spring to an area down stream of Texas Spring tunnel with the intentions of reinoculating the stream with aquatic invertebrates and plants. Presumably, *H.* (*H.*) *sandra* was transported with the sediments that established an introduced population. Extensive sampling has revealed one live specimen of *H.* (*H.*) *muerta* occurring in the surface stream downstream of Texas Spring tunnel. Preliminary investigations therefore suggest that *H.* (*H.*) *muerta* and *H.* (*H.*) *sandra* rarely coexist in Death Valley National Park.

Although Death Valley is one of the driest and hottest deserts in the New World, the climate there has not always been so harsh. During the Pleistocene the climate was cooler and wetter, similar to that found today around Lake Mono, 240 km (150 mi) to the north. Numerous large pluvial lakes occupied the many depressions in this area and at that time Texas Spring would have been at or only slightly above the shoreline of pluvial Lake Manly. The aquatic communities currently found in the springs and streams of Death Valley are largely relicts of these Pleistocene and earlier communities (Shepard 1992, 1993). Grayson (1993) provides an excellent account of both Pleistocene and Recent hydrology for the Death Valley area.

In the desert southwest of the United States, it appears that *H.* (*H.*) *azteca* has been giving rise to new species via populations that have been isolated in thermally constant waters. Thomas et al. (1994, 1997) have proposed ecological isolation for the species pair *H.* (*H.*) *azteca* and *H.* (*H.*) *montezuma,* based on DNA and behavior. Their behavioral studies led them to separate two lineages of *Hyalella* in north-central Arizona; swimmers that inhabit submersed vegetation in lakes and clingers that inhabit springs dominated by emergent macrophytes. Jackson (1912) also noted two distinct locomotion behaviors. *Hyalella* (*H.*) *muerta* and *H.* (*H.*) *sandra* both fall into the clinger behavior category and likely have speciated from local epigean populations of *H.* (*H.*) *azteca.*

Another undescribed *Hyalella* (*Hyalella*) species has also been found in Ash Meadows National Wildlife Refuge, 45 km to the east (in prep.). It also occurs in a warm spring. Because of the discovery of a number of new species in such a small area, we suggest that aquatic biologists more carefully collect and identify specimens in the future, particularly when dealing with thermally constant waters.

Acknowledgments

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Caecidotea cumberlandensis, a new species of troglobitic isopod from Virginia, with new records of other subterranean *Caecidotea* (Crustacea: Isopoda: Asellidae)

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Abstract.—*Caecidotea cumberlandensis* is a subterranean asellid isopod described from two caves in Cumberland Gap National Historic Park in southwestern Virginia. New records of several other subterranean *Caecidotea* are also discussed: *C. incurva, C. jordani, C. barri, C. paurotrigonus* and *C. teresae.* Comparison of the descriptions of *C. paurotrigonus* and *C. dauphina* suggest that these species are conspecific.

In 1976 Dr. John Holsinger told me of a subterranean isopod collected from Cliff Cave in the Cumberland Gap area of southwestern Virginia that had been identified by Fleming (1972a) as *Asellus scrupulosus* (a troglophilic species with eyes and pigmentation). Dr. Holsinger had related that this identification might be in error since the Cliff Cave specimen was eyeless and unpigmented, and suggested that I look at the specimen if the opportunity presented. Fleming's identification was subsequently rejected entirely by Holsinger & Culver (1988).

In 1997 I visited the Smithsonian Institution to assist in the sad task of curating collections that remained in the office of my mentor and friend, Dr. Thomas E. Bowman, at the time of his death. During this process I came upon the Cliff Cave specimen as well as another vial of isopods from Indian Cave, Lee Co., Virginia. Examination of these specimens proved Dr. Holsinger's suspicion correct, that the Cliff Cave specimens represented a distinct taxon new to science.

Family Asellidae G. O. Sars, 1897
Caecidotea Packard, 1871
Caecidotea cumberlandensis, new species
Figs. 1–3

Asellus scrupulosus.—Fleming, 1972a: 241.

Caecidotea species A.—Holsinger & Culver, 1988: 30–31, 37.

Material examined.—Virginia: Lee Co., Indian Cave, David A. Hubbard, Jr., 16 Mar 1993, 5.5 mm male holotype (USNM 291204), 4.5 mm male paratype, 6 female paratypes (USNM 291205); Cliff Cave, Russell M. Norton, 24 Nov 1966, 5.8 mm male paratype (USNM 291206), including a glass slide labelled "8-K *A. scrupulosus*" and signed "LEF" (L. E. Fleming) containing the first and second pleopods.

All specimens remain in the National Museum of Natural History, Smithsonian Institution.

Description.—Eyeless, unpigmented, longest male 5.8 mm, female 4.7 mm; body slender, about 5.2× as long as wide. Head about 1.5× as wide as long, anterior margin concave, postmandibular lobes moderately produced. Pleotelson about 1.4× as long as wide, sides subparallel, caudomedial lobe moderately produced.

Mandibles with 4-cuspate incisors and lacinia mobilis, palp with rows of plumose setae on distal segments. Maxilla 1 with 5 robust plumose setae on inner lobe, 13 spines on outer lobe. Antenna 1 reaching to about mid-point of last segment of antenna 2 peduncle, flagellum of 6-7 segments, esthetes present on last 4 segments. Antenna

2, last segment of peduncle about 1.5× length of preceding segment, flagellum of holotype with 40 segments.

Male pereopod 1, propus 2.6× as long as wide, palmar margin with 2 large spines, processes absent; female pereopod 1.2× as long as wide, palmar margin similar to male. Pereopods 2-7 similar, with moderate setation, sexual dimorphism of pereopod 4 for grasping negligible, carpus about 2.2× as long as wide.

Male pleopod 1, protopod about 0.5 length of exopod, with 2–3 retinacula; exopod about 1.8× as long as wide; lateral margin slightly concave, distolateral margin setae not plumose. Pleopod 2 exopod proximal segment with 2 plumose setae, distal segment with 3–5 plumose setae along margin. Endopod with rounded basal apophysis; tip with 2 distinct processes extending subparallel to one another and approximately perpendicular to the axis of the endopod: (1) lateral process subterminal, slender, tapering slightly, and (2) cannula beak-shaped. Pleopods 3–5, endopods present, but unremarkable. Pleopod 3 exopod distal margin with 3–4 short, non-plumose setae. Pleopod 4 exopod, proximal setae absent; sutures indistinct, suggestive of 2 barely discernible, unconnected false sutures. Pleopod 5 exopod with faint transverse sutures. Uropods of male about 0.5× length of pleotelson, female similar.

Etymology.—The name refers to the Cumberland Gap area in which the species occurs. The suggested vernacular name is the Cumberland Gap cave isopod.

Range.—This species is known only from Cliff and Indian caves in the Cumberland Gap National Historic Park, Lee Co., Virginia. Descriptions of the caves were presented by Holsinger (1975). The caves are about 500 meters apart, occur in the same rock formation (Greenbrier Limestone), and are probably disconnected parts of the large Cudjos-Cumberland Saltpeter Cave system (Holsinger, in litt.). The amphipod *Stygobromus cumberlandus* occurs with *C. cumberlandensis* in Cliff Cave (Holsinger 1978). The range of this amphipod also includes Scott and Wise counties in Virginia, suggesting the possibility of a wider range for *C. cumberlandensis.*

Relationships.—Caecidotea cumberlandensis most closely resembles two other subterranean species, *C. bicrenata* (northern Alabama to southern Illinois; Lewis 1982a) and *C. richardsonae* (Tennessee and Virginia; Steeves 1963). These three species have in common a male pleopod 2 endopod tip with a terminal beak-shaped cannula and subterminal lateral process, both extending approximately perpendicular to the axis of the endopod. These species are most easily separated from one another by the shape of the lateral process, which in *C. cumberlandensis* is thin and tapered distally, in *C. bicrenata* thicker and cylindrical, and in *C. richardsonae* finger-shaped and overlapped by the cannula (the tip processes shown by Lewis & Bowman 1977 for *C. richardsonae* had been spread by pressure from a coverslip; the appearance depicted by Steeves 1963 is more typical). Differences and similarities of key structures in these three species are summarized in Table 1.

Caecidotea jordani (Eberly, 1966)

Material examined.—Indiana: Crawford Co., seep spring flowing from bank of Blue River at former site of Rothrock Mill, Wyandotte, Julian J. Lewis, Victor M. Lewis, James J. Lewis, 30 Jul 1998, 5 males, 12 females; same locality, Julian J. Lewis, Salisa T. Rafail, 1 Aug 1998, 4 males, 5 females.

Range.—The only previously known population (a spring under Jordan Hall on the campus of Indiana University, Bloomington) was extirpated by termiticides. The site reported above is a parafluvial habitat where water seeps from a gravel bed that extends under the floodplain of the Blue River.

Caecidotea incurva (Steeves & Holsinger, 1968)

Material examined.—Tennessee: Blount Co., Whiteoak Blowhole Cave, W. Reeves,

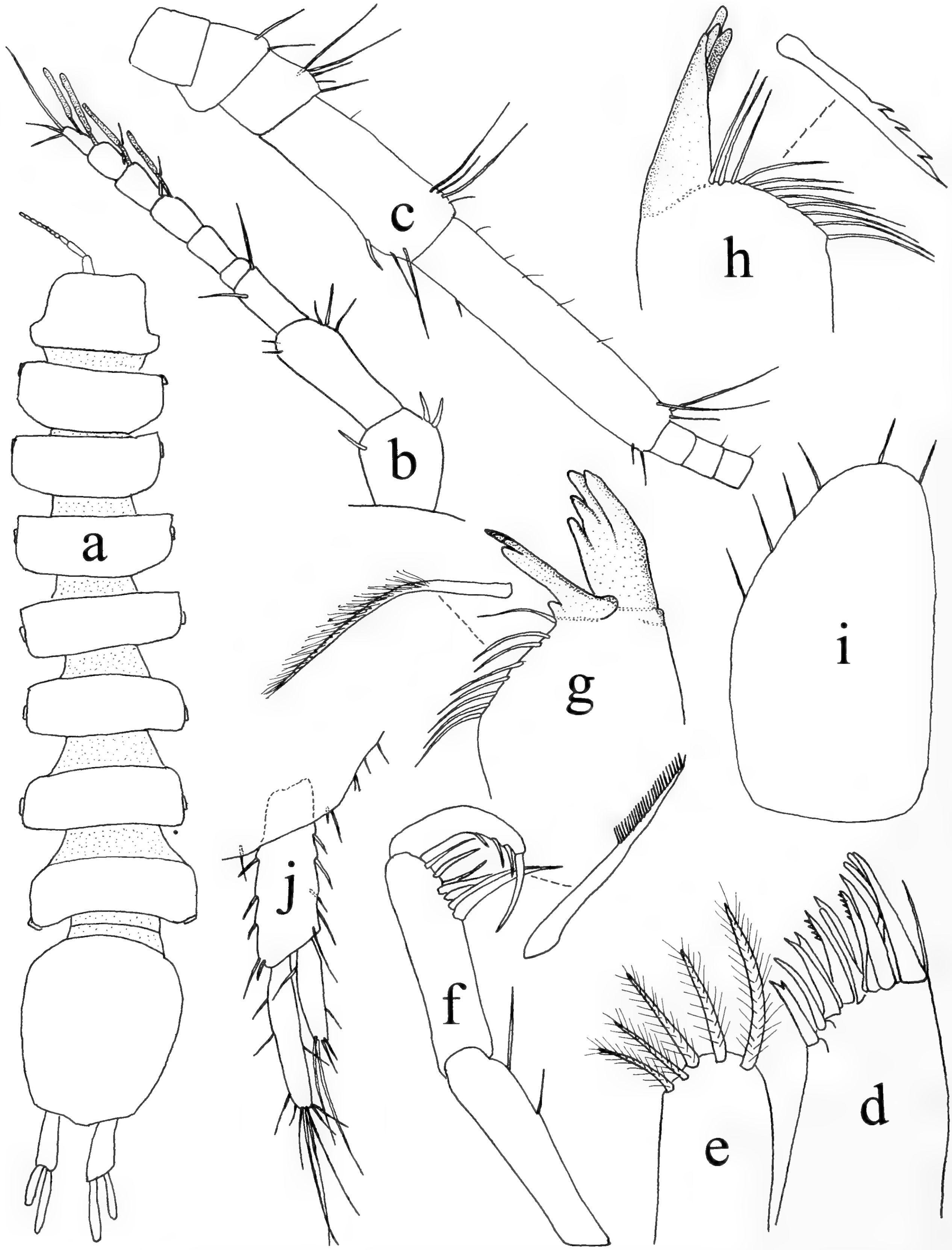

Fig. 1. *Caecidotea cumberlandensis,* 4.5 mm paratype male, Indian Cave, Lee Co., Virginia (a–b, d–h, j); 5.5 mm holotype male, same locality (c); 4.7 mm paratype female, same locality, (i): (a) habitus, (b) antenna 1, (c) antenna 2, (d) maxilla 1, outer lobe, (e) maxilla 1, inner lobe, (f) mandibular palp, (g) left mandible, incisor and lacinia mobilis, (h) right mandible, incisor, (i) pleopod 2, (j) uropod.

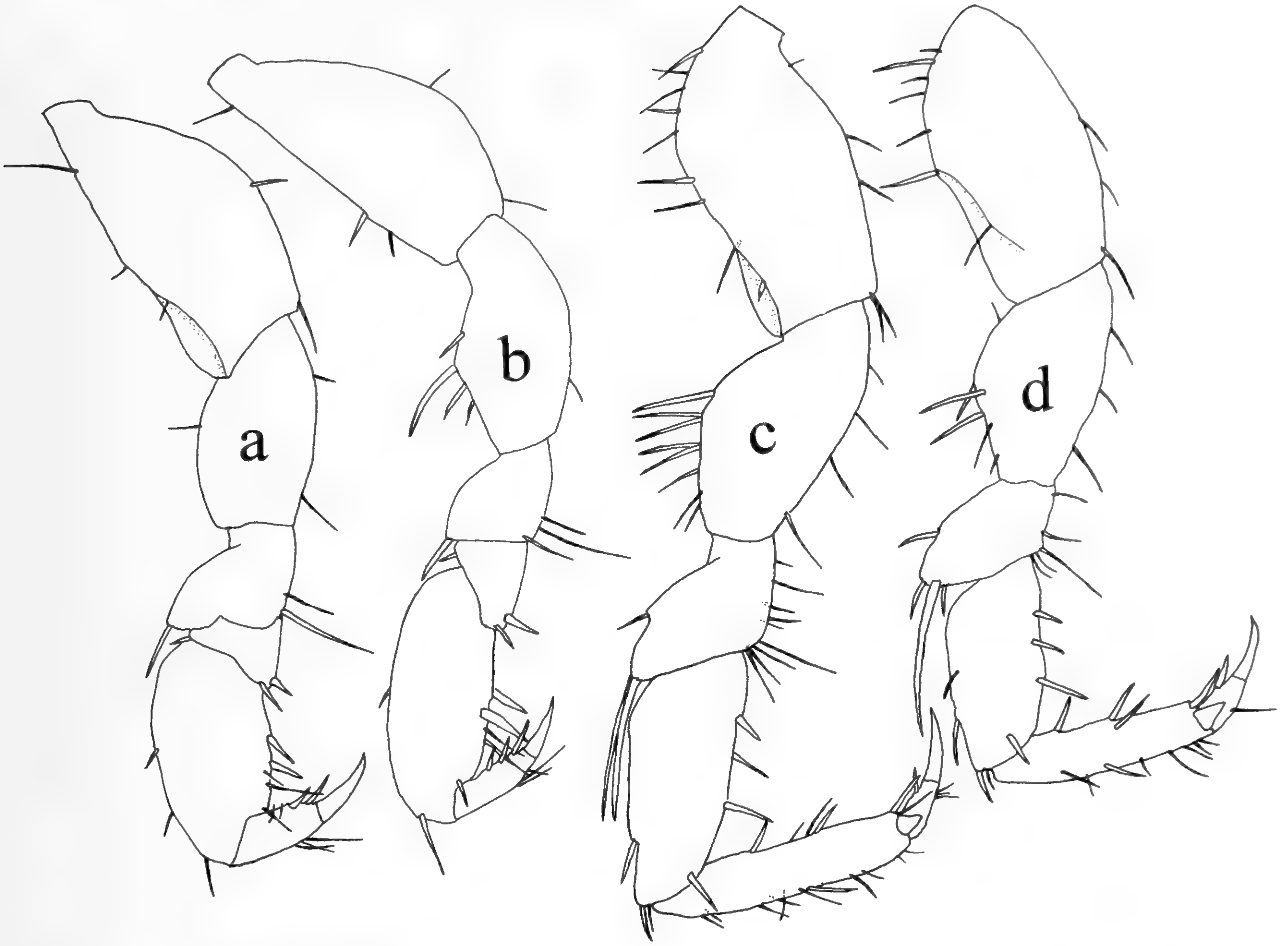

Fig. 2. *Caecidotea cumberlandensis*, 4.7 mm female paratype, Indian Cave, Lee Co., Virginia, (a, d); 5.5 mm male holotype, same locality, (b–c): (a) pereopod 1, (b) same, (c) pereopod 4, (d) same.

12 Aug 1999, 2 males, 2 females; Rich Mountain Blowhole Cave, W. Reeves, 25 Aug 1999, 2 males, 1 female; Virginia: Wythe Co., Early's Cave, D. A. Hubbard, Jr., 7 Jul 1997, 6 males, 4 females; Campbell Cave, D. A. Hubbard, Jr., 14 Sep 1998, 1 male, 1 female; Lone Ash Cave #2, D. A. Hubbard, Jr., 3 Nov 1997, 4 males, 13 females; Mockley Cave, D. A. Hubbard, Jr., 29 Mar 1999, 1 male, 1 female.

Range.—This species was incompletely described, but the endopod of the male second pleopod is so distinct in appearance (Steeves & Holsinger 1968) that a fairly certain identification can be made. Holsinger & Culver (1988) reported this species in Virginia from McMullin Cave, Smyth Co., and Groseclose Cave Number 1, Wythe Co. Other unpublished Virginia records identified and provided by J. R. Holsinger (in litt.) are Deep Spring and Bowles Spring caves, Wythe Co., and Dolingers Cave, Washington Co.

Caecidotea paurotrigonus (Fleming, 1972b)

Material examined.—Louisiana: St. Mary Parish, holes dug in moist area at forest edge beside road, just outside entrance to parish park at Burn's Point, at end of state highway 317, coll. D.W.D., 23 Aug 1981, 1 male, 1 fragment, 9 females.

Range.—This groundwater species was previously known from a single male described by Fleming (1972b) from a ditch in southwestern Mississippi. The new locality is the first report of a subterranean asellid from Louisiana. Identification of *C. paurotrigonus* is obscured by Fleming's description. Based on a single 16.7 mm male, the description provided drawings of key

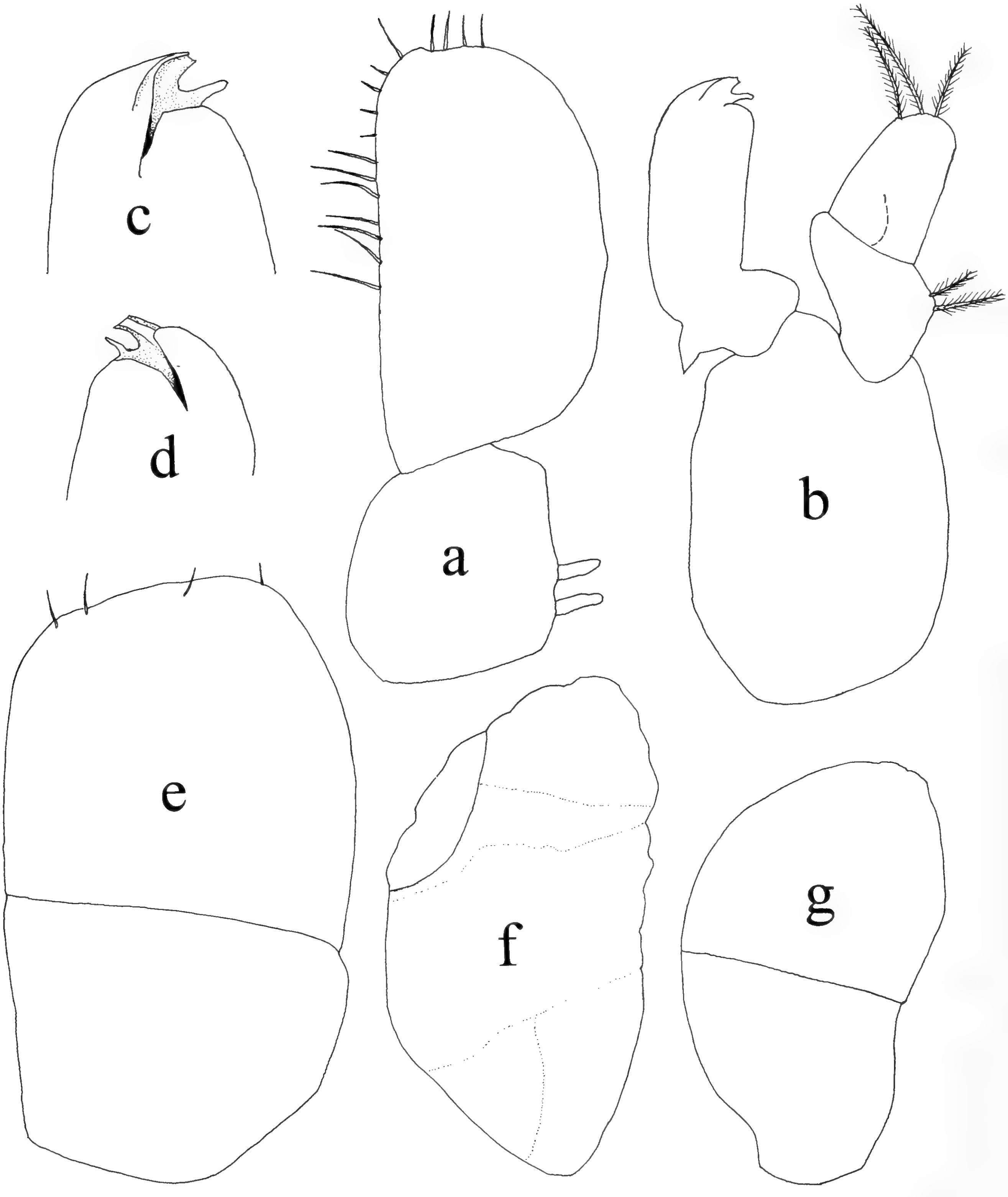

Fig. 3. *Caecidotea cumberlandensis,* 4.5 mm paratype male, Indian Cave, Lee Co., Virginia (a–c, e–g); 5.8 mm male, Cliff Cave, Lee Co., Virginia (d): (a) pleopod 1, (b) pleopod 2, (c) same, endopod tip, (d) same, (e) pleopod 3 exopod, (f) pleopod 4 exopod, (g) pleopod 5 exopod.

structures, but the quality of the drawings and the interpretation of the structures were both questionable. Modlin (1986) on the other hand provided a detailed description of *Caecidotea dauphina* based on a 7.5 mm male. Unfortunately, three of the four structures figured by Fleming for *C. paurotrigonus* bear a strong resemblance to that of *C. dauphina:* (1) pereopod 1 propods of very similar dimensions, margin in *C. dauphina* with basal spine, medial and distal processes, identical in *C. paurotrigonus* ex-

Table 1.—Comparison of selected structures of male *C. cumberlandensis, C. bicrenata* and *C. richardsonae* useful for separating the species.

	C. cumberlandensis	*C. bicrenata*	*C. richardsonae*
Pereopod 1 propod palmar margin processes	absent	present	absent
Pleopod 1 distolateral lobe	absent	absent	present
Pleopod 2 exopod	3–5 setae	12–15 setae	12–15 setae
Pleopod 2 endopod lateral process	thin, tapered distally	cylindrical, not tapered	long digitiform
Proportion of uropod length to pleotelson	0.5× length	1.5–2.0× length	1.5–2.0× length

cept the spine is replaced by a process (as typical of more mature specimens); (2) pleopod 1 with essentially identical shapes, setation patterns and quantity of retinacula; (2) pleopod 2 endopod tips with short apical cannula directed mediad, and short, unremarkable knob-like lateral process. I suspect that *C. dauphina* represents a well described juvenile of the poorly described, but conspecific *C. paurotrigonus*. Unravelling this will require redescription of *C. paurotrigonus* and perhaps more male specimens for comparison from Mississippi and Alabama.

Caecidotea barri (Steeves, 1965)

Material examined.—Kentucky: Woodford Co., small spring 0.6 mile E. Clifton, in side valley above waterfall, elevation about 670 feet, Julian J. Lewis, Victor M. Lewis, James J. Lewis, 19 Feb 1995, 3 males, 4 females.

Range.—This species was previously known only from the type-locality, Clifton Cave, Woodford Co., Kentucky (Steeves 1965), which was bulldozed shut by highway workers. The new locality is across the valley from Clifton Cave.

Caecidotea teresae Lewis, 1982b

Material examined.—Indiana: Floyd Co., well on Grant Line Road, Julian J. Lewis, 26 Apr 1995, 1 male, 1 female.

*Range.*This species was apparently extirpated by termiticides at the two previously known localities on the campus of Indiana University Southeast, New Albany. The well from which the new specimens were taken is found in a pasture across Grant Line Road from the I.U.S. campus. According to the owner, the well was hand dug at the end of the 19th century and was 21 feet deep, with 8 feet in soil and the bottom 13 feet through New Albany Shale.

Acknowledgments

The description of *Caecidotea cumberlandensis* was prepared during a visit to the National Museum of Natural History funded by a Smithsonian visiting scientist grant. *Caecidotea jordani* was rediscovered during the bioinventory of Blue River area caves funded by a Rodney Johnson/Katharine Ordway Stewardship Endowment Grant from The Nature Conservancy. *Caecidotea teresae* was rediscovered during field work funded by the Indiana Non-game and Endangered Wildlife Program. *Caecidotea barri* was found during field work funded by the U.S. Fish & Wildlife Service and Kentucky Nature Preserves Commission (Dr. Thomas C. Barr, Jr. principle investigator). I thank Dr. John R. Holsinger (Old Dominion University), Dr. Brian Kensley (Smithsonian Institution), Dr. Guy Magniez (University of Dijon), Mr. David Hubbard, Jr. (Virginia Division of Mineral Resources), and Mr. Allen Pursell (The Nature Conservancy) for reading the manuscript and making suggestions on its improvement.

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Euphilomedes cooki, a new species of myodocopid ostracode from Moreton Bay, SE Queensland, Australia

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Abstract.—A new species of myodocopid ostracode in the subfamily Philomedinae from Moreton Bay, S.E. Queensland, Australia, is described and illustrated. A key is presented to the ten known species of *Euphilomedes* having primary furcal claws 1, 2, 4, and 6.

This work describes and illustrates a new species of myodocopid ostracode from Moreton Bay, S.E. Queensland, Australia, which is north of Brisbane, near the southern end of the Great Barrier Reef.

Disposition of specimens.—The holotype and paratypes have been deposited at the Queensland Museum (QM), South Brisbane, Queensland.

Superorder Myodocopa Sars, 1866
Order Myodocopida Sars, 1866
Suborder Myodocopina Sars, 1866
Family Philomedidae Müller, 1906

This family contains two subfamilies, Philomedinae Müller, 1906, and Pseudophilomedinae Kornicker, 1967, both with representatives in the vicinity of S.E. Queensland, Australia (Kornicker 1994).

Philomedinae Müller, 1906

This subfamily includes eight genera: *Philomedes* Liljeborg, 1853, *Pleoschisma* Brady, 1890, *Scleroconcha* Skogsberg, 1920, *Paraphilomedes* Poulsen, 1962, *Euphilomedes* Kornicker, 1967, *Anarthron* Kornicker, 1975, *Igene* Kornicker, 1975, and *Zeugophilomedes* Kornicker, 1983. A new species of *Euphilomedes* is described herein.

Euphilomedes Kornicker, 1967

Type species.—*Euphilomedes nodosa* Poulsen, 1962 (subsequent designation by Kornicker 1967).

Composition.—Including the new species described herein this genus includes 19 species plus one subspecies (Kornicker 1991:3; 1995:16).

Distribution.—The genus is cosmopolitan except in Arctic and Antarctic waters. The known depth range is shallow water to 2250 m, but members have been collected mostly from the continental shelf and upper slope (Kornicker & Harrison-Nelson 1997: 14). Three species of the genus have been reported previously from the vicinity of Australia: *E. corrugata* (Brady 1897) from off Port Jackson and in Flinders Passage at depths of 3.7–18.3 m, *E. walfordi* Poulsen, 1962, from the Coral Sea at a depth of 50 m, and *E. erynx* Kornicker, 1995, from the continental slope off New South Wales at a depth of 220 m. The new species described herein is from Middle Banks, northern Moreton Bay, S.E. Queensland, Australia, at a depth of 15–25 m.

Euphilomedes cooki, new species
Figs. 1–9

Etymology.—The species is named in honor of Stephen Cook formerly of the Queensland Museum, Australia, who collected some of the specimens.

Holotype.—Queensland Museum W2492, undissected adult female in alcohol.

Type locality.—Middle Banks, northern Moreton Bay (27.02°S, 153.25°E), Queensland, Australia, about 20 km offshore from the mainland, depth 15–25 m. All specimens part of Queensland Museum Registration Number 11879.

Paratypes.—12 adult females; 3 A-1 males; 1 A-1 female.

Distribution.—Middle Banks, northern Moreton Bay, S.E. Queensland, depth 15–25 m, clean sand or sand and shell. Collected with Smith-McIntyre grab in November 1983 and November 1984.

Description of adult female (Figs. 1-7a–7c).—Carapace elongate with shallow incisur (Fig. 1a). Left valve extends past right valve along free margin. Posterodorsal hinge area straight and without valve overlap.

Ornamentation: Carapace with pits of various sizes and shapes. Each pit with narrow raised border. Some pits two or three times larger than others; pits larger in posterior half of valve. Valve edge with long single bristles. Long single bristles sparsely distributed on valve surface.

Infold: Rostral and anteroventral infold (Fig. 1b,c,e, 7a), infold of caudal process and posteroventral infold (Fig. 1d,f, 7b), each with row of bristles. Anteroventral infold with several parallel ridges (Fig. 1c).

Selvage: Broad lamellar prolongation of right valve in vicinity of rostrum with long marginal hairs; lamellar prolongation narrower and with shorter marginal hairs along ventral margin. Lamellar prolongation of left valve obscured.

Central adductor muscle attachments (Fig. 1g): About 30 attachments on each side. These represented by large pits on each valve just anterior to midlength; most pits ventral to midheight.

Carapace Size (mm): Average length 1.89, range 1.81–1.95; average height 1.36, range 1.29–1.42; average height 72% of length, range 71–74; *n* = 11.

	Length	Height	Height % length
Holotype	1.94	1.39	72
Paratypes	1.84	1.37	74
	1.95	1.40	73
	1.95	1.42	73
	1.87	1.37	71
	1.81	1.31	71
	1.91	1.36	73
	1.93	1.41	72
	1.86	1.33	73
	1.87	1.37	71
	1.81	1.29	71

First antenna (Fig. 2a): 1st joint with distal medial spines forming rows. 2nd joint with dorsal, ventral, and lateral spines, and 3 bristles (1 dorsal, 1 ventral, 1 medial). 3rd joint short with 3 bristles (2 dorsal, 1 ventral). 4th joint with 6 bristles (2 dorsal, 4 ventral). 5th joint about same length as 4th joint, with long sensory bristle with about 7 short marginal filaments. Long medial bristle of 6th joint with base near dorsal margin and with long proximal and short distal spines. 7th joint: a-bristle similar to bristle of 6th joint; b-bristle with 2 filaments near midlength, 2 subterminal filaments, and bifurcate tip; c-bristle long with marginal filaments. 8th joint: d- and e-bristles long, bare, and with blunt tips; f- and g-bristles long with marginal filaments. Not all filaments of bristles of 7th and 8th joints shown in illustration.

Second antenna: Protopodite bare. Endopodite 2- or 3-jointed (Fig. 2b): 1st joint with row of 5 short bare proximal bristles and 1 very long spinous distal bristle; 2nd joint with very long spinous proximal bristle (bristle 2 ½ times length of long bristle of 1st joint) and short bare terminal bristle (the terminal bristle could be interpreted to be on a 3rd joint). Exopodite: 1st joint with minute straight medial terminal bristle; bristle of 2nd joint reaching well past 9th joint, with few dorsal spines and abundant short, fairly stout, ventral spines, no natatory hairs; bristles of 3rd and 4th joints with short slender distal spines, no natatory

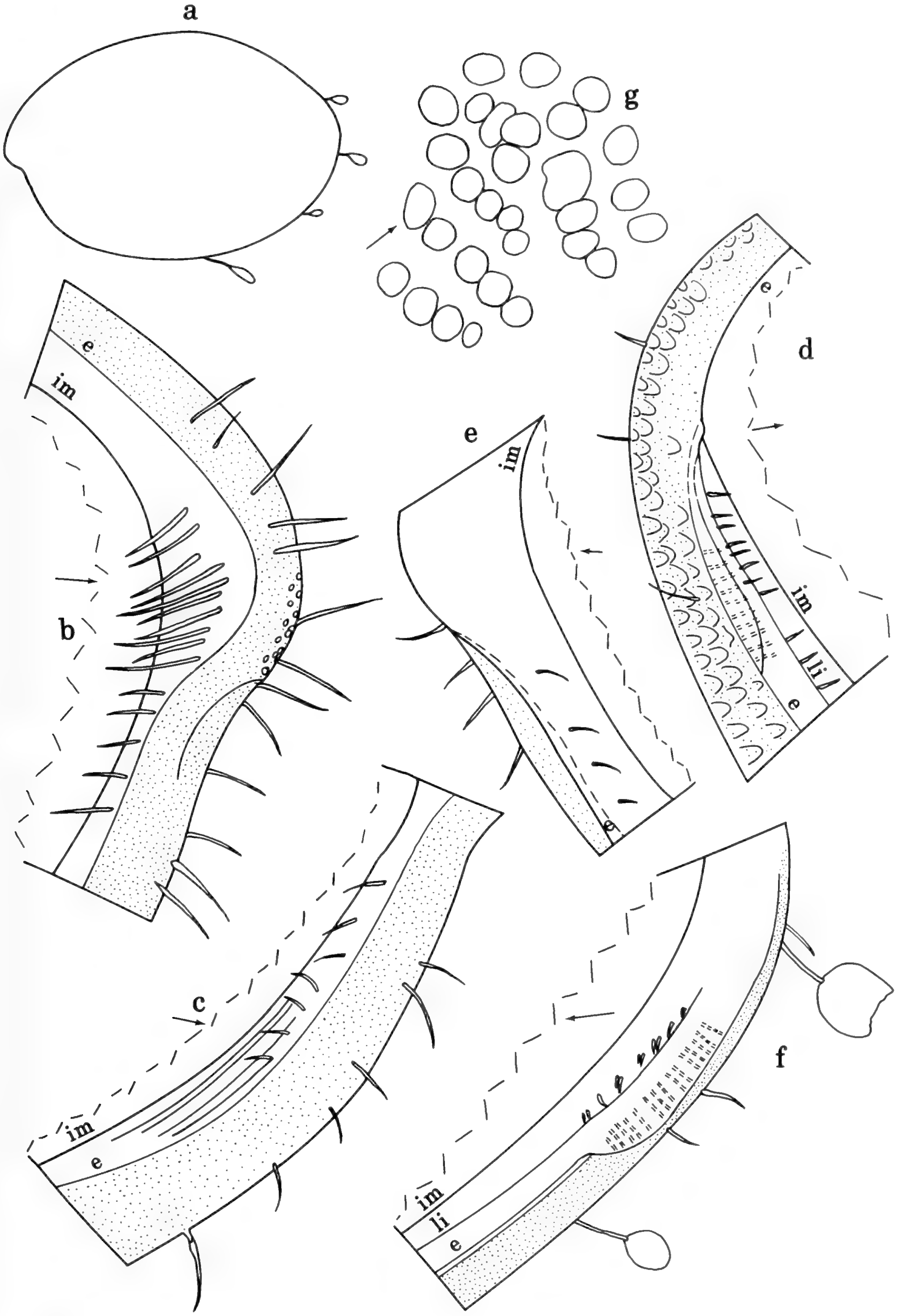

Fig. 1. *Euphilomedes cooki* specimen 12, adult female paratype: a, outline of complete specimen from left side, length 1.84 mm, note four epibionts attached to edge of valve. b–d, interior views of left valve: b, anterior end; c, anteroventral margin; d, posterior end. e, f, interior views of right valve: e, anteroventral margin; f, posteroventral margin. g, ends of central adductor muscles projecting from right side of body, anterior toward right. Abbreviation are: ant: antenna; Bo: Bellonci organ; cx: coxale; e: edge of valve; end: endopodite; ex: exopodite; epip: epipodite; fu: furca; gen: genitalia; gird: girdle; im: inner margin of infold; li:list; lv: lateral view; me: medial eye; mnd: mandible; mv: medial view; mx: maxilla; nabs: not all bristles shown; prot: protopodite; ul: upper lip; Y-scl: Y-sclerite. Roman numerals designate endites. Arrow on illustration indicates anterior.

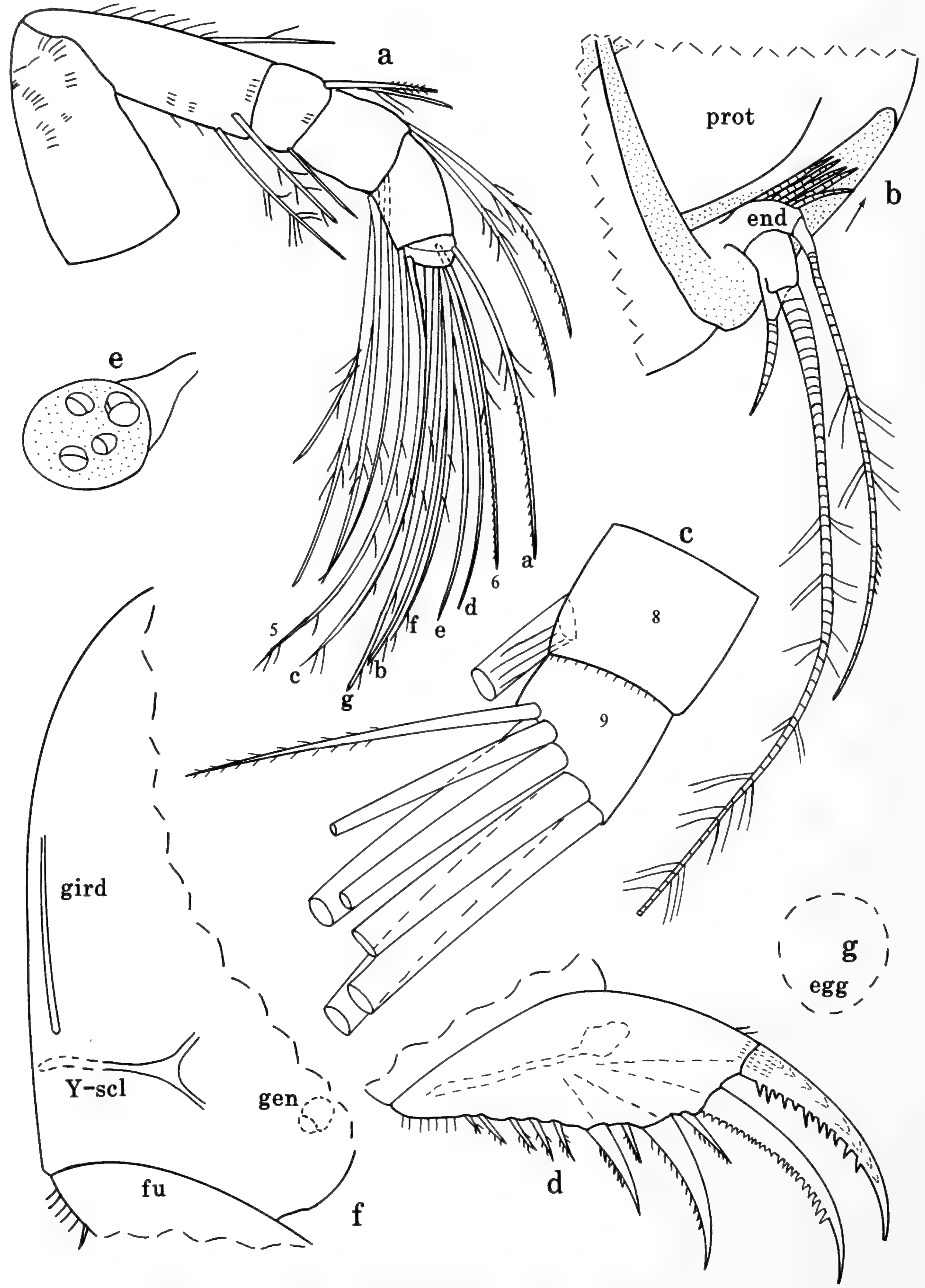

Fig. 2. *Euphilomedes cooki* specimen 12, adult female paratype: a, right 1st antenna, lv; b, left 2nd antenna, endopodite and distal part of protopodite, mv; c, right 2nd antenna, exopodial joints 8 and 9, only proximal parts of some bristles shown, lv; d, right furcal lamella, lv; e, left lateral eye, lv; f, posterior of body from right side; g, outline of unextruded egg, drawn at same scale as "f". (For abbreviations see Fig. 1.)

hairs; bristles of joints 5–8 longer than bristles of joints 2–4, with natatory hairs, no spines; 9th joint with 7 bristles (4 long and 2 short with natatory hairs, 1 very short and with short marginal spines (Fig. 2c, only proximal parts of some bristles shown); joints 2–8 with row of terminal spines.

Mandible (Fig. 3a, b): Coxale endite spinous, tip bifurcate, with small ringed bristle near base. Basale: medial surface and ventral and dorsal margins with rows of spines; medial surface with 5 bristles in proximal ventral corner (3 pectinate unringed, 2 ringed and with long proximal and short distal spines), and 1 short ringed bristle closer to midlength with long proximal and short distal spines; dorsal margin with 3 bristles (1 near midlength, 2 terminal); 7 bristles with long proximal and short distal spines present on or near ventral margin (2 longest bristles distal and with bases on ventral margin; 5 shorter bristles with bases slightly lateral). Exopodite slightly more than ½ length of dorsal margin of 1st endopodial joint, with distinct distal hirsute pad and few terminal spines, and 2 bristles (outer bristle with short marginal spines and about ⅓ length of inner bristle; inner bristle reaching midlength of 2nd endopodial joint, with long spines near midlength and short distal spines). 1st endopodial joint with medial spines and 4 ventral bristles. 2nd endopodial joint: dorsal margin with 2 long bristles in proximal group and 5 spinous bristles in distal group (2 long with basis on margin; 3 short with bases medial (proximal 2 with long spines, distal 1 with short spines)); ventral margin with bristles in 2 groups (2 in proximal group, 3 in distal group); medial surface with spines forming rows. 3rd endopodial joint with 3 pectinate claws (dorsal claw short), and 3 ringed bristles.

Maxilla (Figs. 3b, 4a–c): Precoxale and coxale with fringe of long hairs. Coxale with plumose dorsal bristle. Basale with 3 distal bristles. Exopodite with 3 bristles (proximal short bristle bare, long middle bristle with long spines, other long bristle with short spines). 1st endopodial joint with 1 alpha-bristle and 4 beta-bristles. 2nd endopodial joint with 3 pectinate claw-like bristles and about 7 ringed bristles. Endites with stout spinous and pectinate bristles (endite I with 9 bristles, endite II with 6 bristles, endite III with 8 bristles).

Fifth limb (Figs. 4d–f, 5): Epipodite with 46 bristles. Endite I with 5 bristles (only 3 shown in illustration); endite II with 6 bristles; endite III with 8 bristles. 1st exopodial joint: anterior side with 2 bristles (with long spines) on distal edge; outer corner with 2 small slender bristles with few marginal hairs; main tooth with proximal peg followed by 3 pointed teeth (teeth worn down on specimen 12) and 1 large squarish tooth; ringed spinous bristle proximal to teeth. 2nd exopodial joint: posterior side with 1 proximal bristle and group of 3 distal bristles (middle bristle long, others short (short bristle obscured on right limb of specimen 12)). 3rd exopodial joint: inner lobe with 3 bristles, outer lobe with 2 bristles with long spines. Fused 4th and 5th exopodial joints with 8 bristles.

Sixth limb (Figs. 5a, 6a): Epipodite with 3 spinous bristles. Endite I with 3 bristles; endite II with 4 bristles; endites III and IV each with 9 bristles. End joint with spines and hairs and 18 bristles (most with long proximal hairs and short distal spines).

Seventh limb (Fig. 6b, c): Each limb with 13–15 bristles: proximal group with 8–10 bristles (specimen 12: 5 or 6 on peg side, 4 on comb side; specimen 4 (right limb), 5 on peg side, 3 on comb side), each bristle with 3–5 bells and marginal spines; terminal group with 5 bristles (3 on peg side, 2 on comb side). Each bristle with 3–7 bells and marginal spines. Terminal comb with 12 alate teeth; 2 small curved pegs (with proximal teeth) present opposite comb.

Furca (Fig. 2d, f): Each lamella with 11 claws: claws 1, 2, 4, and 6 primary; claws 3, 5, 7–11 secondary. Primary claws with stout posterior teeth; teeth of claw 1 stouter than teeth of other primary claws and with stout medial teeth; secondary claws with

Fig. 3. *Euphilomedes cooki* specimen 12, adult female paratype: a, right mandible, mv; b, left maxilla and mandible in place on body, nabs, mv; c, medial eye and Bellonci organ from left side. (For abbreviations see Fig. 1.)

Fig. 4. *Euphilomedes cooki* specimen 12, adult female paratype: a–c, right maxilla: a, complete limb, lv; b, bristle of distal end of 1st exopodial joint, mv; c, bristles and claws of 2nd endopodial joint, mv. d–f, left 5th limb, endites I, II, and III, respectively. (For abbreviations see Fig. 1.)

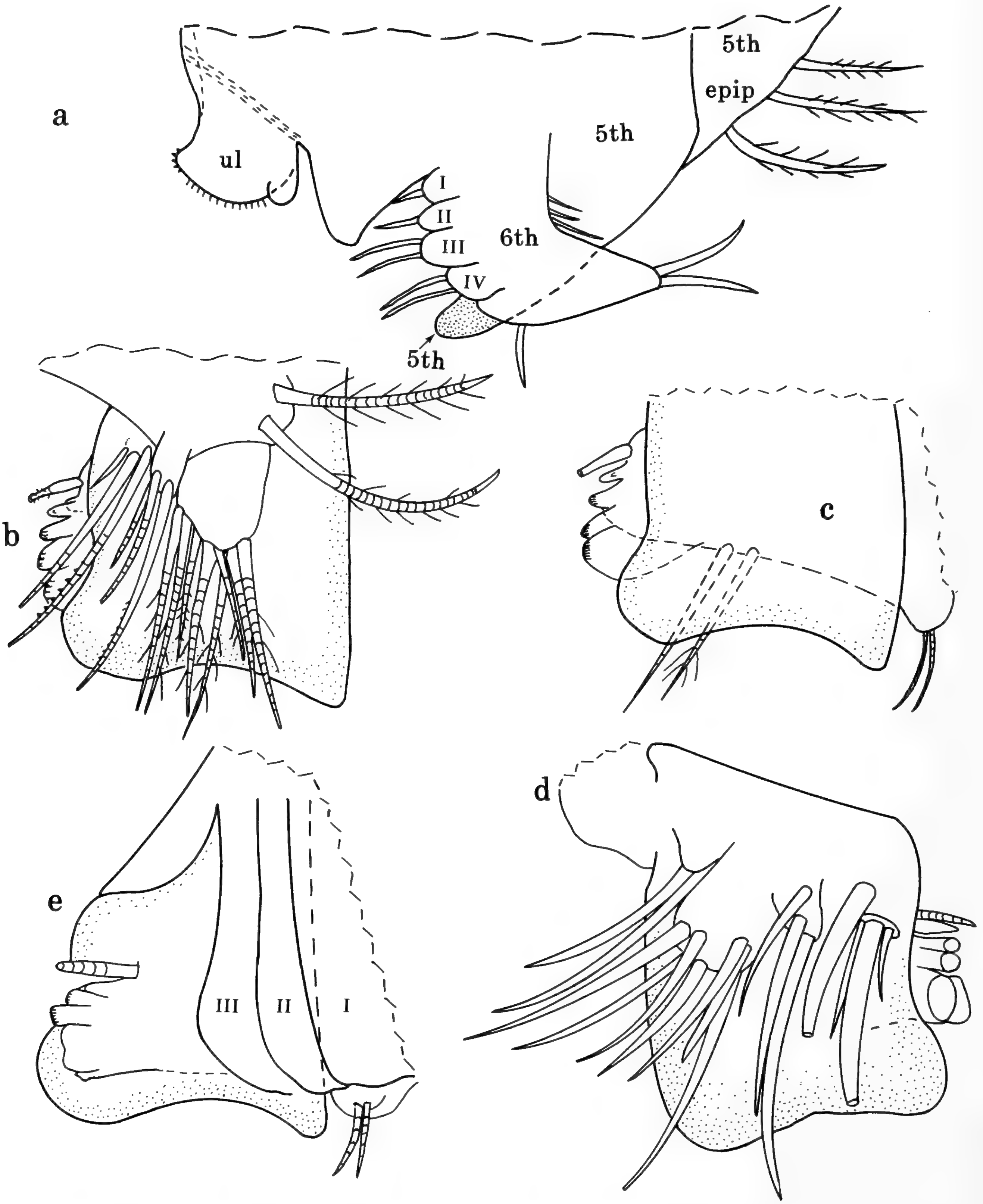

Fig. 5. *Euphilomedes cooki* specimen 12, adult female paratype: a, upper lip, left 6th limb, and right 5th limb in place on body, not all bristles shown. b, c, posterior views of distal end of right fifth limb, respectively. d, e, posterior and anterior views of distal end of left fifth limb, respectively. (For abbreviations see Fig. 1.)

marginal spines. Right lamella with few distal anterior spines and also spines medial and proximal to claw 1. Right lamella anterior to left by ¾ width of claw 1.

Bellonci organ (Fig. 3c): Elongate with short wide part (bearing striations) near midlength and narrow tapered tip bearing minute spines.

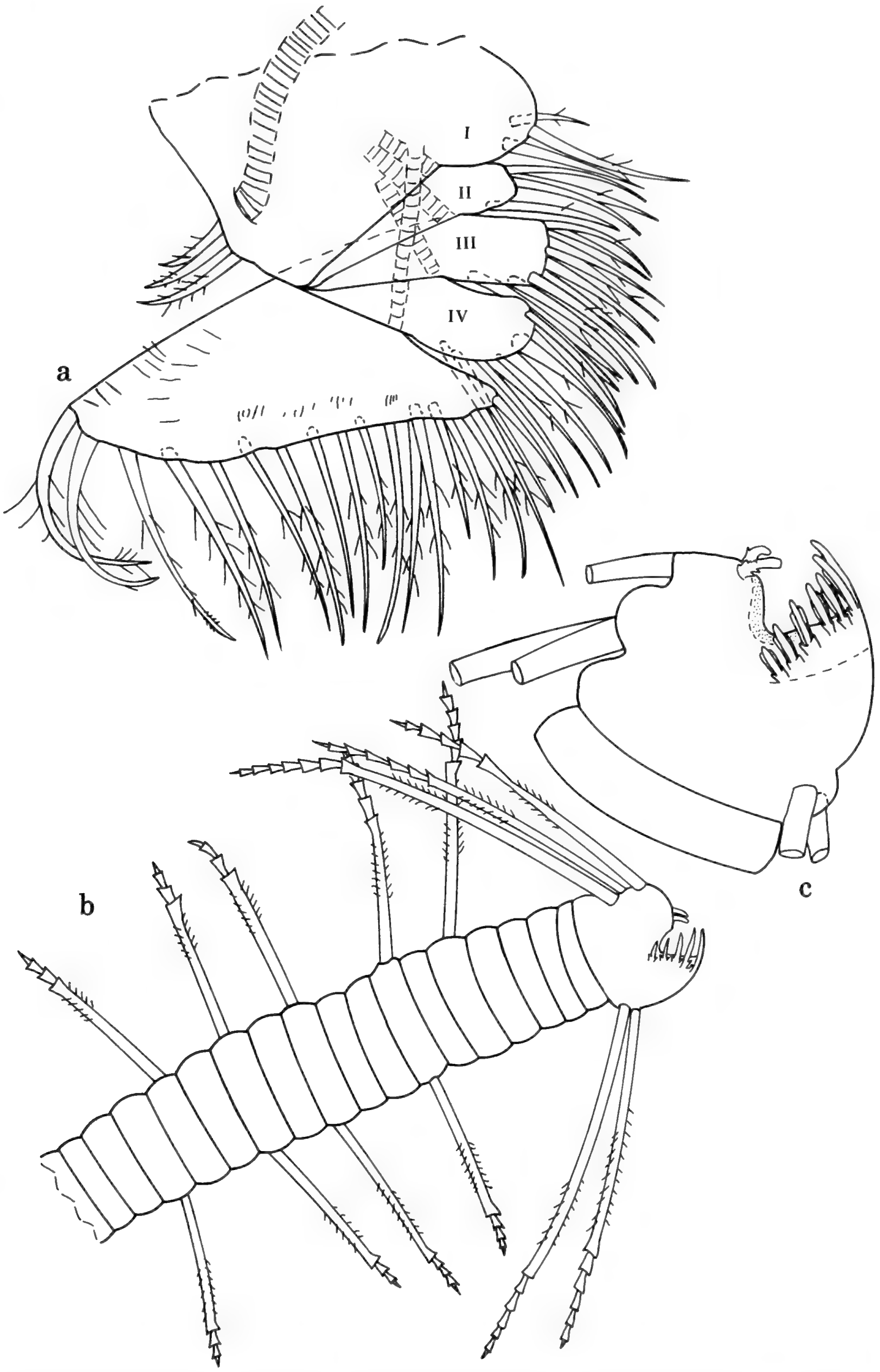

Fig. 6. *Euphilomedes cooki* specimen 12, adult female paratype: a, right 6th limb, lv; b, right 7th limb; c, tip of left 7th limb, only proximal part of bristles shown. (For abbreviations see Fig. 1.)

Eyes: Medial eye with brown pigment (Fig. 3c). Lateral eye smaller than medial eye, unpigmented, with 4 divided amber-colored ommatidia (Fig. 2e).

Upper lip (Figs. 5a, 7c): Projecting slightly anteriorly, with anterior and lateral glandular processes.

Genitalia (Fig. 2f): Small oval.

Anterior of body: Convex.

Posterior of body (Fig. 2f): Evenly rounded, bare.

Y-sclerite (Fig. 2f): With ventral branch.

Number and lengths of eggs: Specimen 12 with about 16 unextruded eggs (Fig. 2g). Specimen 4 with 18 eggs in marsupium (lengths of 2 eggs 0.406 mm, 0.408 mm).

Gut content: Specimen 12 with unrecognizable amber-colored particles in gut.

Epizoa: Specimens 12 and 4 with vase-shaped protistans along posterior margin (Fig. 1a, f).

Description of A-1 male (Fig. 7d–f).—Carapace similar in shape and ornamentation to that of adult female.

Carapace size (length, height in mm): 1.59, 1.06, height 67% of length (specimen 13); 1.58, 1.13, height 72% of length.

Second antenna: Protopodite bare with narrow slightly curved proximal pivotal sclerite. Endopodite 3-jointed (Fig. 7d): 1st joint short with 4 small proximal ringed bristles and 1 distal long stout ringed bristle (broken off in illustrated endopodite (Fig. 7d)); 2nd joint elongate with 3 small ringed bristles; 3rd joint elongate with 2 small ringed terminal bristles with short spines. Exopodite 9-jointed: 1st joint with small medial terminal spine; bristle of 2nd joint less than twice length of exopodite, with spines along ventral edge; bristles of joints 3–8 fairly short, longer than bristle of 2nd joint, but less than twice length of exopodite, with ventral spines stouter than those of bristle of 2nd joint, without natatory hairs; 9th joint with 6 bristles (2 short lateral at distal dorsal corner, 4 longer terminal (longest at ventral end and less than twice length of exopodite)), all with marginal spines, without natatory hairs; joints 2–8 with row of spines along terminal edges.

Fifth limb (Fig. 7e, f): Similar to that of adult female.

Sixth limb: With 3 epipodial bristles. Endite I with 3 bristles; endite II with 4 bristles; endite III with 8 bristles.

Seventh limb: Limb with 12 tapered bristles with marginal spines: proximal group with 7 bristles (3 on comb side, 4 on peg side), each with 2 or 3 bells; terminal group with 5 bristle (2 on comb side, 3 on peg side), each with 2–5 bells. Terminus with comb of about 11 alate teeth opposite 2 small pegs.

Furca: Similar to that of adult female except with only 4 secondary claws following primary claw 6.

Lateral eye: Well developed with many ommatidia and black pigment between them.

Description of A-1 female (Figs. 8,9).—Carapace similar in shape and ornamentation to that of adult female, but narrower.

Carapace size (length, height in mm): 1.58, 1.02; height 65% of length (specimen 1).

Remarks.—The absence of natatory hairs on bristles of the exopodite of the 2nd antennae of A-1 males and females indicates that the juveniles of this species are incapable of efficient swimming.

Comparisons.—Each lamella of the furca of the new species *E. cooki* bears primary claws 1, 2, 4, and 6, secondary claws 3 and 5, and 5 additional secondary claws following primary claw 6. Only one species of *Euphilomedes* having a similar distribution of primary and secondary claws has been described previously from the vicinity of Australia, *E. walfordi,* which is known from only the adult male, and so is not directly comparable in all morphological characters to the adult female and A-1 instar male of *E. cooki* described herein. However, the following differences between the adult male of the *E. walfordi* and the adult female of *E. cooki* are considered significant: 1, The carapace length of the adult female *cooki* is

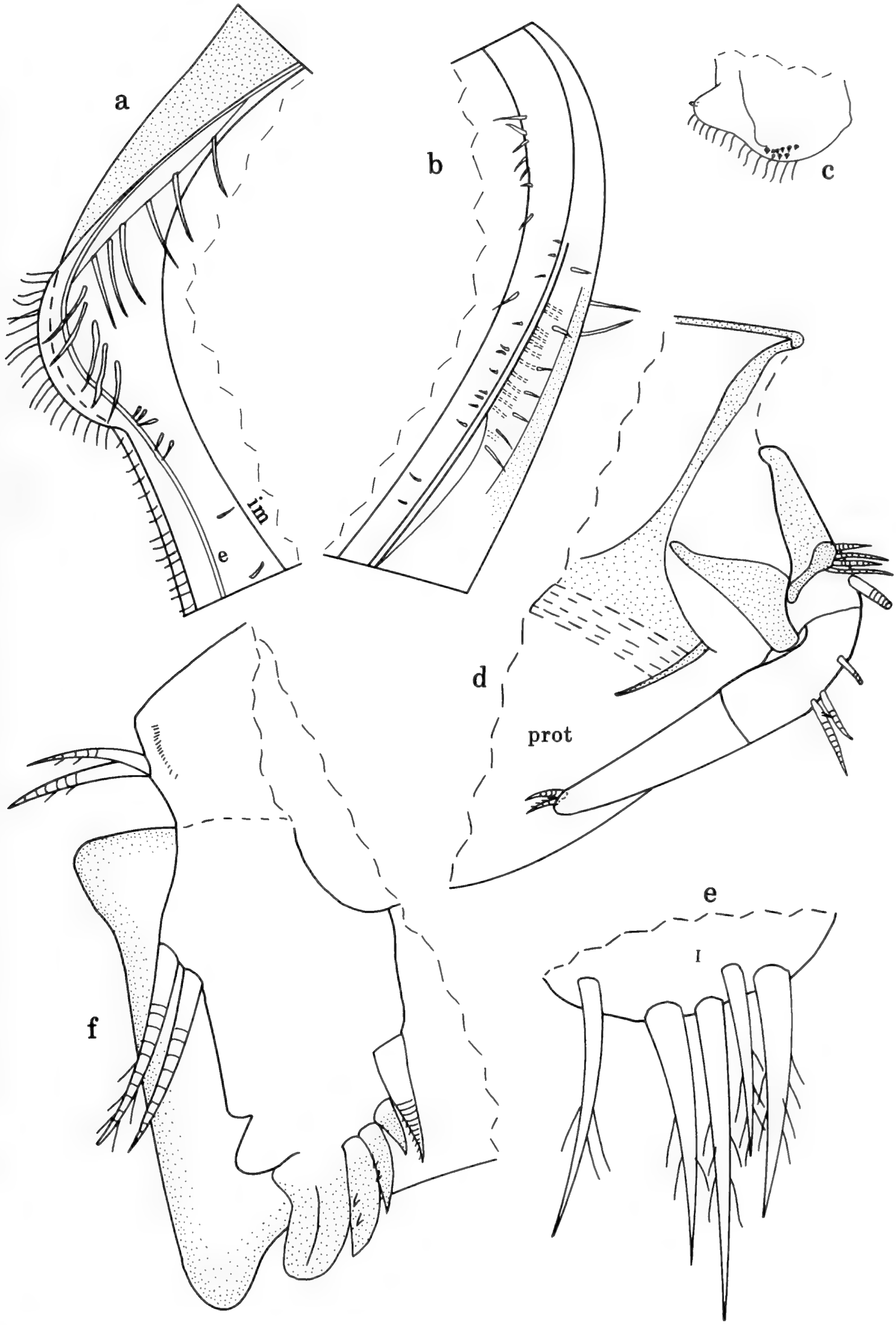

Fig. 7. *Euphilomedes cooki* specimen 2, adult female paratype: a, b, interior views of anterior and posterior ends of right valve, respectively; c, upper lip, anterior toward left. d, specimen 13, A-1 male paratype, left 2nd antenna, endopodite and distal part of protopodite, mv. e, f, right 5th limb, av: e, distal end endite I. (For abbreviations see Fig. 1.)

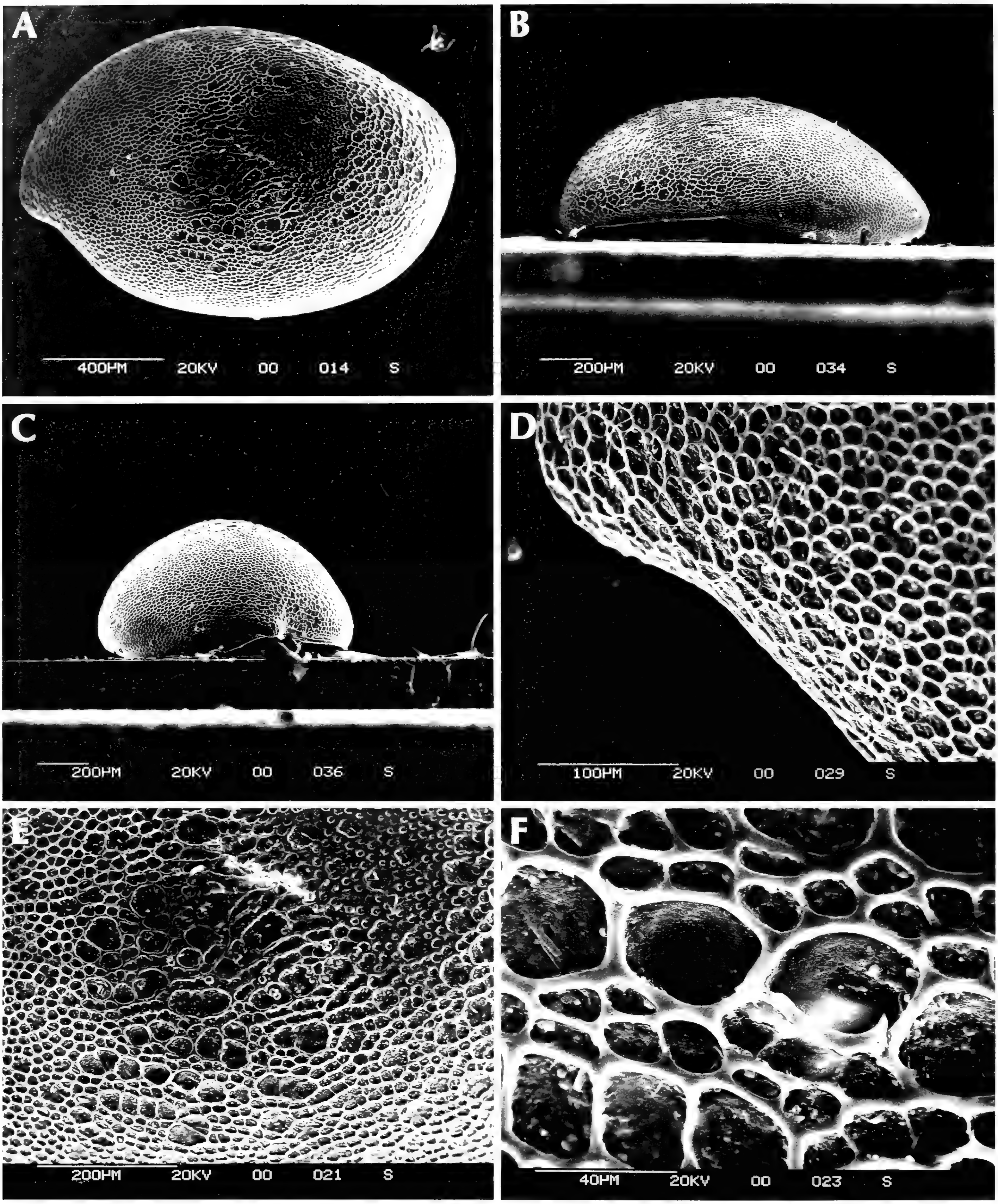

Fig. 8. *Euphilomedes cooki,* A-1 female paratype (specimen 1), left valve: a, lateral view of valve, length 1.58 mm; b, dorsal view of valve, anterior to left; c, anterior view of valve, ventral to right; d, anteroventral margin of valve, lv, from "a"; e, area in vicinity of central adductor muscle, from "a"; f, detail of reticulations, from lower left part of "e".

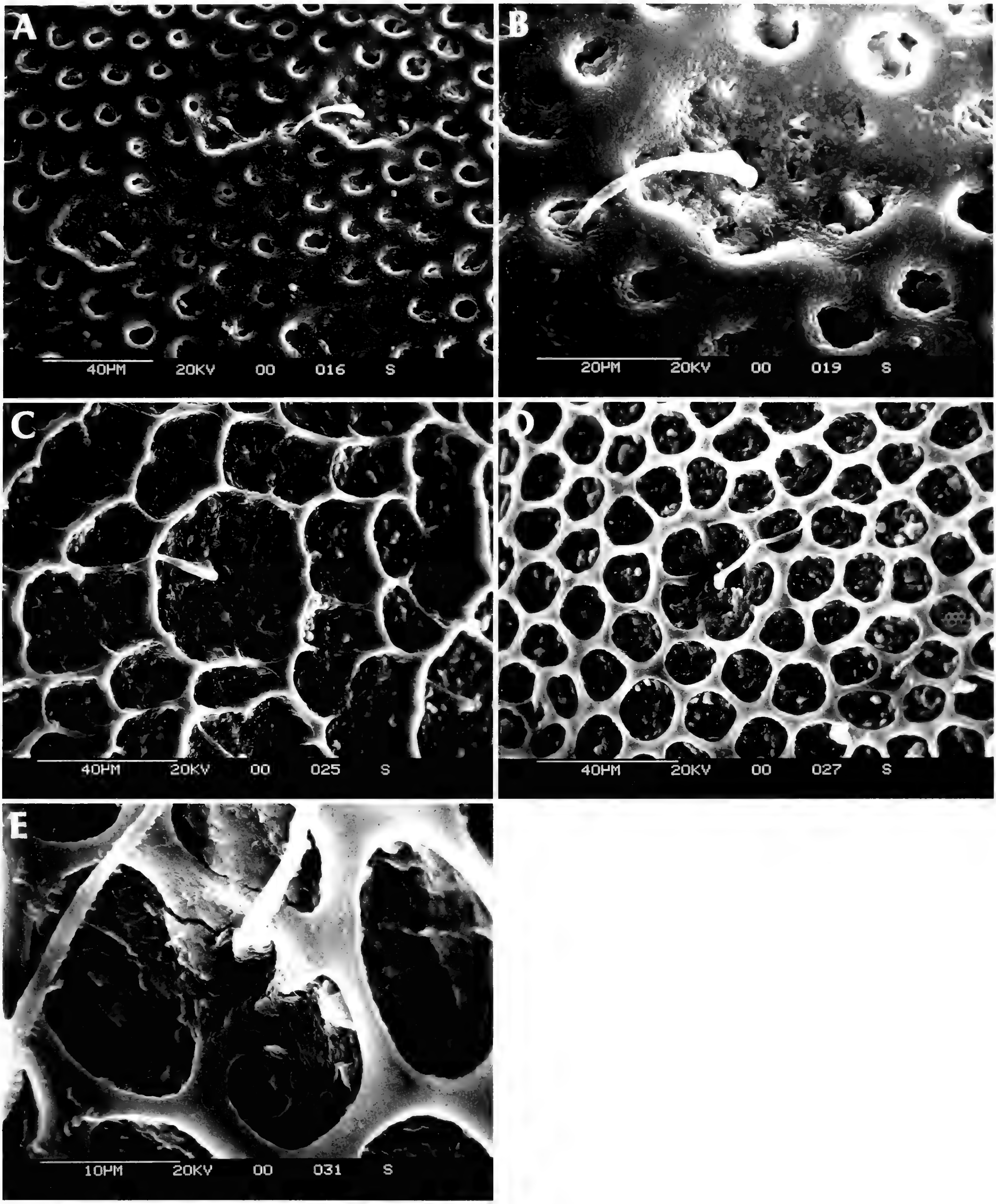

Fig. 9. *Euphilomedes cooki* A-1 female paratype (specimen 1), left valve: a, detail of pits and bristles in upper right part of Fig. 8a; b, detail of bristle shown in upper right of "a"; c, detail of bristle and reticulations in posterior part at midheight of Fig. 8a; d, detail of bristle and reticulations in anterior part at midheight of Fig. 8a; e, detail of bristles and reticulations near incisure in Fig. 8d.

1.73–1.95 mm compared to 3 mm for the adult male *walfordi*; 2, the outer surface of the carapace of the adult female *cooki* has few hairs, whereas that of the adult male *walfordi,* according to Poulsen (1962:371), "is densely covered with short hairs". The seventh limb of the adult male *walfordi* has 19 bristles without marginal spines (Poulsen 1962:372), whereas that limb of the adult female *cooki* has 13–15 bristles with marginal spines (when differences occur in the number of bristles on the 7th limbs of male and female myodocopids, the male generally has fewer bristles than the female).

The key to species of *Euphilomedes* presented below is restricted to those species having furcal lamellae with primary claws 1, 2, 4, and 6, and secondary claws 3, 5, and 7+.

Key to species of *Euphilomedes* having furcal claws 1, 2, 4, and 6 primary*

1\. Lower angle of posterior shell margin with small tooth . . . . *E. sinister* (Kornicker, 1974)
1\. Lower angle of posterior shell margin without tooth 2
2\. Seventh limb with less than 12 cleaning bristles 3
2\. Seventh limb with 13–15 cleaning bristles . . . . *E. cooki,* n. sp.
2\. Seventh limb with more than 15 cleaning bristles . . . . . . *E. walfordi* (Poulsen, 1962)
3\. 2nd joint of endopodite of female 2nd antenna with only the long plumose bristle . . . . *E. africana* (Klie, 1940)
3\. This joint with an additional distal bristle 4
4\. The distal bristle is only a spine, shorter than the width of the joint . . . . *E. japonica* (Müller, 1890)
4\. This bristle slightly longer than width of joint . . . . *E. morini* (Kornicker & Harrison-Nelson, 1997)
4\. This bristle longer than twice the width of the joint 5
5\. This bristle is placed dorsally on the joint . . . . *E. nodosa* (Poulsen, 1962)
5\. This bristle is placed on the narrow tip of the joint 6
6\. Furca with more than 12 pairs of claws . . . . *E. smithi* (Poulsen, 1962)
6\. Furca with 11 or less pairs of claws . . . 7
7\. Shell with a dorso-posterior, chitinized process . . . . . . *E. producta* (Poulsen, 1962)
7\. Shell without such process . . . . *E. longiseta* (Juday, 1907)

* Key adapted in part from the key to species of the genus *Euphilomedes* in Poulsen (1962:362).

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A new record of *Cornechiniscus madagascariensis* Maucci, 1993 (Tardigrada: Echiniscidae) from India

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Abstract.—*Cornechiniscus madagascariensis* Maucci, 1993 which has been known only from its type locality, Madagascar, is reported from Himachal Pradesh, northern India. Some taxonomic emendations to the original description are made from the paratypes.

Recently, through the courtesy of Dr. H. Dastych of the Zoologisches Institut und Zoologisches Museum der Universität Hamburg, we had an opportunity to examine an unidentified *Cornechiniscus* species collected from Himachal Pradesh, northern India. After the direct comparison with the paratypes of *C. madagascariensis* Maucci, 1993 deposited in the Museo Civico di Storia Naturale di Verona, it was concluded that the specimen from India should be identified with *C. madagascariensis* which has previously been known only from its type locality, Madagascar. In this paper, we describe this species in detail based on the specimen from India, and make some taxonomic emendations from the paratypes.

The specimens mounted on the microslides were closely examined by a phase and Nomarski differential interference contrast microscope (Zeiss Axiophot) at maximum magnification (×2500), illustrated with the aid of camera lucida, and measured using an eyepiece micrometer.

Terminology is mainly that used in Abe et al. (1998). Abbreviations used in the text are as follows, CT: Museo Civico di Storia Naturale di Verona (Italy), ZMH: Zoologisches Institut und Zoologisches Museum der Universität Hamburg (Germany).

Genus *Cornechiniscus* Maucci & Ramazzotti, 1981

Diagnosis.—Echiniscidae with horn-shaped cirrus A. Granulation on body surface consists of cuticular swellings. Pseudosegmental plate present. Secondary clava hemispherical. Venter with longitudinal cuticular grooves.

Type species.—*Echiniscus cornutus* Richters, 1907

Cornechiniscus madagascariensis Maucci, 1993

Figs. 1, 2, 3A–E

Cornechiniscus madagascariensis Maucci, 1993:383, figs. 1–4.—Antananarivo, Madagascar.

Material examined.—Paratypes: two adult females, Madagascar "Antsirabe, 8/v/1989, *Cornechiniscus lobatus madagascariensis* Maucci, paratipo, 19/v" mounted in polyvinyl-lactophenol (CT 13915, 13918). One adult female, India "Himal [sic Himachal] Pradesh, 1500 m asl., moss from rocks, Sep 1976, lg. J. Błoszyk, (T. 4), *Cornechiniscus*" (ZMH).

Comparative material.—*Cornechiniscus lobatus* (Ramazzotti, 1943): syntypes: Italy "I-44, *Pseudechiniscus cornutus* f. *lobata,* Montirone (Abano), 12-5-42, G. Ramazzotti, 1 Muta con 2 uova, 6 [sic 7] Individui, forma *lobata,* (Muschi su roccia), -solo Faure-, 24, TIPO, *P. cornutus* f. *lobata*" (CT).

Female from India.—Body length 295.0 μm excluding leg IV, width 136.0 μm; body width : body length, 1:2.17. Eyespot well-marked, black, subelliptical, 9.7 μm wide, situated in posterior part of head plate. Body color evenly translucent in preserved material.

Dorsal plates thick. Dorsal surface including intersegmental lateral plates wholly covered with fairly coarse granulation that consists of pillar-shaped cuticular granules; adjacent granules distantly spaced, interconnected with conspicuous cuticular striae; granules near edge of each plate much smaller than those at median part; granules on scapular, segmental paired, median, intersegmental lateral (1 and 2), pseudosegmental, and terminal plates ca. 2.5 μm in diameter; granules on head plate and anterior part of neck plate ca. 1.5 μm in diameter; granules on posterior part of neck plate ca. 0.2 μm in diameter. Lateral region of neck plate and basis for cirrus A only with very fine, densely distributed punctations that consist of pillar structures of epicuticle.

Head plate well-developed, with two zigzag-sutures, showing facetted appearance.

Neck plate conspicuous, subdivided vertically into three parts; posterior part of neck plate developed as a lobe which is narrowly overlapping anteriormost part of scapular plate.

Scapular plate well-developed, anterior with poorly defined W-shaped sculpture; posterior to W-shaped sculpture, scapular plate shallowly subdivided vertically at middorsal line of body; an oblique cuticular line at each lateral side.

Median plate 1 clearly subdivided into anterior and posterior parts; anterior part fairly larger than posterior part; anterior and posterior parts trapezoidal and inverted subtriangular in shape, respectively.

Intersegmental lateral plates 1 and 2 similar to each other in size and shape.

Segmental paired plates II and III well developed, similar to each other in size and shape, both with lateral segmental plates; small, triangular spines developed posterior part of lateral segmental plates II and III each (spines C and D).

Median plate 2 clearly subdivided into anterior and posterior parts; anterior part subpentagonal, fairly larger than posterior part; posterior edge of posterior part sinuate.

Median plate 3 well-developed, rhomboidal, undivided.

Pseudosegmental plate clearly subdivided vertically at middorsal line of body; lobe on its posterior margin well-developed, unpaired, but shallowly bilobate, 11.4 μm high, 33 μm wide at base; tips of lobe smooth, without spine.

Terminal plate with obvious, long incision which is slightly effaced near middorsal line of body; minuscule, triangular spine developed posteriormost of incision (spine E).

Leg plates developed on outer surfaces of legs I–III and dorsal surface of leg IV; each leg plate with coarse granulation similar to those on dorsal plates, i.e. adjacent granules interconnected with cuticular striae; granules larger but sparse on median part of leg plate, smaller but dense on peripheral part. Plate of leg IV without true dentate collar, but with very blunt triangular process posterior to leg plate. Sensory organ on leg I conical, 6.3 μm long, 1.7 μm wide at base; sensory organ on leg IV papillate, 6.9 μm long, 5.1 μm wide at base.

Dense patches of cuticular granulation situated below mouth opening, between each pair of legs I–III, and around gonopore; these patches each without perceptible edge. Venter longitudinally costate, with some shallow, linear grooves that developed from cuticular patch between leg I to gonopore, along with midline of body.

Mouth opening and cephalic sensory organs situated ventrally. Internal cirrus onion-shaped, tapering sharply toward tip, 8.6 μm long, 5.1 μm wide at base; external cir-

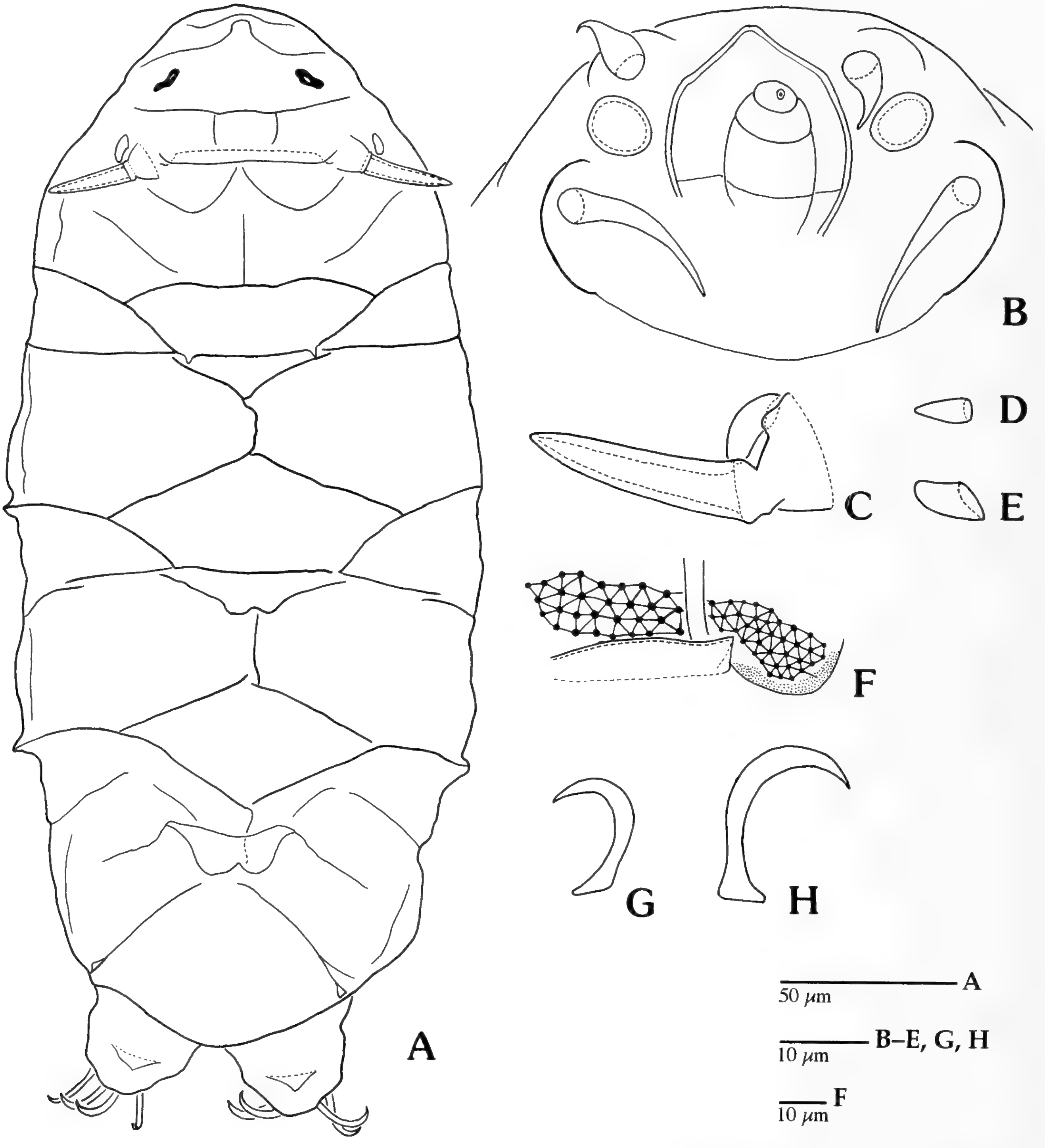

Fig. 1. *Cornechiniscus madagascariensis* Maucci, 1993. A, habitus, dorsal view; B, cephalic region, ventral view; C, cirrus A and primary clava on the left, dorsal view; D, sensory organ I; E, sensory organ IV; F, left side of segmental paired plate III and pseudosegmental plate; G, external claw of leg I; H, internal claw of leg IV. (A–E, G, H: ZMH; adult female; Himachal Pradesh, N India. F: CT 13918; paratype adult female; Antsirabe, Madagascar).

rus stout, tapering gradually, 21.4 μm long, 4.0 μm wide at base; both internal and external cirri without true cirrophores, but their proximal portions swollen in appearance; furthermore, internal and external cirri each with hemispherical cuticular swelling beneath own base; both sides of cuticular swellings of external cirri interconnect each other with arcuate cuticular line. Secondary clava hemispherical, 7.4 μm in diameter, situated nearer to internal cirrus than to external cirrus.

Cirrus A clearly longer than external cirrus, 28.6 μm long, 9.7% of body length, 6.9

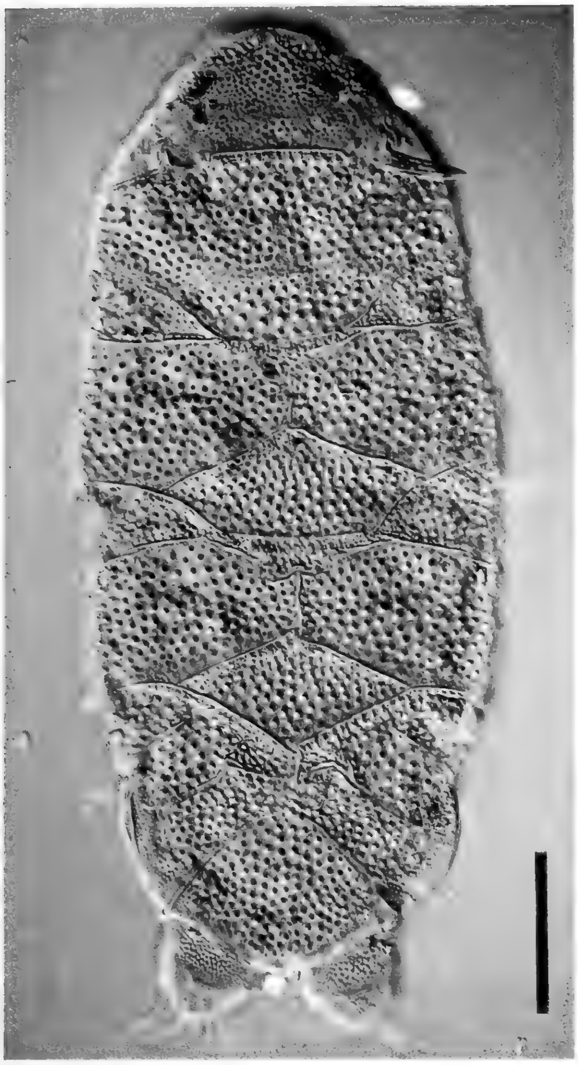

Fig. 2. *Cornechiniscus madagascariensis* Maucci, 1993. Habitus, dorsal view. (ZMH; adult female; Himachal Pradesh, N India). Differential interference contrast. Scale = 50 μm.

μm wide at base, directed laterad; cirrus A provided with normally developed cirrophore; primary clava situated just behind cirrophore of cirrus A, clavate, curved, apex directed posteriad, 8.0 μm long, 4.8 μm in diameter at base.

Claws I–III distally curved, whereas claw IV less curved compared with claws I–III; all claws thickened basally, without spur; internal claw slightly longer than external claw on all legs; claws I–III 12.8–14.3 μm long; claw IV clearly longer than claws I–III, ca. 18 μm long.

Female gonopore normal, consists of rosette-like structure, 16 μm in diameter. Anus large, situated posteriad, near base of legs IV.

Emendatory notes on the paratypes.—Body 282.1 and 322.4 μm long. Neck plate tripartite vertically. Scapular plate ornamented with ill-defined W-shaped sculpture. Cuticular grooves on venter well-marked. Small spines developed at positions C, D, and E. Other characters in concordance with Maucci (1993).

Remarks.—We examined two paratypes (lengths 295.0 and 322.4 μm) of *C. madagascariensis.* The specimen from India is almost identical with the paratypes including the following important characters: pattern of the dorsal granulation, shape and size of each claw, morphology of the cephalic and leg sensory organs. Although we were able to examine only one specimen from India, there seems to be no problem for us to identify the specimen with *C. madagascariensis.*

Maucci (1993) considered that *C. madagascariensis* is most closely related to *C. lobatus* Ramazzotti, 1943, and we agree with him on this point. He pointed out that the consistent absence of the dorsal and lateral body spines is one of the most important characters to distinguish *C. madagascariensis* from *C. lobatus.* We confirmed, however, that, as in *C. lobatus,* the small spines are actually present at positions C, D, and E also in *C. madagascariensis* (both in the paratypes and specimen from India).

There are some reports of *C. lobatus* provided with cuticular striae among dorsal granules, viz. Binda & Pilato (1972) from Sicily (Italy), Dastych (1979) from Afghanistan, and Moon & Kim (1991) from South Korea. Furthermore, we have verified recently that the cuticular striae are rather conspicuous, especially in the terminal plate, in the syntypes of *C. lobatus* (Fig. 3F). The cuticular striae were not mentioned in the original description (Ramazzotti, 1943) and subsequent redescription (Maucci, 1979).

From the evidence discussed above, the presence or absence of body spines and cuticular striae among granules cannot be used as taxonomic characters in discrimi-

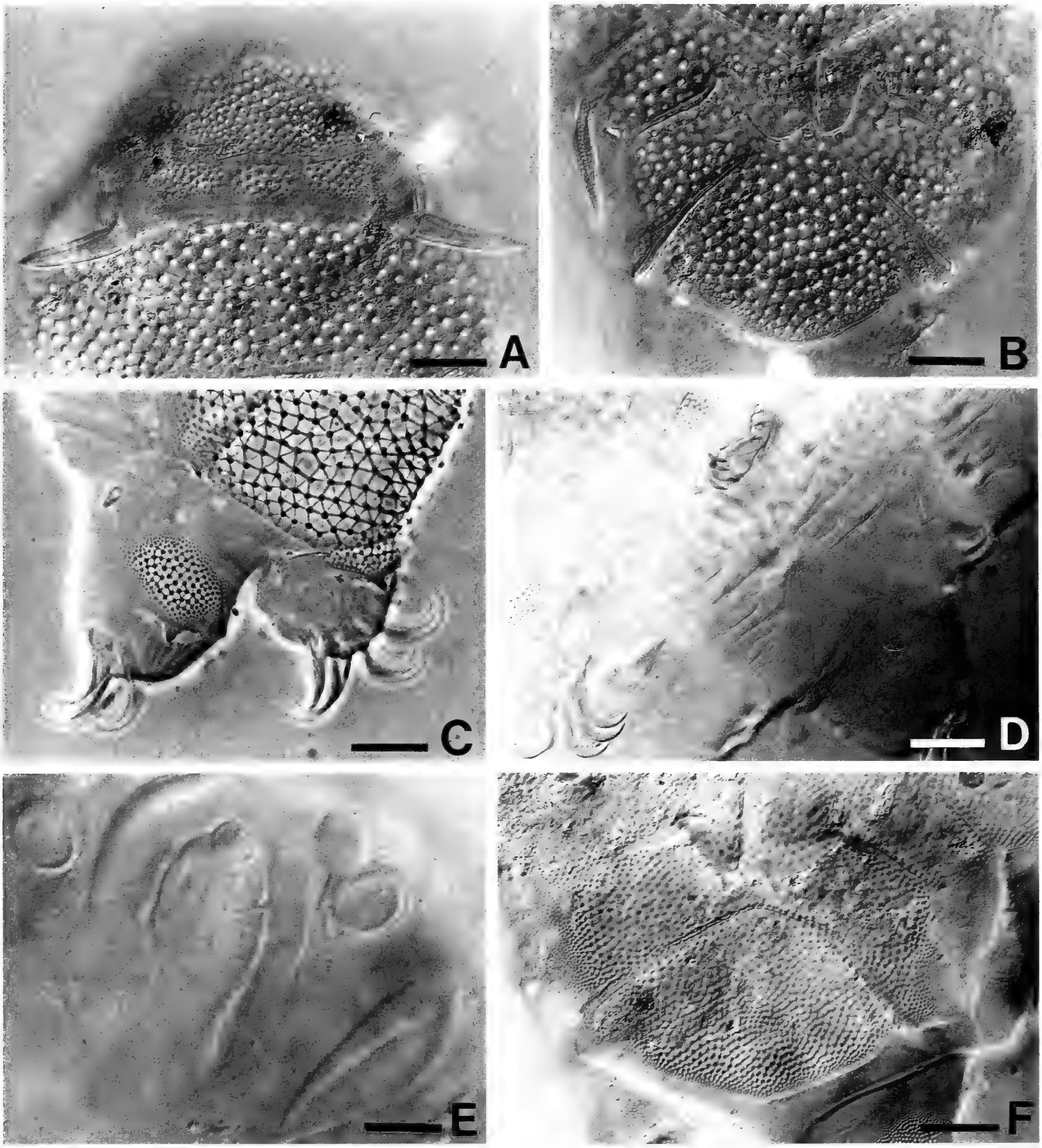

Fig. 3. A–E: *Cornechiniscus madagascariensis* Maucci, 1993. A, anterior body, dorsal view; B, pseudosegmental and terminal plates, dorsal view; C, posterior body, dorsal view; D, venter between legs I to III, showing cuticular grooves; E, mouth and cephalic sensory organs. (A, B, E: ZMH; adult female; Himachal Pradesh, N India. C, D: CT 13918; paratype adult female; Antsirabe, Madagascar). F: *C. lobatus* (Ramazzotti, 1943), pseudosegmental and terminal plates, dorsal view (CT; a syntype adult female). A, B, D–F: differential interference contrast; C: phase contrast. Scales = 20 μm (A–D, F), 8 μm (E).

nating *C. madagascariensis* from *C. lobatus.*

In *C. madagascariensis,* however, granulation on body surface consists of fairly large, distantly spaced granules (Fig. 3A–C), and this can be considered as the most important criterion to distinguish *C. madagascariensis* from *C. lobatus* (Fig. 3F).

Discussion

In the original description of *C. madagascariensis,* Maucci (1993) implied that this species may be referred to a subspecies of a cosmopolitan species, *C. lobatus* Ramazzotti, 1943. This also can be inferred from his specimen labels on microslides (see Material examined). Considering the present record from India which is quite far from Madagascar, however, the subspecific status cannot be supported. We are in agreement with Maucci (1993) who recognized *C. madagascariensis* as a good species based on the differences mainly discussed above.

We have confirmed that the ventral cuticular grooves, which have been omitted from the previous descriptions, are also commonly developed in many other *Cornechiniscus* species (unpublished data). In *Pseudechiniscus,* which is a closely related genus to *Cornechiniscus,* the venter is ornamented with net-like pattern in many species (Dastych 1984, Kendall-Fite & Nelson 1996). It is thus mentioned at present that the longitudinal groove character-condition is unique for the genus *Cornechiniscus.*

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Ophryotrocha lipscombae, a new species and a possible connection between ctenognath and labidognath-prionognath eunicean worms (Polychaeta)

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Abstract.—One new species of dorvilleid, *Ophryotrocha lipscombae,* is described based on material from the U.S. Atlantic slope. This new species is unique in its presence of 5 pairs of accessory plates, which are never found in any other dorvilleids, but are present in all labidognath-prionognath euniceans. A brief discussion of the phylogenetic position of *Ophryotrocha lipscombae* in the Eunicida is provided.

Ophryotrocha has been extensively studied by many polychaetologists (e.g., Jumars 1974, Åkesson 1984, Hilbig & Blake 1991, Eibye-Jacobsen & Kristensen 1994, Pleijel & Eide 1996); this may due to a number of factors: *Ophryotrocha* is common in both shallow and deep water environments; furthermore, it is easily cultured for study of reproductive and developmental patterns; in addition, its phylogenetic position within the Dorvilleidae has turned out to be interesting. As a part of the study of Eunicida phylogeny, a new *Ophryotrocha* species was found by chance. In a jar containing mixed small-sized eunicean specimens labeled only as "Eunicidae", not only one eunicid larva was found, but also two species of *Ophryotrocha* and one juvenile lumbrinerid could be identified. All specimens were observed using stereo and compound light microscopes; illustrations were made using a camera lucida.

Abbreviation.—Mx refers to maxillae. The species description is in a similar format as that used by Hilbig & Blake (1991).

Ophryotrocha lipscombae, new species
Figs. 1–4.

Material examined.—North Atlantic Ocean, United States, 110 miles south of Woods Hole, Massachusetts, 29 Jul 1977, 39°47′N, 70°40′W, *Alvin* Dive 773, STA DOS-1 (N-34), 1830 m (Holotype, USNM 186571; 7 paratypes, USNM 186572). North Atlantic Ocean, United States, 110 miles south of Woods Hole, Massachusetts, 15 Jun 1976, 39°47′N, 70°40′W, *Alvin* Dive 658, 1830 m (Paratype, USNM 186573).

Description.—Holotype complete with 31 chaetigers, 2.75 mm long, 0.41 mm wide (Fig. 1A). Other complete specimens 0.90–2.43 mm long, 0.17–0.44 mm wide (Figs. 1B, C; 2). Largest specimen incomplete with width of 0.77 mm. Body slender, oval in cross section. Chaetigers two times wider than long throughout body. One ciliary girdle present on each peristomial ring and each chaetiger. Color whitish in specimen collected in 1976 and brownish in specimens collected in 1977.

Prostomium distally bluntly triangular in smaller specimens (Fig. 1B), rounded in larger ones (Fig. 1A); two times longer than wide in holotype. Two short and stout, knob-like antennae, not reaching anterior end of prostomium. No evidence of palps and eyes observed in any specimen. Prostomium same length and width as peristomium. Peristomium consisting of two apodous, achaetigerous rings, each ring slightly shorter than adjacent chaetigers. Distinct lateral incisions present between peristomial rings; first peristomial ring distinctly fused with prostomium.

Parapodia uniramous, with one acicular lobe; inferiormost simple chaetae in a separate chaetal lobe. Dorsal and ventral cirri absent. Chaetae of three types: type 1, 3–4 serrated cultriform simple chaetae (Fig. 1E) tapering to slender distal teeth in supra-acicular fascicle (Fig. 1D), their subdistal end finely serrated; type 2, 4–7 (the number variable in different body regions and different specimens) heterogomph bifid compound falcigers (Fig. 1F) arranged in two rows in subacicular fascicle, their blades short and serrated; type 3, single, slender, simple cultriform chaeta (Fig. 1G) emerging from long chaetal lobe in inferiormost position, forming an angle with acicula at the base. Each parapodium with one sharply pointed acicula distinctly deeper into parapodium than other chaetae. Pygidium relatively long, as long as last two chaetigers in 24-chaetiger specimen. Anal cirri easily broken, one small knob-like pair observed on 24-chaetiger specimen. No distinct middle pygidial stylus present.

Mandible rod-like, black, two pieces forming X-shape. In 0.17 mm-wide specimen, distal end of each mandible piece with about 20 small teeth (Fig. 3B); in 0.44 mm-wide specimen, distal end of mandible without teeth (Fig. 3C). Maxillae K-type, with 8 paired pieces in roughly four rows; on each side, MX-I, II, and V-VII each forming one main row, while Mx-III and Mx-IV each as a separate row sitting outside (Fig. 4A). Mx-I (Figs. 3A, 4A) heavy, generally ice-tong shaped and facing each other, with 3 large teeth in addition to main fang. Mx-II (Figs. 3A, 4A) thin plates, forming an arc over distal part of Mx-I. Mx-II with about 12 large teeth and a few irregularly placed small teeth in the middle. Mx-V to Mx-VIII (Fig. 4A) smaller than Mx-II, but structurally similar, plate shaped, with 4–8 large teeth and several small teeth. Mx-III and Mx-IV elongate and fang-shaped with additional 1 or 2 smaller teeth, sitting anterior to Mx-II and outside of Mx-V. One pair of short carriers (Figs. 3A, 4A) fused to each other, and to posterior end of Mx-I. Two rows of 5 sclerotinized black accessory plates (Fig. 4A) in erect position inside main maxilla row, each plate corresponds to Mx-II and Mx-V to VIII. Jaw structure symmetrical.

Remarks.—Ophryotrocha lipscombae can be easily distinguished from other *Ophryotrocha* species by the presence of 3 teeth in addition to the main fang on Mx-I, the presence of five accessory plates and the anterior end formed by the prostomium and the first peristomial ring. The above features are novel in dorvilleids, especially the accessory plates which have never been reported in the Dorvilleidae but are present in all other major families of the Eunicida (personal observation). When it is compared to other dorvilleids, such as *O. akessoni* and *O. geryonicola, O. lipscombae* appears to have a larger jaw apparatus for a similarly sized specimen; its maxillae can reach through the anterior four to five chaetigers, while those of the other species usually reach through the anterior two chaetigers. The over-all jaw structure is similar in all four *Ophryotrocha lipscombae* specimens dissected whose size ranged from 0.17 mm to 0.77 mm wide.

This species reaches a relatively large size (as wide as 0.77 mm) among dorvilleids. While no gametes have been observed, we do not believe these specimens to be juveniles of any other reported eunicean worms. The type material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C.

Geographic distribution.—110 miles south of Woods Hole, Massachusetts, Atlantic slope.

Etymology.—The species is named after Prof. Diana Lipscomb of George Washington University for her many contributions to systematic biology.

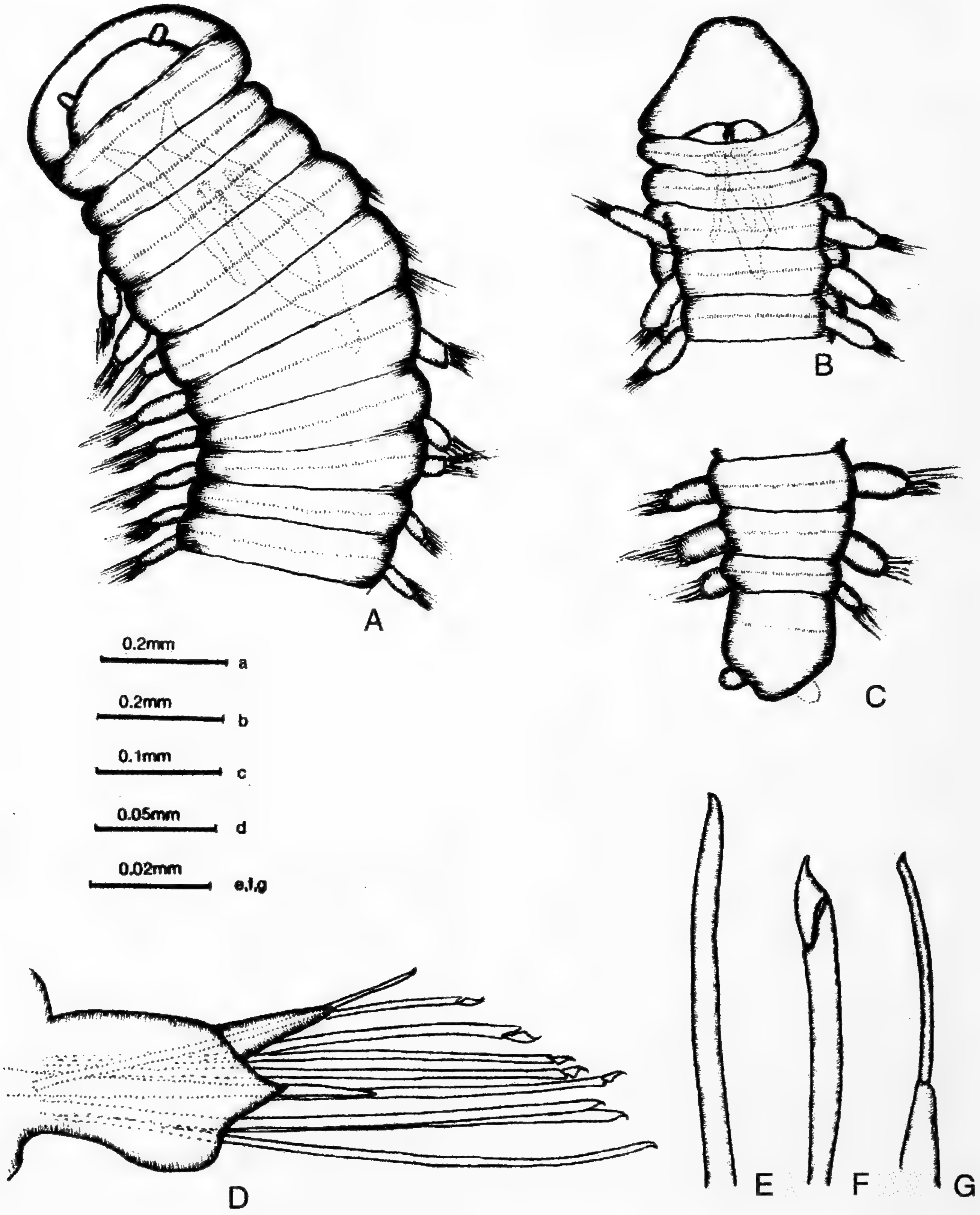

Fig. 1. *Ophryotrocha lipscombae:* A, anterior end, 31-chaetiger specimen, dorsal view; B, anterior end, 18-chaetiger specimen, ventral view; C, posterior end, 24-chaetiger specimen, ventral view; D, parapodium 3, anterior view; E, supra-acicular chaetae; F, compound falciger; G, most inferior simple chaeta.

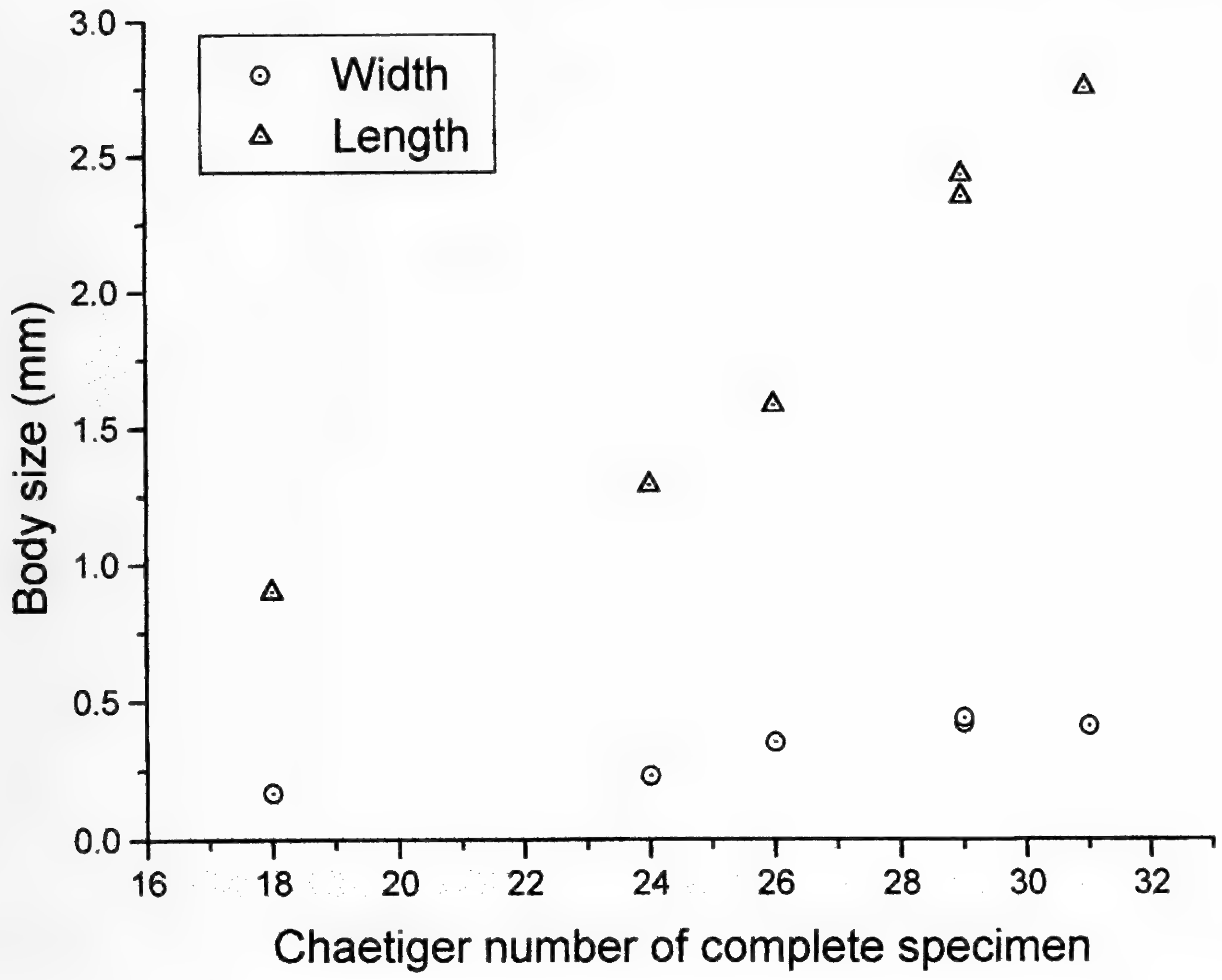

Fig. 2. Correlation between body size and chaetiger number in *Ophryotrocha lipscombae.*

Discussion

The eunicean worms share a set of complex jaws composed of a ventral mandible and dorsal maxillae, and they are classified into five types based on jaw morphology: labidognath (Ehlers 1868) includes Eunicidae, Onuphidae, Lumbrineridae and Hartmaniellidae. This type has a pair of well separated short carriers; Oenonidae have prionognath jaws (Colbath 1989, Fauchald & Rouse 1997) characterized by the presence of a median plate inside the muscular bulb; Dorvilleidae has 4 rows of maxillae and is called ctenognath; xenognath (Mierzejewski & Mierzejewska 1975) and placognath (Kielan-Jaworowska 1966) are represented only by fossil taxa. The above classification of eunicean jaws might be arbitrary if cladistic tree-thinking is applied. Usually ctenognath is considered as monophyletic, and it is a sister group of labidognath-prionognath taxa (Kielan-Jaworowska 1966, Kozur 1970, Jumars 1974, Orensanz 1990). The assessment of jaw homology can be relatively easily made between prionognath and labidognath (Orensanz 1990), but both are generally considered difficult to compare to the ctenognath. The overall phylogenetic construction of Eunicida by Tzetlin (1980) may be problematic when a cladistic analysis is performed based on additional evidence (unpublished data); however, his scheme connecting the K-type *Ophryotrocha* jaw with those of labidognath-prionognath jaws is reasonable based on the following evidence: first, the Mx-I of labidognath-prionognath is homologous with the Mx-I of both P- and K-type

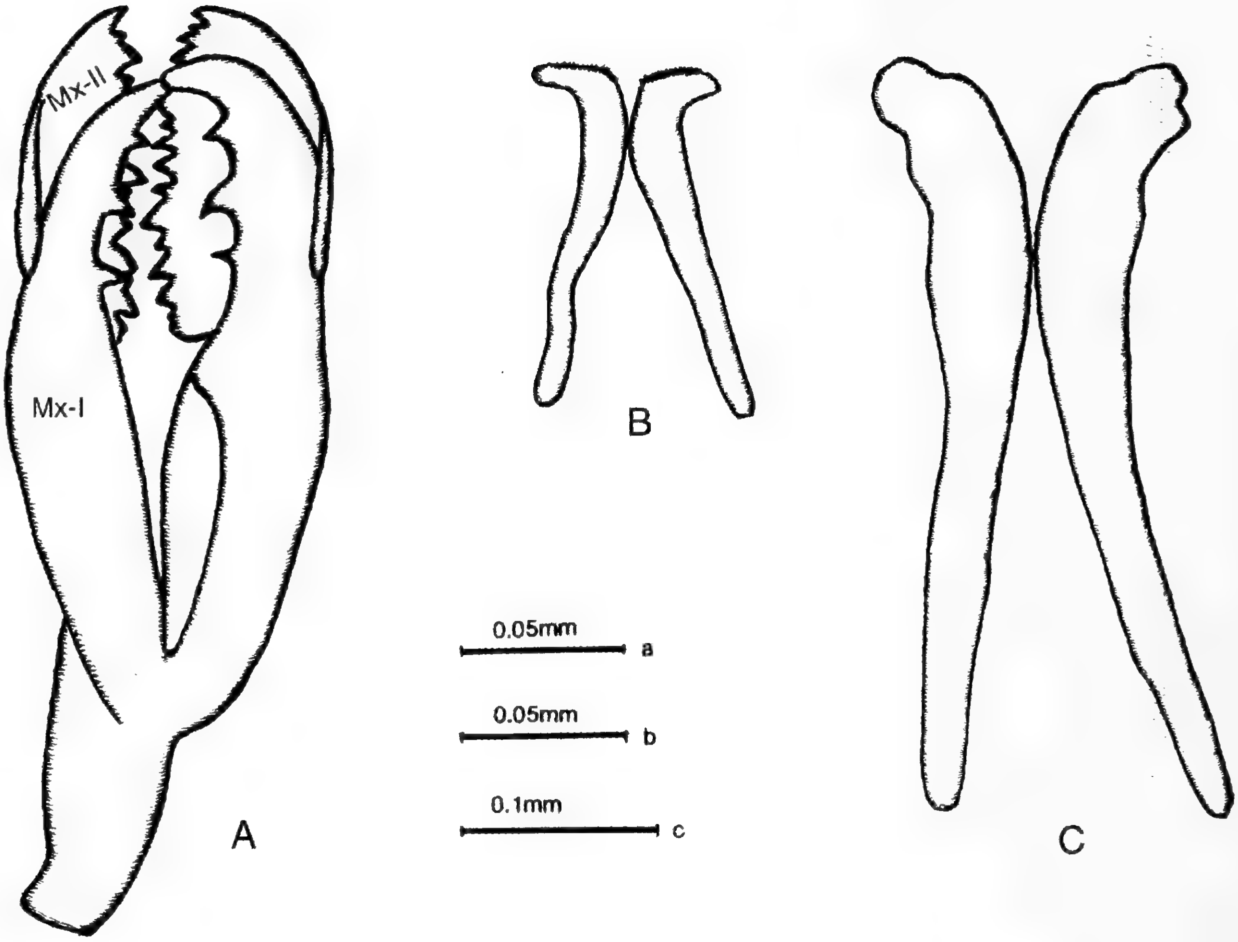

Fig. 3. *Ophryotrocha lipscombae:* A. jaw structure in dorsal view, only Mx-I, Mx-II and the carrier are depicted; B. mandible of 18-chaetiger specimen, dorsal view; C. mandible of 31-chaetiger specimen, dorsal view.

Ophryotrocha, based on extensive studies of larval and adult jaw morphology of Dorvilleidae, Onuphidae and Oenonidae (H. L., unpublished data); second, the accessory plates, or attachment lamellae (Paxton 1986), are present in all members of the labidognath-prionognath taxon (personal observation), and the presence of such plates in *Ophryotrocha lipscombae* is the first record for any dorvilleid. Accessory plate numbered 5 pairs in *O. lipscombae,* 3 pairs in Oenonidae (Fig. 4B) and Lumbrineridae (Fig. 4C), and 2–3 in Onuphidae and Eunicidae. All accessory plates are located median to the corresponding maxillae in erect position; no plate corresponds to Mx-I.

The presence of accessory plates may provide a substantial primary homology for *O. lipscombae* and the labidognath-prionognath taxa; the relationship will be tested in a systematic study of Eunicida based on morphology, ontogeny and fossil data. At present, the new species is considered as a member of *Ophryotrocha* based on its overall morphological characters. Though the phylogenies of *Ophryotrocha* (Pleijel & Eide 1996) and Dorvilleidae (Jumars 1974, Westheide 1982, Hilbig & Blake 1991, Eibye-Jacobsen & Kristensen 1994) have been studied using various methods, better overall understanding might be gained from a relatively broader study of the phylogeny of the order Eunicida, including detailed studies of members of all major groups.

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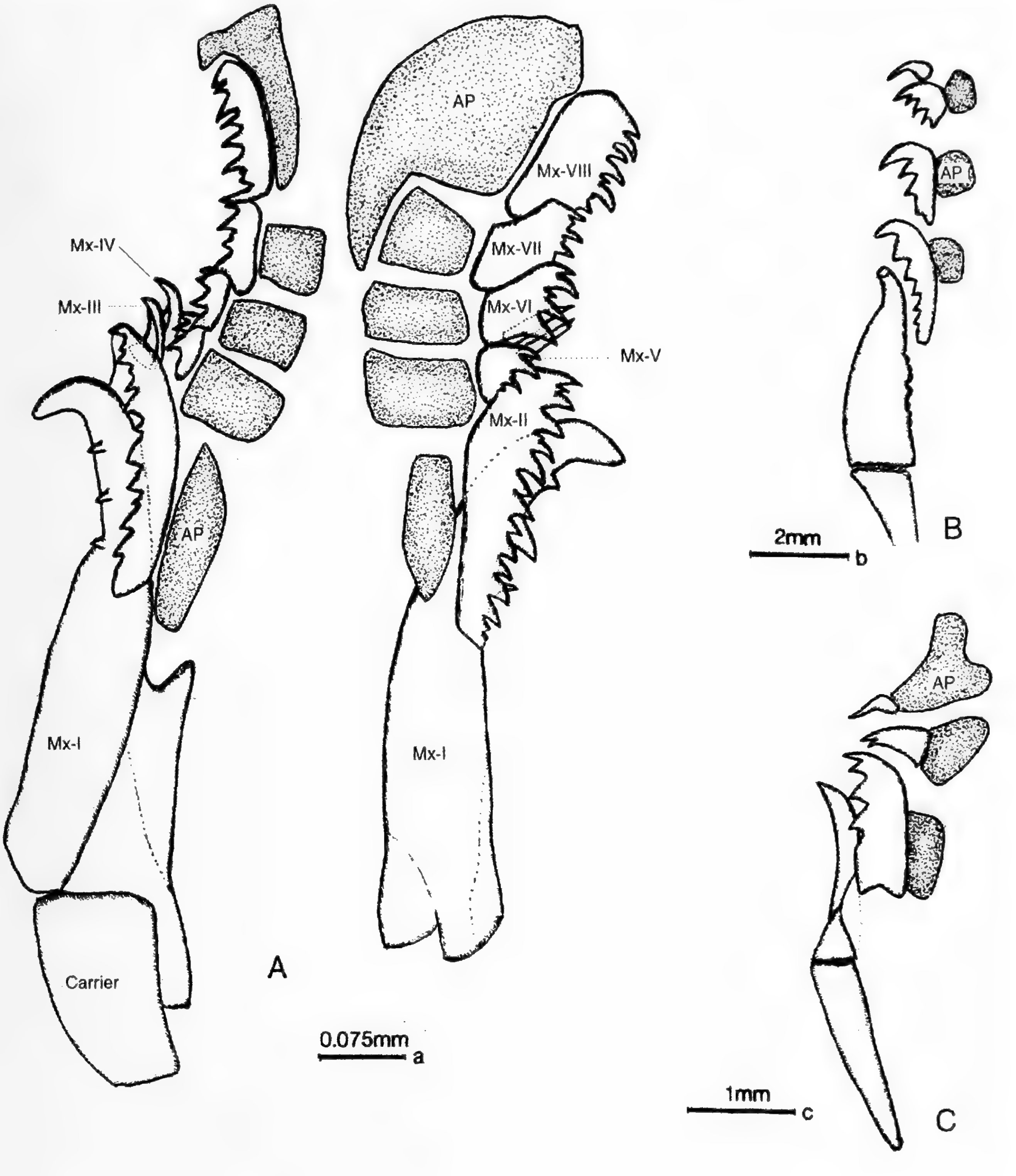

Fig. 4. A. Detailed jaw structure of 31-chaetiger specimen, *Ophryotrocha lipscombae,* in ventral view; note that left and right sides are cut apart, the carrier is broken, and the whole structure is displayed in an unnatural way in order to show the detailed structure; B. jaw structure in ventral view, *Arabella iricolor* (USNM 10355); C. jaw structure in ventral view, *Lumbrineris zonata* (USNM 30611).

other colleagues from the Department of Invertebrate Zoology, NMNH, Smithsonian Institution, and Diana Lipscomb and the Systematics Group, Department of Biological Sciences, the George Washington University. We thank Stephen Gardiner and Kirk Fitzhugh for their reviews. HL is supported by the Research Enhancement Funds and Weintraub Research Fellowship from the George Washington University, and research contract 9822uu04278 from the Smithsonian Institution.

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Aphrodita bisetosa (Polychaeta: Aphroditidae), a new species of sea mouse from the southeastern Pacific Ocean off central Chile

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Abstract.—A new species of Aphroditidae, *Aphrodita bisetosa* from the southeastern Pacific Ocean off central Chile, is described. Specimens were collected in soft bottoms, 27–37 km from the coast line in front of Los Vilos (31°56′S) and Papudo (32°31′S), at 250–400 m depth. The new species was compared with *A. magellanica* Malard, 1891 from the Magellan area, Chile and *A. alta* Kinberg, 1855 from Rio de Janeiro, Brazil, and the Antarctic region, with which it appears to be more closely related.

Aphroditids are commonly named "sea mice," because of the thick mat of very fine notopodial fibers which form a felt-like covering over the dorsum, giving them a furry appearance. Although they are rather large and conspicuous inhabitants of marine soft muddy bottoms, they are frequently absent from most collections because of the great depths at which they usually live, and in general they have been poorly studied. The most recent and comprehensive study of aphroditids was by Hutchings & McRae (1993) on species found in Australian waters and the Indonesian Archipelago.

There is almost no information about aphroditids of the southeastern Pacific Ocean along the Chilean coast. Only one species, *Aphrodita magellanica* Malard, 1891, has been previously recorded from the Magellan area (49°S) south to Cape Horn (56°S) in southern Chile (Rozbaczylo 1985); the specimens, had been collected during the Challenger Expedition (1873–1876), and identified by McIntosh (1885) as *Aphrodita echidna* Quatrefages.

Four specimens of aphroditids collected by commercial shrimp trawlers at two sites off central Chile were given to the first author for study; after examination, they were considered as belonging to a new species.

Materials and Methods

Specimens were collected by the shrimping boat *Goden Wind,* as part of a benthic survey obtained 27–37 km from the coast between Los Vilos and Papudo, in October 1976. At 2 of 5 stations sampled, specimens of aphroditids were found in sandy-mud bottom (Fig. 1). Additional information on the accompanying macrofauna collected during the trawls can be found in Andrade (1986).

Polychaetes were fixed in 4% formalin and preserved in 70% ethanol. Figures were prepared with a drawing tube on a Wild M-5 stereoscopic microscope and a Leitz compound microscope.

Type specimens of the new species are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the Sala de Sistemática, Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago (SSUC).

Aphrodita bisetosa, new species
Figs. 1–3

Material examined.—Central Chile: in front of Los Vilos, St. 1, ca. 31°56′S, 71°49′W, 300–400 m, H. Andrade, coll., 14 Oct 1976, holotype (USNM 186512) and female paratype (SSUC 6868); in front of Papudo, St. 3, ca. 32°31′S, 71°47′W, 250–280 m, H. Andrade, coll., 14 Oct 1976, paratype (N° 2 USNM 186513) and female paratype (SSUC 6869).

Description.—Holotype. Body ovate, arched dorsally, widest at setigers 14–16, with tapering caudal region (Fig. 2a); 27 mm long, 16 mm wide, excluding setae, with 41 setigers. Dorsum with thick felt, approximately 1.5 mm thick at middle region of body, with fine sediment entrapped giving it greyish appearance. Ventral surface of body whitish, covered with minute spherical papillae (Fig. 2d).

Prostomium small, rounded with pair of ocular areas, pale to light brown in color, located on slightly raised prominences (Fig. 2b). Median antenna with basal ceratophore and elongated style, slightly shorter than prostomium, attached dorsally, near anterior border of prostomium. Palps biarticulate, finely papillated, wide basally, tapering gradually, extending approximately to sixth setiger. Facial tubercle minutely papillated, approximately half of length of prostomium, partly hidden by palps dorsally and extending ventrally as digitiform process over mouth (Fig. 2b, c).

Elytra (Fig. 2e, f) 15 pairs, completely hidden by dorsal feltage, on setigers 2, 4, 5, 7, 9, . . . 25, 28, 31, imbricate, completely covering dorsum, semi-transparent; smooth except for few scattered microscopic digitiform papillae (Fig. 2g), mostly concentrated on inner lateral area of upper surface and less on posterior area of elytra. First pair of elytra smallest, gradually increasing in size to approximately pair 7–9, then decreasing posteriorly. First and second pair of elytra ovate, longer than wide, with elytrophores attached centrally and laterally, respectively; following elytra wider than long; last three pairs noticeably longer than wide; last pair smaller.

Dorsal tubercles from segment 6 to 30 provided with branched fimbriated papillae on posterolateral margins (Fig. 3d).

First setiger or tentacular segment with elongated, uniramous parapodia, flattened, projecting anteriorly and laterally to prostomium (Fig. 2b), with one tuft of fine silky fibers emerging dorsally forming the dorsal felt, and 3 fascicles of fine, faintly iridescent, mud-covered capillary setae; one tuft supra-acicular and two others sub-acicular; with few scattered papillae covering parapodium (Fig. 2b). Parapodial dorsal and ventral cirri with cylindrical cirrophores and subulate styles. Dorsal cirri approximately one-third length of palps. Ventral cirri slightly shorter than dorsal.

Following setigers with biramous parapodia. Second setiger with first pair of elytra. Notopodia rectangular, with one tuft of fine silky fibers forming dorsal felt, 2 supra-acicular fascicles of stout acicular setae, with hooked tips, similar in shape and distribution to that of parapodium 3, and a sub-acicular fascicle with capillary notosetae forming lateral fringe, and on posterior surface of notopodia at level of acicula, a small tuft of fine silky fibers forming dorsal felt. Neuropodia cylindrical, covered with spherical papillae; tip of acicula emerging at distal end of neuropodial lobe. Neurosetae, brown, arranged in 3 tiers: upper consisting of 2–3 acicular setae, middle 1–2 acicular setae, and lower of numerous capillary setae (Fig. 31), slender bipinnate and spirally twisted, with two rows of thick teeth that continue in subdistal region as fine spines, and with distal end smooth. Ventral cirri subulate, located near base of neuropodium, about one and one-half length of neuropodia (Fig. 2d).

Third setiger similar to second, but with dorsal cirri instead of elytra. Dorsal cirri long, subulate, approximately 3–4 times length of ventral cirri.

Parapodia of middle region of body (Fig.

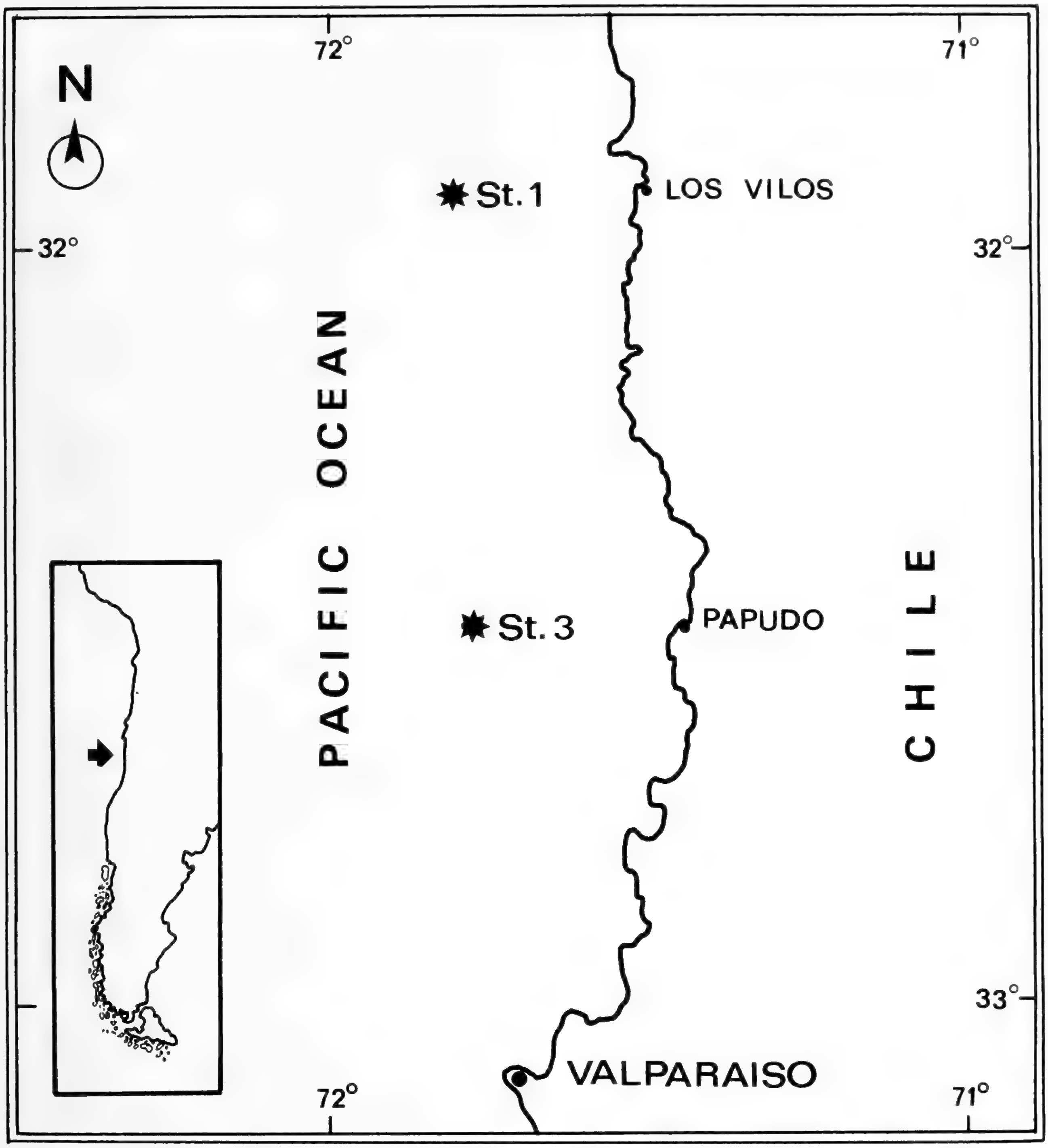

Fig. 1. Map showing the stations (*) where specimens of *Aphrodita bisetosa,* new species, were found.

3a, b) with notopodial lobe large, nearly triangular, with dorsal cirri with cirrophores large, basally bulbous, projecting on posterior faces of notopodia; styles subulate, long, slender, smooth, directed dorsally; dorsal cirri approximately 3–4 times longer than ventral cirri; notoacicula stout, light brown, emerging at vertex of distal end of notopodial lobe.

Notopodia with tufts of fine silky fibers emerging dorsally forming dorsal felt, with hooked ends (Fig. 3i); arranged in three main groups on cirrigerous segments, one above and one below upper fascicle of supra-acicular notosetae, and third one on posterior surface of notopodia at level of acicula; on elytrigerous segments appearing in two main groups, one between upper and lower fascicle of long supra-acicular notosetae, and one on posterior surface of notopodia at level of acicula. Three fascicles of notosetae present, one sub-acicular and

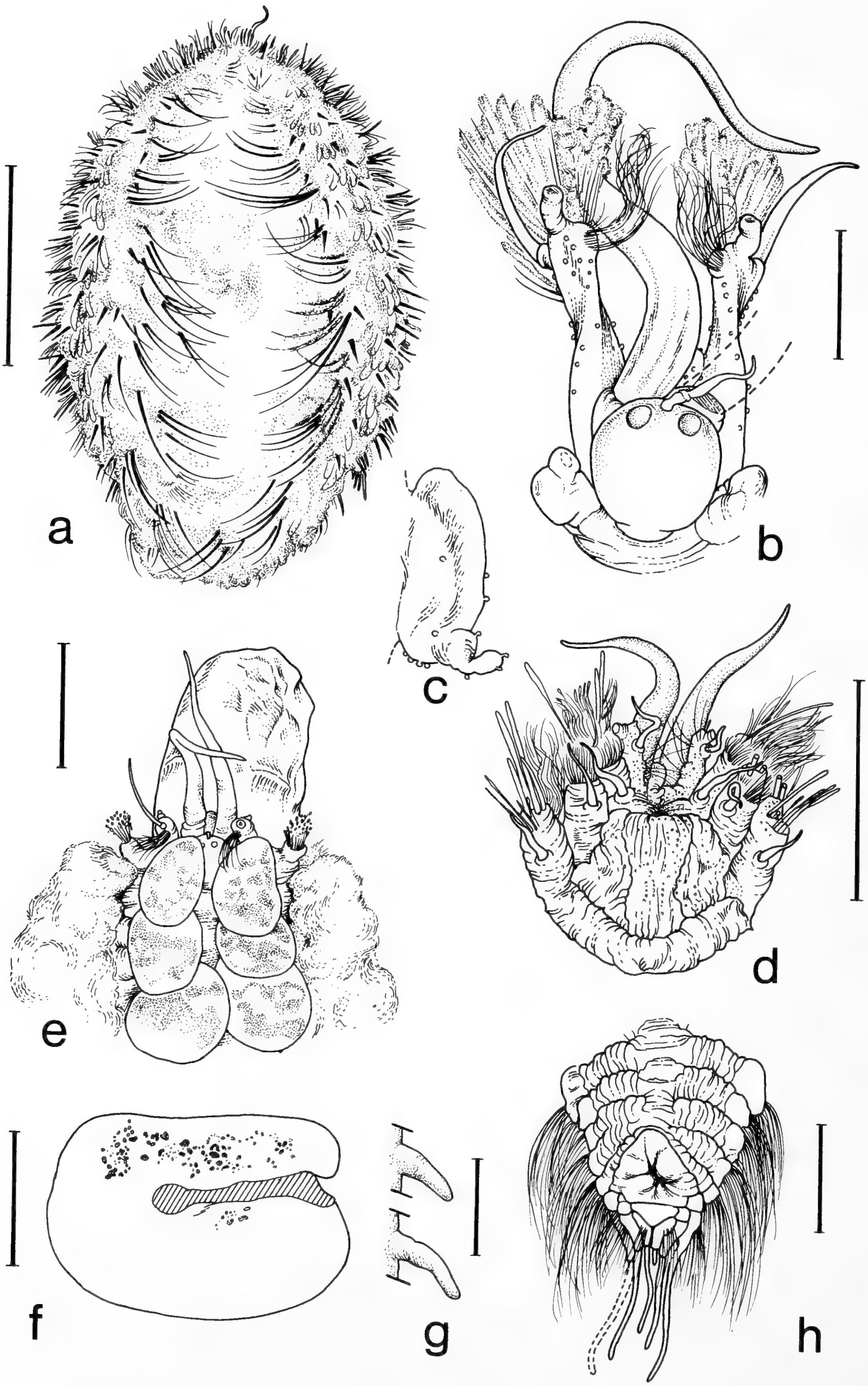

Fig. 2. *Aphrodita bisetosa,* new species (Holotype USNM 186512). a, dorsal view, whole animal; b, dorsal view of prostomium and first segment, with first pair of elytra omitted (right palp and dorsal parapodial cirri missing); c, facial tubercle (Paratype SSUC 6869), antero-lateral view; d, anterior end (Paratype SSUC 6869), ventral view; e, anterior end (Paratype USNM 186513), dorsal view, with proboscis everted and feltage set aside, showing first three pairs of elytra, style of median antenna missing; f, ninth left elytron, inner surface (Paratype USNM 186513); g, papillae from ninth elytron; h, posterior segments around the anus (Paratype SSUC 6869), dorsal view. Scales = 10 mm for a; 5 mm for d, e, f; 1 mm for b, h; 0.05 mm for g.

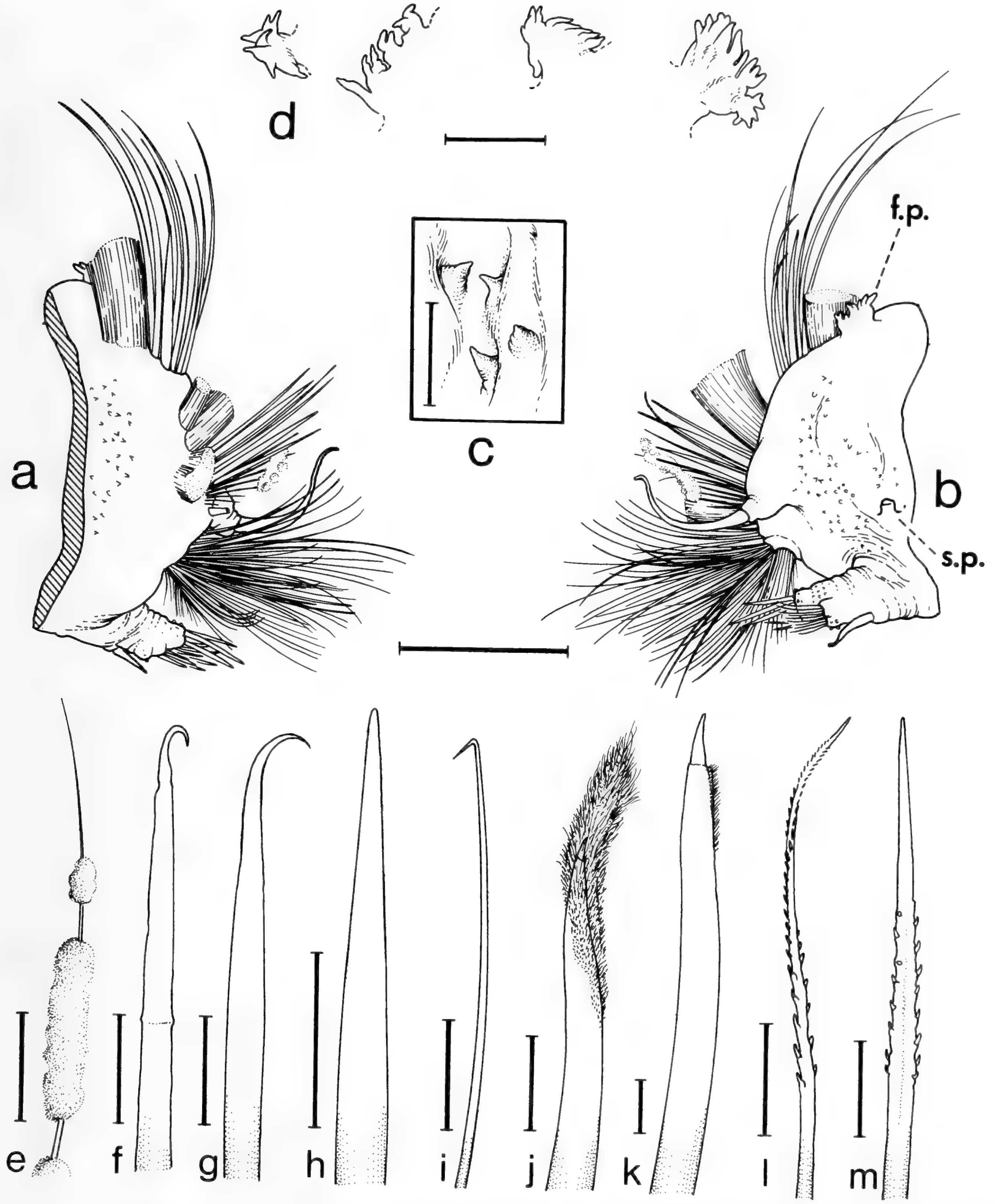

Fig. 3. *Aphrodita bisetosa,* new species, a, parapodium 14 (Paratype SSUC 6868), in anterior view (tufts of silky fibers are shown cut off); b, same parapodium in posterior view (f. p. = fimbriated papilla; s. p. = segmental papilla); c, conical papillae from notopodium of same parapodium; d, fimbriated papillae (Paratype SSUC 6869), from segments 6, 8, 10, and 12, respectively; e, capillary notoseta from parapodium 14; f, g, acicular notosetae of stout type, with hooked tips, from parapodium 14; h, acicular notoseta of stouter type, with straight tip, from parapodium 18; i, fine silky fiber, from parapodium 20; j, acicular neuroseta, with heavily bearded end, from lower tier, parapodium 22; k, acicular neuroseta, partially bearded, from lower tier, parapodium 14; l, capillary bipinnate neuroseta, spirally twisted, from lower tier, parapodium 2; m, capillary, partially bipinnate neuroseta, from lower tier, parapodium 29. Scales = 5 mm for a, b, j; 1 mm for d, h; 0.5 mm for c; 0.01 mm for k, l, m; 0.005 mm for e, f, g, i.

two supra-acicular. Sub-acicular fascicle made up of numerous iridescent capillary setae (Fig. 3e), extending laterally, with distal end straight and pointed; most covered with fine silky fibers and fine mud resembling cotton in appearance. Two supracicular fascicles made up of 2 kinds of acicular setae emerging through dorsal feltage: many stout acicular setae with hooked tips (Fig. 3f, g) and 1–2 stouter acicular setae with straight tips (Fig. 3h), short, conical, dark brown to blackish, spine-like, extending dorso-posteriorly (tips may be broken off), with fine silky fibers at base. In upper fascicle, stout protective notosetae present (Fig. 2a), long, brown-colored basally and shiny golden light brown color distally, tapering gradually, with flexible hooked tips (may be broken off), sometimes partially covered with fine silky fibers. In lower fascicle, stout protective notosetae short with, distal region having fine silky fibers and covered with fine mud presenting finger-like appearance, peppered with ferruginous color.

Notopodia covered with two kinds of papillae: globular, small, few, scattered on subacicular area near distal margin of notopodial lobe, and conical (Fig. 3c), larger and more abundant, scattered on basal area of notopodial lobe.

Neuropodia (Fig. 3b), cylindrical, ending distally in three step-like lobes, covered with minute spherical papillae. Ventral cirri small, subulate, located in middle region of neuropodia, approximately one-third the length of dorsal cirri.

Neurosetae stiff, stout, dark brown, slightly curved distally, with heavily bearded ends (Fig. 3j), which can be broken; pointed subdistal tip visible through beard, exposed when the distal tip of beard ends lost (Fig. 3k). Neurosetae arranged in three tiers with 2 setae in upper, 2 in middle and 4–6 in lower tier in anterior parapodium (setiger 4), 2 in upper, 3–4 in middle and 5–9 in lower tier in middle parapodium (setiger 15), and 2 in upper, 2 in middle and 7 in lower tier in parapodium of posterior region of body (setiger 25). Upper group with stoutest and longest setae; lowest most slender and shortest. Neuroacicula, stout, light brown, emerging through upper lobe.

Ventral neurosetae of posterior region of body, capillaries, with two rows of teeth subdistally (Fig. 3m), and distal region smooth with tips from slightly curved to straight. Neurosetae of more posterior setigers all capillaries.

Anus (Fig. 2h) located dorsally, anterior to 2 small segments. Without anal cirri.

Variation.—Additional material examined ranges from 47–80 mm long, 20–35 mm wide, excluding setae, with 42 setigers. Body varies from ovate to elongated in largest specimens. Fascial tubercle extends ventrally as digitiform process over mouth in all except one specimen (paratype SSUC 6868). Only one specimen with everted proboscis (Fig. 2e) with opening surrounded by numerous, leaflike, dichotomously branched papillae; chitinous jaws lacking. Elytra in largest specimens are light brown to cream in color; irregularly stained ferrugineous to olive in colour on inner surface (Fig. 2f). Holotype without segmental papillae, but present in largest specimens as small knobs on posterior faces of parapodia between rami, on segment 14, and subsequent setigers (Fig. 3b).

In paratypes neurosetae varied as follows: 2 setae in upper, 2–3 in middle and 3–6 in lower tier in anterior parapodium (setiger 4), 2–3 in upper, 3–5 in middle and 10–12 in lower tier in middle parapodium (setiger 15), and 2–3 in upper, 3–4 in middle and 7–11 in lower tier in parapodium of posterior region of body (setiger 25).

Etymology.—The species name *bisetosa* is derived from Latin *bi*-meaning double, and *setosa* meaning with bristles, because of the presence of two kinds of notosetae which emerge through the dorsal feltage.

Distribution.—The species has been found at two sites off Central Chile: between 27 and 37 km off the coast in front of Los Vilos, 300–400 m and in front of Papudo, 250–280 m depth, in sandy-mud bottoms.

Remarks.—The new species *Aphrodita bisetosa* is characterized by two kinds of acicular setae emerging through dorsal feltage: numerous stout setae with hooked tips, and some stouter, short, dark brown, spine-like setae, with straight tips, forming two distinct rows of protective notosetae along each side of body. The acicular notosetae appear in two fan-shaped fascicles of different length: an upper fascicle of long setae, shiny golden brown-colored distally, extending dorsomedially, nearly touching medially, and a lower fascicle of short setae extending backwards, bearing a mud cover, peppered with ferruginous colour, presenting finger-like appearance.

Aphrodita bisetosa appears to be most closely related to *A. magellanica* Malard, 1891, from the Magellan area and to *A. alta* Kinberg, 1855 from Rio de Janeiro, Brazil, and the Antarctic region. *A. magellanica* is the most similar to *A. bisetosa* n. sp. Both species have two rows of acicular notosetae along each lateral region of the body that are short, brown, and spine-like with straight tips emerging through the dorsal feltage. Both species have similar neurosetae of the acicular type, brown, with bearded ends (which can be broken), and in both species the dorsal felt is formed of very fine silky fibers with hooked tips; the lateral regions are of ferruginous color. *A. bisetosa* differs from *A. magellanica* by having two kinds of protective notosetae; its spine like acicular notosetae are conical toward the tip, 1–2 of these notosetae are present in each supracicular tuft; ventral cirri of parapodia lack papillae; and the body has 41–42 setigers. In *A. magellanica,* in contrast, has only one kind of protective notosetae. The spine like notosetae are flattened toward the tip, 2–3 of these notosetae can be present in each supracicular tuft; ventral cirri of parapodia possess numerous papillae and the body has about 35 segments.

Aphrodita bisetosa resembles *A. alta* in that the protective notosetae end in a hook, the acicular neurosetae of the middle region of the body are slightly curved and have heavily bearded ends and in both species the proboscis bears leaflike papillae surrounding the opening. *A. bisetosa* differs from *A. alta* by the following characteristics present in the latter species: only one type of protective notosetae that do not project through the felting, only one type of ornamentation in capillary neurosetae of second setiger; without segmental papillae and proboscis with jaws.

Acknowledgments

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Exogone breviantennata Hartmann-Schröder, 1959 (characters emended) (Annelida: Polychaeta: Syllidae), a new record for the Bahamas with a key to selected *Exogone* species

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Abstract.—The syllid polychaete *Exogone breviantennata* Hartmann-Schröder, 1959 is reported from the Bahamas, where it was collected from epiphytic communities on submerged red mangrove roots in Osprey Lake and Reckley Hill Pond located on San Salvador Island. The external morphology of both paratype and Bahamian specimens is described and species characters emended. Observations on reproduction, biology, habitats and distribution are reported. The essential characteristics used to identify the genus *Exogone* are discussed and a key to Caribbean species with a dorsal cirrus on setiger 2 is provided.

Several polychaete species were collected from algal covered red mangrove roots in Osprey Lake and Reckley Hill Pond, landlocked bodies of water on San Salvador Island in the Bahamas. One of them, reported here for the first time from the Bahamas, *E. breviantennata* Hartmann-Schröder, 1959, has features unique to interstitial polychaetes normally associated with sand or mud. The species characters are emended based on examination of paratype material and the specimens collected from the Bahamas. Included is a discussion of the important characters used to identify the genus *Exogone* and a key to species related to *E. breviantennata* that are found in the Caribbean.

Materials and Methods

Two subtidal *Rhiziophora mangle* prop roots, extensively colonized by algae, were collected from Osprey Lake, San Salvador Island, Bahamas, 5 May 1996, and from Osprey Lake and Reckley Hill Pond (sometimes given as Reckley Hill Settlement Pond), 19 Jun 1997. The polychaetes were removed, relaxed in 5% magnesium sulfate and fixed in a 5% formalin/seawater solution. Specimens were transferred to 70% ethanol for long-term storage. Some of the specimens were mounted in Hoyer's solution in order to clear body tissue so that teeth and setae would be clearly visible (Zottoli & Long 1998) or in Glycrogel Mountant (Gurr 1962), which allowed close examination of body surfaces.

Measurements were made under compound or dissecting microscopes with a calibrated grid. Body length was measured from the tip of the prostomium to the end of the pygidium; for twisted specimens, the grid was rotated along the body. Body width was measured from the tip of the right neuropodium to the left across the dorsal surface of the fourth setiger.

Comparative material was borrowed from the Zoologisches Museum, Hamburg (ZMH) and the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C., U.S.A.

Identifying Specimens of the Genus *Exogone*

Most syllids, because of their small size, are difficult to identify, requiring careful examination under a compound microscope. For this and other reasons, Fauchald (1977:79) stated: "the identification of syllids [is] a time-consuming occupation." Larger specimens should have the pharynx isolated and appropriate parapodia removed for examination under a compound microscope. Smaller specimens should be cleared in an appropriate medium such as Hoyer's solution (see Zottoli & Long 1998) or mounted permanently in Glychrogel Mountant (Gurr 1962). During examination, it is important to keep in mind that what you see may be an artifact resulting from the degree of relaxation prior to fixation, the type of preservative used, or the length of time stored, especially with regard to the size and shape of soft parts and the appearance of setae (see Riser 1991:214). The quality of equipment, which determines the fineness of detail seen, and the experience of the investigator, may also influence what is observed. These factors may be responsible for the lack of detail in many original descriptions, which in some cases are now considered incomplete because they did not illustrate or discuss what are now considered essential characters.

The following is a discussion, on a character by character basis, of features commonly used to identify species of *Exogone*. Size should not be used to classify specimens because local and regional variations have been inadequately studied for most polychaetes. The degree of fusion of the palps must be viewed both dorsally and ventrally. The number of antennae (if not lost) is reliable, although antenna shape, length, and placement on the prostomium need to be measured on a large number of specimens; antennae are easily distorted due to relaxation and fixation techniques. Russell (1991) refuted the use of the number of muscle cell rows of the proventriculus as a diagnostic character in the family Syllidae, and we have found sufficient variation in *E. breviantennata* to agree; the number of setigers in which the proventriculus is found varies according to how far the pharynx is retracted, thus making this a questionable character for species distinction. For comments regarding the usefulness of nuchal organs in identifying some syllids, see Riser (1991). The shape of the neuropodia and the shape and position of the dorsal, ventral, and tentacular cirri are easy to determine even in small specimens. The presence or absence of dorsal cirri on setiger 2 in adult specimens is an important and stable species characteristic; however, the apparent absence of dorsal cirri on setiger 2 should be verified on several specimens as the structures can easily be detached. All parapodia should be scanned for modified setae of any kind and all setae should be carefully examined dorsally, laterally, and ventrally under oil immersion along the entire length of the animal. Setae of the same type can appear quite different from setiger to setiger depending on the degree of rotation. For example, blades may appear smooth if viewed from either a dorsal or a ventral aspect but toothed from a lateral aspect. The tips of setal blades that appear unidentate may, on closer examination, be seen to be bidentate. The type and extent of denticulation or spination on the setal shafts also become more apparent with increasing magnification. The importance of care in observing setae is illustrated in a comparison of figures 75–78 in the original description of *E. breviantennata* by Hartmann-Schröder (1959), which show no decoration on the setae, and, yet, painstaking reexamination of a type specimen revealed obvious decoration (blades and shafts). Finally, every specimen in a collection should to be checked individually, to ensure that all belong to the same species (Perkins 1981).

Genus *Exogone* Ørsted, 1845

Key characters.—Small worms (usually less than 3 mm in length but up to 8 mm); palps sometimes fused; three antennae and one pair of tentacular cirri; dorsal and ventral cirri well developed but shorter than setal lobes; all appendages papilliform or ovoid; eversible pharynx with single anterior tooth (Fauchald 1977, Pascual et al. 1996). San Martín (1991) reviewed this genus based on his work with Cuban syllids and expanded the number of key characters to include presence or absence of eyes, extent of palpal fusion, presence of two long anal cirri, smooth body surface, and reproductive habits.

In summary and in decreasing order of reliability, we use the following characters to distinguish various species in the genus *Exogone:* presence or absence of a dorsal cirrus on setiger 2; position, shape, and length of the antennae; shape, size, development and placement of eyes; placement and relative length of the proboscis and proventriculus; and shape and denticulation and spination of setae and acicula.

Biology of the genus Exogone.—Members of this genus have been reported from soft and hard bottoms (Uebelacker 1984: 30–37 through 30–43), associated with sponges (Pascual et al. 1996) and on unshaded algal flats dominated by *Caulerpa verticillata* and *Halimeda opuntia* f. *trilobata,* reported by Russell (1991). In the Canary and Madeira Islands, six species of this genus comprised 6.6% of all polychaetes collected from sponges. When they are associated with living in sponges, some members of this genus exhibit morphological characters such as decrease in the blade length of compound setae and/or blades fused with the shafts, as is the case in other syllid genera, e.g., *Haplosyllis* (Pascual et al. 1996). However, *Exogone* species that are not exclusively associated with sponges do not show these adaptations, e.g., *E. breviantennata* (see below). Members of the subfamily Exogoninae usually undergo reproductive metamorphosis that includes changes in various external structures (eyes, antennae, parapodial structures, and setae) and internal structures (nephridia and musculature) (Schroeder & Hermans 1975, Kuper & Westheide 1998). Based on the literature and our observations, *E. breviannenata* appears to be an exception in that reproductive modifications have never been observed for either sex.

Of interest is the fact that, based on the original descriptions of 34 species in this genus, there is about a one to one ratio of those that have a dorsal cirrus on setiger 2 and those that lack this character. Of the latter group, many species were reported to have a minute median antenna; very few of those species were said to have a median antenna longer than the palps. Of the former group, most species had a median antenna that reached at least to the tip of the prostomium, and many were much longer, reaching to or beyond the palps. An exception to this is *E. breviantennata,* which has a shorter median antenna, not even reaching to the tip of the prostomium.

Exogone breviantennata Hartmann-Schröder, 1959
characters emended
Figs. 1–5

Exogone breviantenna Hartmann-Schröder, 1959:125–127, figs. 75–78; San Martín, 1991:728–729, 730–731, fig. 8; Núñez et al., 1992:47, fig. 3; Pascual et al., 1996: 70, 77, table 2.

Exogone occidentalis Westheide, 1974:113; Russell, 1991:59–61, fig. 4 (emended).

Material examined.—El Salvador: paratype P-14590, ZMH; Belize: Twin Cays, West Bay, D. E. Russell, Nov 1993, Sta. M-4, 3 specimens labelled *Exogone occidentalis,* USNM 102085; and Bahamas: San Salvador Island (from amongst filaments of the algae *Batophora* sp. and *Vaucheria* sp. taken from the prop roots of *Rhiziophora mangle*), Oyster Pond, R. Zottoli & C. D. Long, 6 specimens, 4 May 1996; Osprey Lake, R. Zottoli, 13 specimens, 5 May 1996, USNM 186554; Reckley Hill Pond, R. Zottoli, 2 specimens, 5 May 1996 and 17 specimens, 19 Jun 1997, USNM 186555-186561; and southern edge of Bimini Lagoon, from plastic mesh sponges anchored and floating in 1–3 feet of water, collected at intervals up to 11 months from

1970–1971, Amy Schoener, 12 specimens (labelled as *Exogone verugera*), USNM 51542, and 5 specimens, USNM 51545.

Key characters.—Syllid in the genus *Exogone* with dorsal cirri on all setigers and median antenna shorter than prostomium.

Description of the paratype.—Specimen 1.95 mm long, 0.2 mm wide, 24 setigers (Fig. 1). New segment, without setae, forming between last setiger and pygidium. Prostomium about four times as wide as long; anterior and lateral margins rounded. Eyes not discernible. In the original description of type material, Hartmann-Schröder (1959) described and figured four eyes, one at each corner of a trapezoid, in the posterior half of the prostomium. Single median and two lateral digitiform antennae. Antennae similar in shape to tentacular, dorsal, and ventral cirri. Palps completely fused dorsally, extend anteriorly well beyond the prostomium. Tentacular segment short, about three times as wide as long; clearly separated from the prostomium, but not from the following first setiger. One pair of lateral tentacular cirri, about 0.02 mm long and 0.01 mm basal width. Uniramous parapodia (neuropodium only) as short lobes, similar on all setigers. Digitiform dorsal (about 0.024 mm long and 0.02 mm basal width) and ventral (about 0.024 mm long and 0.012 mm basal width) cirri. One dorsal simple seta (3 μm basal width) per setiger; terminates with short spines (Fig. 2A); tip slightly concave. One heterogomph spiniger (Fig. 2B) just below the dorsal simple seta; blade length 20 to 30 μm, increases from anterior to mid-body and then decreases posteriorly; blade with about 25 deeply cut teeth, rounded at the base. Terminal end of shaft where it meets the blade with cusps. Two to four heterogomph falcigers (Fig. 2C) below the spiniger, blades 5–10 μm long, bidentate (first tooth much smaller than second), with about five deeply cut teeth; base rounded. Generally four falcigers per setiger from anterior to mid-body setigers, then posteriorly diminishing to two; blade length increases in mid-body and then decreases again (Table 1). Outline of single aciculum visible in some setigers; details not clear. Ventral simple seta (base width about 3 μm) in setigers 14–24; tip strongly hooked and with short spines (Fig. 2D). Pygidium with two cirri, 0.13 mm long and 0.03 mm long. Pharynx short, retracted, extends forward from posterior portion of setiger 2; single dorsally attached tooth. Proventriculus 0.13 mm long and 0.1 mm wide, extends from setiger 2 to 5, with about 13 muscle rows.

Description of San Salvador Island specimens.—The following description is based on 32 complete specimens and 13 attached larvae, with 5–31 setigers, and ranging in length from 0.34 to 2.7 mm and 0.09 to 0.22 mm in width; see Table 2 and Figs. 3–5. Prostomium (Fig. 3A) about twice as wide as long. Two pairs of dark red eyes placed lateral to the antennae; anterior-most, largest pair about half way along lateral antennal length; posterior-most pair at antennal bases. No obvious modification of eyes in sexually mature specimens. Median antenna 0.01 to 0.026 mm long and two lateral antennae 0.01 to 0.015 mm long, all short and originating slightly anterior to prostomial-tentacular segment junction. Tentacular segment about four times as wide as long. Tentacular cirri 0.01 to 0.024 mm long (Figs. 3, 4). Digitiform dorsal (0.02 to 0.03 mm long) and ventral (0.01 to 0.03 mm long) cirri on all setigers.

Setal structure and pattern similar for all specimens examined. Dorsal simple seta (2.4 to 3 μm base width) terminates bluntly with about 15 short spines. Heterogomph spiniger blade length 17 to 28 μm; blades with approximately 30 teeth; spines on terminal end of shaft. One to four heterogomph falcigers (blade length 5 to 9 μm) and spines on terminal end of shaft. One ventral simple seta on posterior segments, found in all setigers in attached larvae (6–13 setigers) but are lost anteriorly in later stages. Single, smooth aciculum (6 μm basal width) in each setiger, with rounded slightly concave tip. Pygidium with two lat-

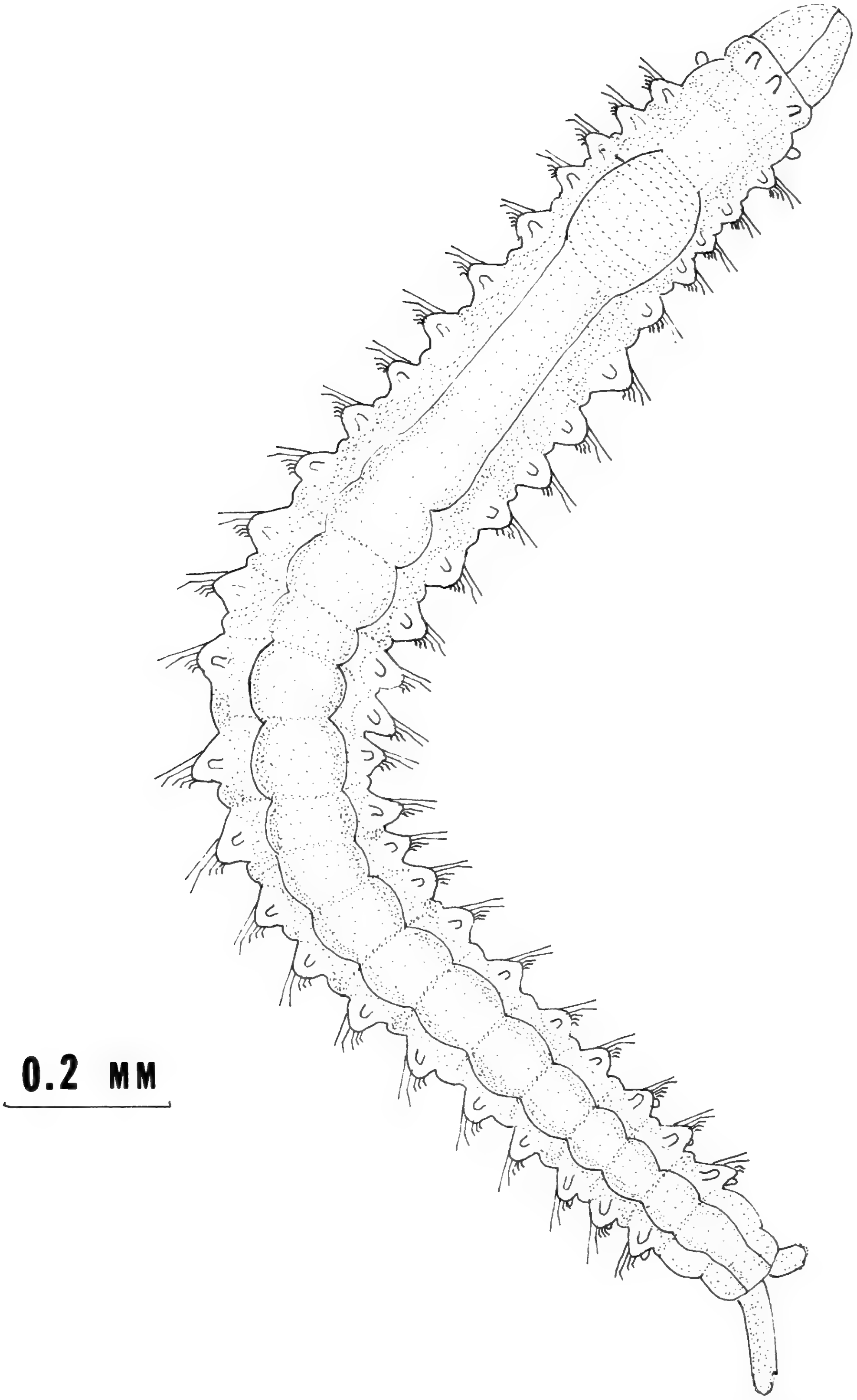

Fig. 1. Dorsal view of *Exogone breviantennata* paratype (P-14590, ZMH) from El Salvador, 1.95 mm long, 0.2 mm wide, and with 24 setigers.

eral cirri (0.05 to 0.15 mm long), sometimes uneven in length, apparently due to regeneration.

Pharynx (Figs. 3B, 4, 5) short, extends to setigers 1, 2, or 3 depending on degree of contraction; anterior rim with 10 soft papillae in addition to the large, curved, pointed, dorsally attached tooth, more easily seen when pharynx is everted. Proventriculus (0.07 to 0.2 mm long and 0.05 to 0.12

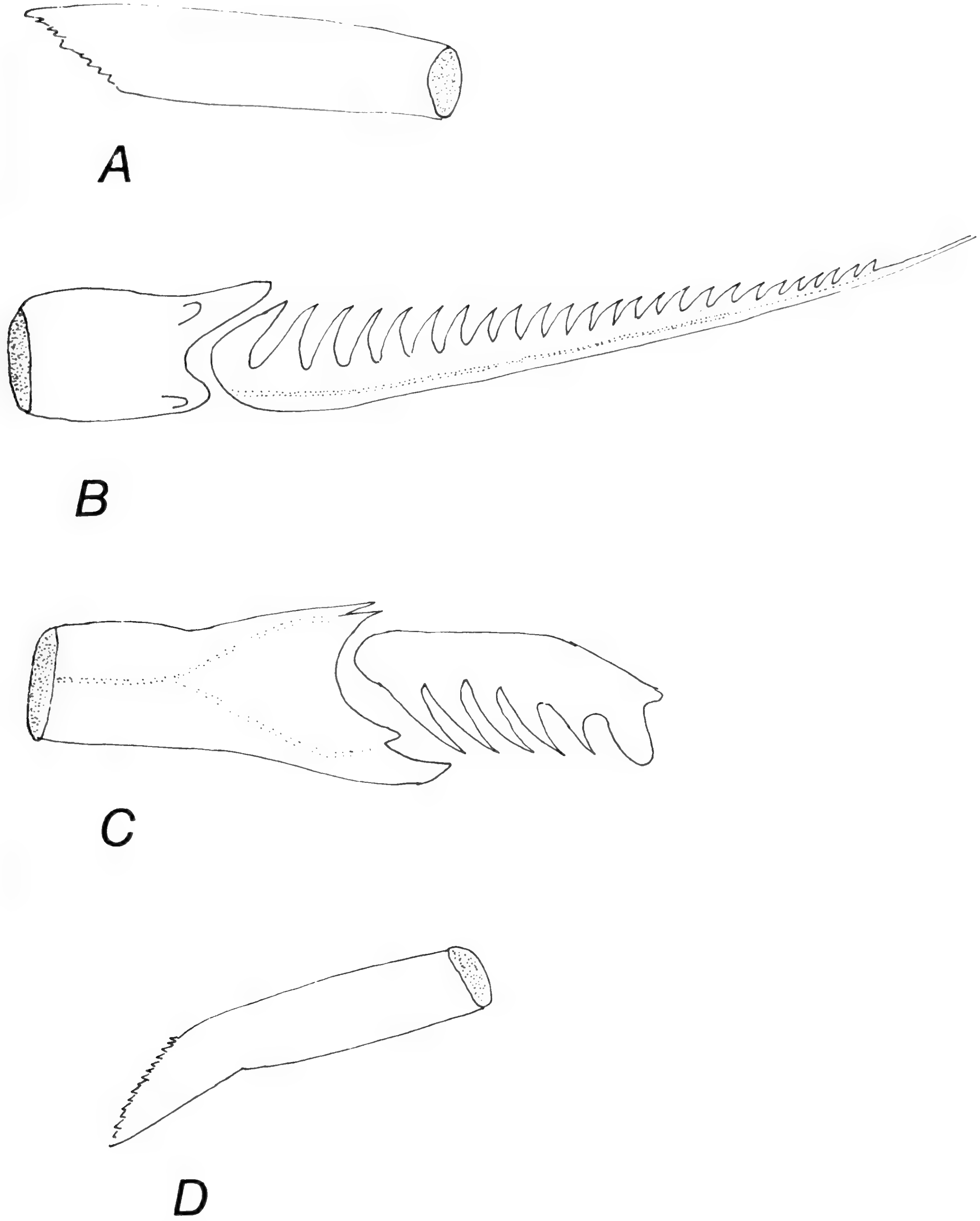

Fig. 2. Setae from *Exogone breviantennata* paratype (P-14590, ZMH) from El Salvador, 1.95 mm long, 0.2 mm wide, and with 24 setigers. A. Distal portion of dorsal simple seta, 3 μm basal width; B. Heterogomph spiniger, 30 μm blade length; C. Heterogomph falciger, 10 μm blade length; D. Ventral simple seta, 3 μm basal width.

Table 1.—Length in μm of spinigers and blades of compound setae from right side of *Exogone breviantennata* paratype (P-14590, ZMH) from El Salvador, 1.95 mm long, 0.2 mm wide and with 24 setigers. utm = unable to measure; avg = average; 0 = not present.

Setiger number	Heterogomph spiniger	Heterogomph falciger#1	Heterogomph falciger#2	Heterogomph flaciger#3	Heterogomph falciger#4
1	24	7	7	6	5
2	24	7	7	6	5
3	30	7	7	6	5
4	30	10	6	6	6
5	30	10	6	6	6
6	32	utm	utm	utm	utm
7–14	utm	utm	utm	utm	0
15	24	7	7	5	0
16–20	utm	utm	utm	utm	0
21	20	5	5	0	0
22–24	utm	utm	utm	utm	0
Averages	26.75	7.67	6.33	5.80	5.5

mm wide) extends posteriorly from setigers 1–4, 2–4, 2–5, 2–6, 3–5 or 3–6 (Figs. 1, 5) depending on degree of contraction during fixation; about 15 rows of muscle cells.

Sexually mature females with internal eggs or ventrally attached eggs or larvae (Fig. 5). Six internal eggs, average diameter 0.08 mm in setigers 12–17 of a 25-setiger female; five eggs 0.09 to 0.096 mm in diameter, attached ventrally, one to two per setiger on setigers 12, 14, and 15, of a 25-setiger female; and six eggs 0.08 to 0.1 mm in diameter, attached ventrally, two per setiger on setigers 15, 19, and 22 of a 31-setiger female. Five, 6-setiger larvae, (Fig. 5) average length and width 0.43 mm and 0.9 mm, one or two on setigers 12, 13, and 15 of a 21-setiger female; eight, 5-setiger larvae, average length and width 0.26 mm and 0.11 mm, one each on setigers 11–14 and 16–19 of a 27-setiger female. One 26-setiger male found with sperm packed in body cavity of setigers 18–25. No reproductive modifications observed for either sex. The only morphological differences between juveniles and sexually mature specimens are fewer setigers and more ventral simple setae in the younger stages (Table 2).

Discussion.—Two species of *Exogone* that have a dorsal cirrus on the second setiger and a short median antenna have been reported from the Caribbean: *E. breviantennata* and *E. exmouthensis.* A third species, *E. occidentalis,* was not compared to *E. breviantennata* when it was described from the Galapagos Islands (Westheide 1974). When Russell (1991) emended Westheide's (1974) description of *E. occidentalis,* based on a study of the type material and on specimens from a Belizean barrier reef, he described most setae as bearing spination as well as denticulation, thus bringing its description closer to *E. breviantennata.* Our examination of the Belize specimens leads us to agree with San Martín (1991) who listed *E. occidentalis* as a junior synonym of *E. breviantennata.*

We reexamined a paratype of *E. breviantennata* and found that the setae showed the spination and denticulation (also present in Bahamian specimens), which were referred to as indistinct in the type description. San Martín (1991) figured the denticulation of the blades of the compound setae and spination on the shafts on most setae for *E. breviantennata* from Cuba.

Exogone exmouthensis was described from Australia (Hartmann-Schröder 1980) without comparison to *E. breviantennata* and reported from Cuba by San Martín (1991) without description. He placed *E. breviantennata* and *E. exmouthensis* in separate subgenera based on details of the se-

Table 2.—Morphological measurements of specimens of *Exogone breviantennata* from Osprey Lake and Reckley Hill Pond, San Salvador, Bahamas. Measurements in mm. Spec. = specimen; set. = setiger; provent. = proventriculus; vent.SS = setiger number on which ventral simple setae begin; coll. = collected; loc. = collection site; Loc. 1 = Osprey Lake; Loc. 2 = Reckley Hill Pond; utm = unable to measure. Figures for specimens numbered 33–37 are averages from 5 larvae attached to specimen #4 and those for specimens 38–45 are averages from 8 larvae attached to specimen #15.

Spec. #	Set. #	Body length	Body width	Provent. length	Provent. width	Vent. SS	Date coll.	Loc.	Comment
38–45	5	0.30	1.00	0.07	0.05	1	05/05/96	2	on spec. 15
33–37	6	0.43	0.09	0.07	0.05	1	05/05/96	1	on spec. 4
16	6	0.34	0.10	utm	utm	1	06/19/97	2	
17	10	0.52	0.10	0.08	0.07	1	06/19/97	2	
18	10	0.70	0.10	0.08	0.05	1	06/19/97	2	
19	12	0.63	0.12	utm	utm	1	06/19/97	2	
20	12	0.71	0.12	0.10	0.06	8	06/19/97	2	
5	13	0.85	0.17	0.12	0.09	4	05/05/96	1	
21	13	0.70	0.11	0.12	0.07	1	06/19/97	2	
3	15	1.00	0.12	0.14	0.11	10	05/05/96	1	
22	16	0.88	0.14	0.13	0.07	10	06/19/97	2	
1	16	1.20	0.12	0.15	0.1	9	05/05/96	1	
23	17	1.03	0.14	0.11	0.07	11	06/19/97	2	
24	17	1.10	0.14	utm	utm	10	06/19/97	2	
2	17	1.35	0.16	0.14	0.1	9	05/05/96	1	
25	19	1.21	0.14	0.15	0.08	12	06/19/97	2	with eggs
7	19	1.40	0.18	0.15	0.09	12	05/05/96	1	
26	20	1.22	0.18	0.17	0.10	utm	06/19/97	2	
27	20	1.30	0.16	0.14	0.08	13	06/19/97	2	
4	21	1.40	0.2	0.19	0.11	22	05/05/96	1	with larvae
12	21	2.10	utm	0.17	0.1	14	05/05/96	2	
28	11	2.10	0.17	0.17	0.1	15	06/19/97	2	
9	22	1.75	utm	0.2	0.1	16	05/05/96	1	
29	23	1.80	0.16	0.16	0.10	17	06/19/97	2	
13	23	2.25	utm	0.17	0.1	14	05/05/96	2	
30	25	1.72	0.18	0.18	0.10	19	06/19/97	2	
6	25	1.90	utm	0.18	0.1	18	05/05/96	1	with eggs
31	25	2.00	0.16	utm	utm	20	06/19/97	2	
32	26	1.90	0.19	0.20	0.10	20	06/19/97	2	with sperm
8	27	1.95	0.20	0.2	0.12	23	05/05/96	1	
14	27	2.25	0.22	0.19	0.12	23	05/05/96	2	
15	27	2.70	0.20	0.17	0.1	22	05/05/96	2	with larvae
11	31	2.15	0.20	0.18	0.1	18	05/05/96	1	with eggs

tae, e.g., head of the shaft of compound setae with or without spination, the determination of which is dependent upon variables unassociated with morphology of the specimens themselves (see above). We have not seen specimens of *E. exmouthensis* and so are unable to comment on its relationship to *E. breviantennata.*

Two other species, *E. ovalis* Hartmann-Schröder, 1960, and *E. breviantennata ovalis* Hartmann-Schröder, 1974, have been made synonyms of *E. breviantennata* (San Martin 1991).

Most species of the genus *Exogone* that are described as having a dorsal cirrus on setiger two also have a median antenna that reaches at least to the tip of the prostomium, if not longer. In this regard, *E. breviantennata* is unique in that its median antenna is much shorter, not even reaching to the tip of the prostomium.

Because new species are sometimes

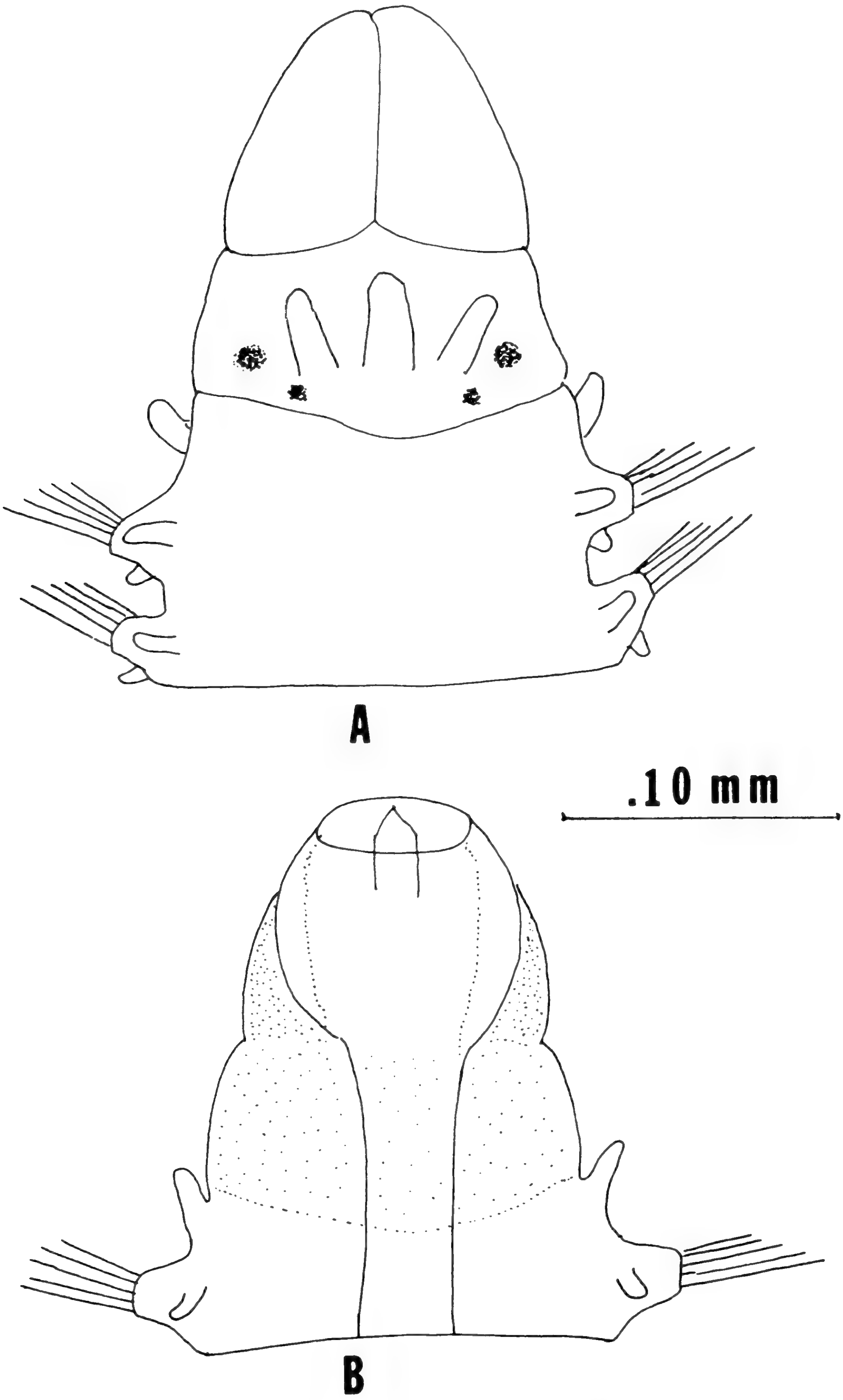

Fig. 3. Anterior end of *Exogone breviantennata* from Reckley Hill Pond, San Salvador, Bahamas. 1.72 mm long, 0.18 mm wide, and with 25 setigers. A. Dorsal view of prostomium including first two setigers; B. Ventral view including first setiger, showing anterior end of pharynx with tooth.

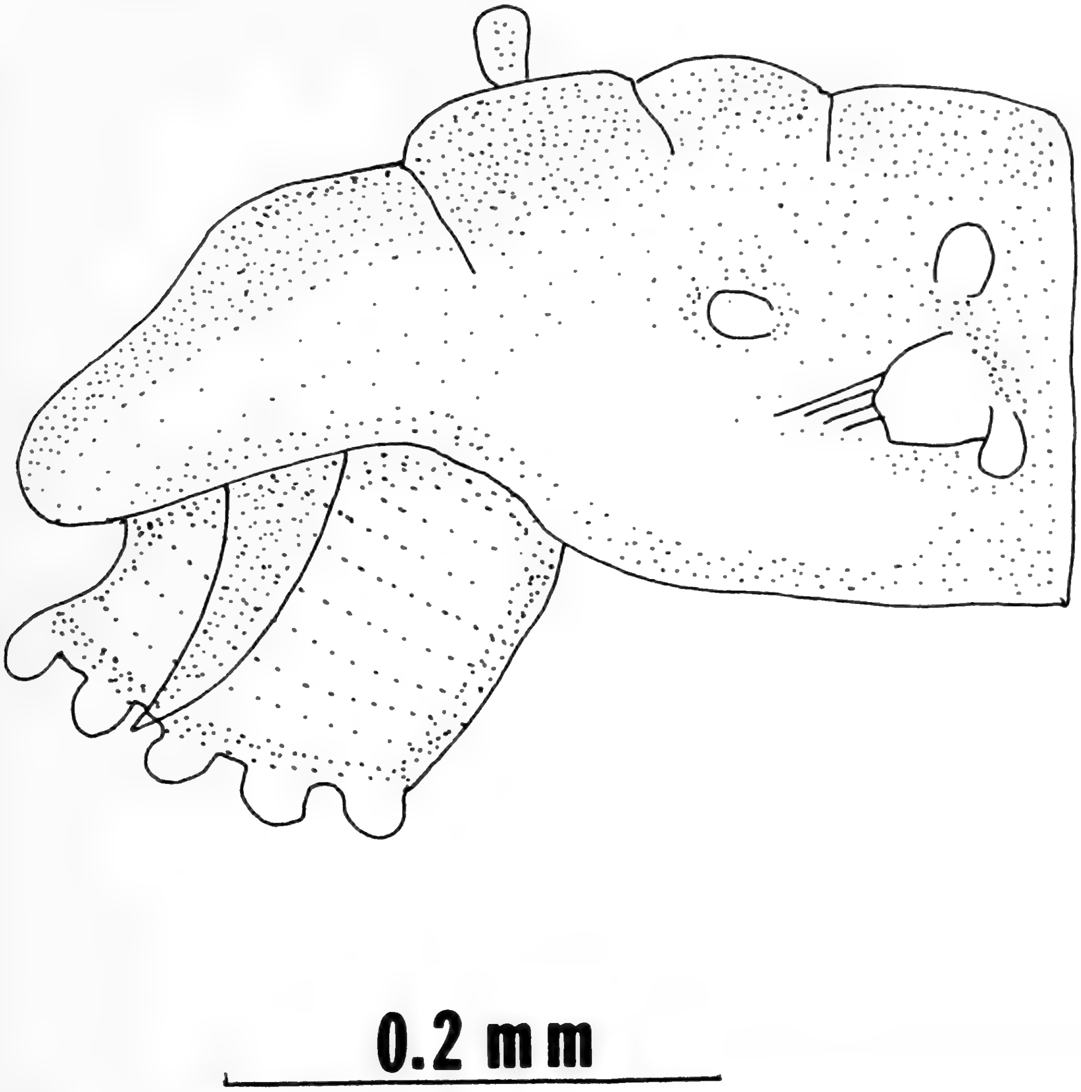

Fig. 4. *Exogone breviantennata* from Osprey Lake, San Salvador, Bahamas. 1.4 mm long, 0.18 mm wide, and with 19 setigers; lateral view of anterior end, showing tooth in extruded pharynx.

erected for minor setal differences, we carefully measured as many characters as possible for the paratype (from El Salvador) and for specimens from Osprey Lake and Reckley Hill Pond on San Salvador. We found no significant differences from site to site.

Habitat.—Type material collected in mud around mangroves in El Salvador (Hartmann-Schröder 1959). In the Bahamas, *E. breviantennata* was found amongst filaments of the algae *Batophora* sp. and *Vaucheria* sp. and on the prop roots of *Rhizophora mangle*. Pascual et al. (1996) summarized its habitat as intertidal to shallow depths, sand and shell gravel, in sponges and amongst hydroids on *R. mangle* roots, *Halimeda* sp. in beds of *Thalassia testudinum, Lobophora variegata* and calcareous crusts, *Vermetus* sp., photophilic algae and living inside the cavities of six species of infralittoral demosponges, where it constituted 0.6% of the total number of polychaetes and 9.7% of *Exogone* specimens extracted from the sponges. These habitats define it as part of an interstitial and crevice fauna.

Distribution.—Equatorial Pacific: Galapagos Islands (Westheide 1974), North East Pacific: La Herradura, El Salvador (Hartmann-Schröder 1959); North Atlantic: Bahamas (reported here), Belize (Russell 1991, as *E. occidentalis*), Canary and Madeira Islands (Pascual et al. 1996), and Cuba (San Martin 1991). San Martin (1991: 731) says "Probably circumtropical."

Biology.—The lack of solid material in

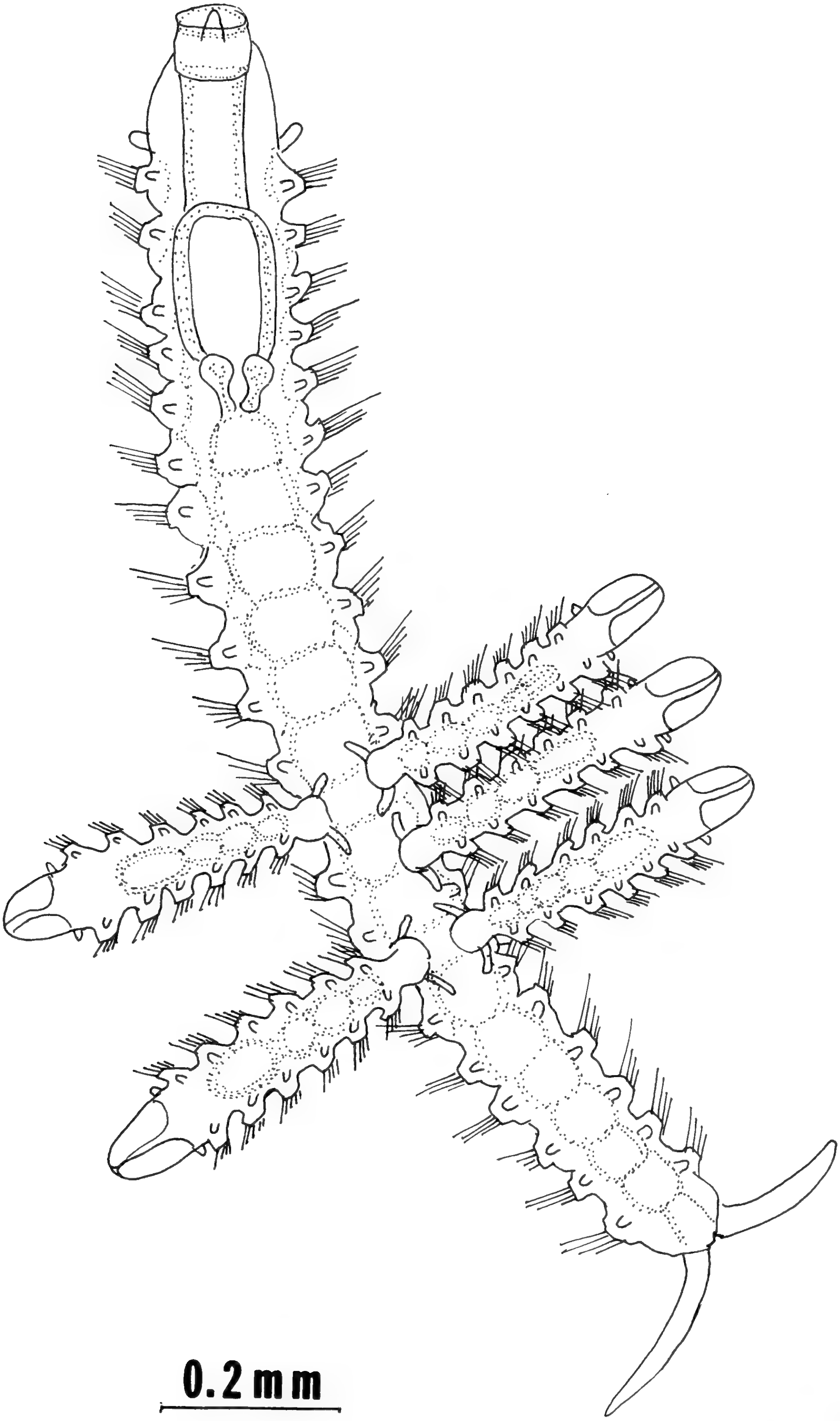

Fig. 5. Ventral view of *Exogone breviantennata* female with attached larvae from Osprey Lake, San Salvador, Bahamas, 1.4 mm long, 0.2 mm wide, and with 21 setigers.

the digestive tract of the Bahamian specimens suggests that they were fluid feeding, most likely using their tooth to penetrate algal filaments and then sucking out the contents with the aid of the muscular proventriculus. See Figs. 3B and 4 for the tooth in position for feeding. In live material, the gut is often dark green along its entire length, thus supporting this interpretation. Pascual et al. (1996) reported that, in the Canary and Madeira Islands, spicules of the species of sponges from which specimens were collected were found in their gut, suggesting that the worms were actually eating sponge tissue. There did not seem to be any preference for a particular species of sponge. They speculated as to whether polychaetes that are found with sponges function at times as parasites, mutualists, or commensals. Members of the subfamily Exogoninae had been previously thought to be selective deposit-feeders of mud or detritus (Uebelacker 1984:30–4).

Reproduction.—San Salvadoran sexually mature females were found with up to six eggs or eight larvae (Fig. 5, Table 2) attached to their ventral surface. Extrusion of eggs from the body cavity and fertilization were not observed. One male was found with sperm. There was no evidence of reproductive modifications of any kind. Hartmann-Schröder (1959) found gametes in, and eggs attached ventrally on, setigers 11–15 in the type material from El Salvador. In Belize, Russell (1991) found a sexually mature female with oocytes in six setigers beginning about setiger 16. Since attached larvae from both San Salvador and Belize females (Russell 1991) had no more than six setigers, they probably detach and become benthic at this stage.

Previous Bahamian records of the genus Exogone.—Worldwide, nearly 50 species of the genus *Exogone* have been described (Pascual et al. 1996). As of 1992, 19 of these species that are considered valid have been reported from the Caribbean and associated waters: *E. arenosa* Perkins, 1981; *E. atlantica* Perkins, 1981; *E. breviantennata* Hartmann-Schröder, 1959; *E. caribensis* San Martín, 1991; *E. dispar* Webster, 1879; *E. exmouthensis* Hartmann-Schröder, 1980; E. *gemmifera* Pagenstecher, 1862; E. *longispinulata* San Martín, 1991; *E. lourei* Berkeley & Berkeley, 1938; *E. naidina* Ørsted, 1845; *E. naidinoides* Westheide, 1974; *E. parhomoseta mediterranea* San Martín, 1984; *E. pseudolourei* San Martín, 1991; *Exogone* sp. A and sp. B, Uebelacker, 1984; *E. rolani* San Martín, 1991; sp. A, San Martín, 1991; *E. verugera* Claparède, 1868; and *E. wolfi* San Martín, 1991. See Perkins & Savage (1975), Salazar-Vallejo (1992) and Camp et al. (1998) for references to Caribbean reports. Of these, two have been reported from the Bahamas: *Exogone dispar* (Webster) (based on Vittor & Johnson 1977 and our examination of USNM 51541, from Bimini Lagoon) and *E. verugera* (Claparède) (in the collections of the USNM, L. Ward, pers. comm., 29 Aug 1995). San Martín (1991) notes that the original description of *E. verugera* is confused, and therefore not reliable, and synonymizes a series of Atlantic reports with *E. breviantennata.* Seven of the species reported from the Caribbean have a dorsal cirrus on the second setiger: *E. arenosa, E. breviantennata, E. dispar, E. exmouthensis, E. lourei, E. pseudolourei, E. rolani,* and *E. wolfi.* As any of the remaining six might be found in Bahamian waters, they are included in the key below.

Key to Caribbean *Exogone* species with dorsal cirrus on second setiger

1a. Median antenna does not reach tip of prostomium . . . . *E. breviantennata* Hartmann-Schröder, 1959
1b. Median antenna, much longer than lateral antennae, reaches to or exceeds tip of prostomium 2
2a. Tips of shafts of spinigers on setiger 2 with greatly enlarged triangular process 3
2b. Tips of shafts on setiger 2 not greatly enlarged 4
3a. Superior simple setae with well-defined

spine on tips; proventriculus with up to 28 rows of muscle cells .... *E. arenosa* Perkins, 1981
3b. Superior simple setae without spine; proventriculus with at most 20 rows of muscle cells .... *E. lourei* Berkeley & Berkeley, 1938
4a. Dorsal simple setae of median and posterior setigers enlarged and modified, strongly bidentate; proventriculus short, with ca 15 muscle cells rows .... *E. pseudolourei* San Martín, 1991
4b. Dorsal simple setae of median and posterior setigers not enlarged 5
5a. Median antenna club shaped .... *E. dispar* (Webster, 1879)
5b. Median antenna elongate 6
6a. Dorsal simple setae similar throughout body .... *E. wolfi* San Martín, 1991
6b. Dorsal simple setae increasing in thickness posteriorly and changing in shape .... *E. rolani* San Martín, 1991

Acknowledgments

We were alerted to the interesting polychaete fauna of the land-locked marine lakes of San Salvador, The Bahamas, by William Lindsay (Elmira College, New York), who, along with the staff of the Bahamian Field Station, have made this work possible. We thank them and Fitchburg State College for its continued support. We especially appreciate the constructive comments on the manuscript by Drs. Nathan Riser and David Russell.

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Podarke aberrans Webster & Benedict, 1887 - resolution, with descriptions of two new species in the genus *Microphthalmus* (Annelida: Polychaeta)

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Abstract.—Reference is made to individuals with "fan-shaped" caudal appendages from two different regions in the Gulf of Maine and to two different life-history stages in the original description of *Microphthalmus aberrans* (=*Podarke aberrans* Webster & Benedict, 1887). Intertidal meiofaunal investigations in the region over the past forty years have yielded three species that correspond to parts of the description. Two fragments of the "adult form" labeled Type, from Eastport, Maine, upon which most of the type description is based, exist as one of the syntype slides deposited by Webster & Benedict in the National Museum of Natural History. The species has been encountered occasionally in clean coarse sand beaches along the coast of Maine, and in the subtidal of Nahant Bay, Massachusetts. A second species with a fimbriate anal lamella, *M. aggregatus* n.sp., occurs in the intertidal of Cape Cod Bay, Massachusetts. The "half grown specimens", *M. pettiboneae* n.sp., to which the epithet *aberrans* has been incorrectly applied, is also present among the syntype slides, and has been collected in intertidal samples from New Brunswick, Canada to the south shore of Cape Cod, Massachusetts.

Webster & Benedict (1887) assumed that badly damaged specimens from Provincetown, Massachusetts collected in 1879, but not retained, were the same species as the one being described as *Podarke aberrans* from the Eastport area in Maine, because of the "peculiar fan-shaped" anal lamella. One "adult" specimen was encountered by the authors at Eastport, and the description of *Microphthalmus abberans* is based upon that individual with additional remarks on the morphology of "half-grown specimens." The figures accompanying the description are of both the "adult" and juvenile form, and the type material of *Microphthalmus aberrans* (Webster & Benedict, 1887) (=*Podarke aberrans* W. & B.) deposited in the National Museum of Natural History (USNM), is a mixture of two species. Southern (1914) reported that he had examined the "original types" deposited in the USNM and at Union College and that they did not agree with the type description. He transferred the species from *Podarke* to *Microphthalmus,* accepting the specific epithet *aberrans* for the material available to him and furnished a figure of the notopodial setae to support his contention; thus, we must assume that the slide of the specimen upon which Webster & Benedict based their description was not encountered. Eliason (1920) accepted Southern's statements about the type material while describing material from the Öresund, which he ascribed to the Webster & Benedict species, thus establishing a precedent of applying the epithet *aberrans* to a species that does not agree with the type description. The failure of subsequent authors to examine the type material has resulted in a perpetuation of this error.

A few individuals fitting the description of *Microphthalmus abberans* have occurred in intertidal meiofaunal collections I have made along the coast of Maine over the past forty years and in subtidal substrate from Nahant Bay, Massachusetts. Numerous specimens of a second species with a fimbriate anal lamella have routinely been encountered in the intertidal dunes on the sand flat at Ellisville, Massachusetts, as well as on the beach at Manomet, Massachusetts across Cape Cod Bay from Provincetown. The initial description of *Podarke aberrans* refers to three different species belonging to the genus *Microphthalmus,* two of which, including the species that has born that name since Southern's publication, must be described as new.

Materials and Methods

Specimens were obtained from substrate collected in 18 fl. oz. plastic bags for meiofaunal studies. Each sample was washed with fresh sea water in the laboratory 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 were anaesthetized with 7.5% $MgCl_2$ prior to fixation in Hollande's cupri-picri-formal-acetic. Whole mounts were stained with Ranvier's picro-carmine or Mayer's alcoholic HCl carmine; some were counterstained with alcoholic indigo-carmine. All measurements were obtained from living specimens.

Material labeled *Microphthalmus aberrans* in the collections of the Atlantic Reference Centre (ARC), St. Andrews, New Brunswick, and the National Museum of Natural History were obtained on loan. The syntypes (USNM 447) of *Podarke aberrans* from Eastport, Maine deposited by Webster & Benedict consist of five slides and two specimens in alcohol.

Microphthalmus aberrans (Webster & Benedict, 1887)

Figs. 1–6

Podarke aberrans Webster & Benedict, 1887:713–715, p.p., "adult form", figs. 14, 15, 18. *Microphthalmus aberrans.*—Pettibone, 1963:104, p.p.

Diagnosis.—Sexual individuals to 9 mm in length with 30–45 setigers. Ocelli absent. Dorsal cirri more than four times as long as neuropodial lobe. Anal cirri slightly longer than dorsal cirri. Notopodia with up to 15 pointed simple and one pectinate seta and a sturdy aciculum. Presetal neuropodial ligule with thin aciculum associated with one or two bidentate simple setae (Fig. 3). Neuropodial setal bundle with thick aciculum, one apically bidentate simple seta and about 15 finely denticulated apically bidentate falcigers. Falciger blades range from 6–32 μm in length. Testes in setigers 9 through 16, ovaries in following setigers. Penis anterior to parapodia of setiger 3 on both sides, with tubular stylus 25 μm long, muscle bulb large with large posterior papilla. Anal lamella with about 30 short, blunt, fimbriae.

Lectotype.—USNM (447), slide 502, labeled "*Podarke aberrans* adult fragments" (two fragments; one of three setigers from the female region of the body, and one of four setigers and anal lamella).

Material examined.—Data and photographs obtained from living specimens collected in the intertidal at Liberty Point, Robbinston, Maine; Crowe Neck, Cobscook Bay, Maine; Griffith's Head, Georgetown, Maine, and 16 m depth off Egg Rock, Nahant Bay, Massachusetts, in addition to the lectotype slide, have made it possible to complete the description of the species. One adult (USNM 186552) collected on 27 Mar 1980 at Liberty Point and one immature specimen (USNM 186533) encountered at Griffith's Head on 20 Apr 1999, have been deposited, in alcohol, in the USNM.

Morphological notes.—The acicula taper toward the slightly expanded apex; that of the presetal neuropodial lobe is hooded. The diameter of the presetal neuropodial aciculum is almost one-half that of the other two, <3 vs. 6 μm, however it runs at an angle, and its base varies in position from the same level to 4 μm distal to that of the neuropodial aciculum. The acicula are all approximately the same length, 76 μm. The pectinate notopodial seta ranges from 91–99 μm in length with the blade occupying almost one-half of the length. The blade is finely denticulated almost to the tip (Fig. 6). The difference in construction of the blade and shaft allows for great flexibility at the juncture so that at times the seta takes on the appearance of being jointed; the twisted appearance figured for the pectinate seta of *M. bermudensis* Westheide, 1973, (Abb. 4, fig. D) has also been encountered. The pectinate setae of species with several simple notopodial setae can rarely be recognized in the clump (Fig. 2) but can usually be distinguished in some of the parapodia of living specimens under coverslip pressure. The simple notopodial setae vary in appearance, depending upon the angle at which they are viewed and if they are retracted into the body or are projected. The majority of the simple notosetae of preserved specimens are strongly hooked apically. The striated fibrillae forming the cortex spiral (180° ?) but can not be traced to the apex. This spiraling may account for the flexibility which results in the hooked configuration.

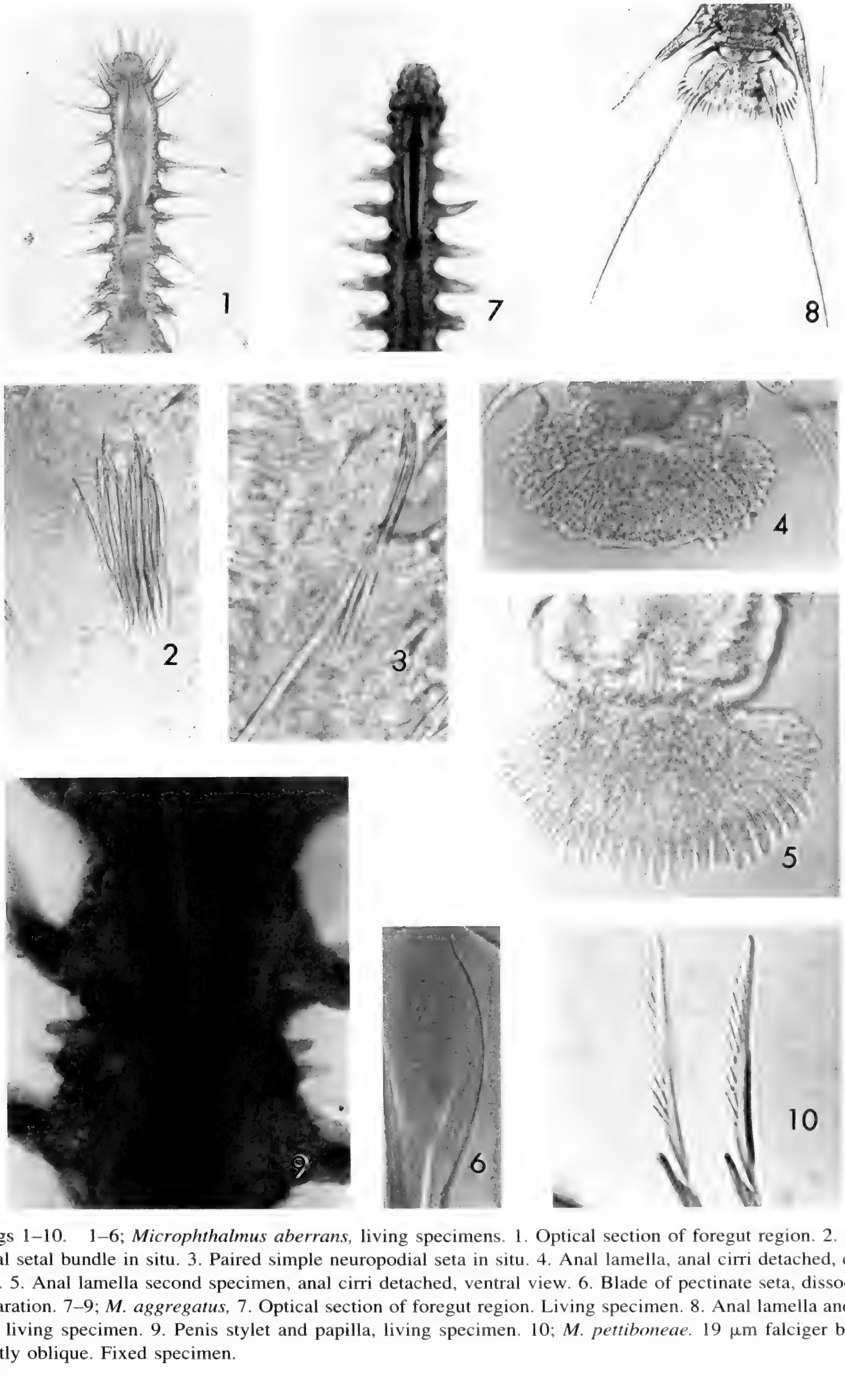
There appear to be eight digitiform papillae on the pharynx cap. The pharynx extends posteriorly to setiger 5 which is occupied by the ventriculus. The epithelium of the pharynx is thick and when the organ is inflated, develops longitudinal ridges (Fig. 1). There is a well-developed valve and sphincter separating the pharynx and ventriculus. The latter is globular and comprised of radial muscle and glandular cells. Retractor muscles extend from the base of the pharyngeal cap to the body wall at the juncture of the third tentacular segment and first setiger at which point protractors originate passing to insert at the juncture of the pharynx and ventriculus. Strongly developed retractor muscles extend from the ventriculus to the longitudinal muscles of setiger 8.

One of the 18 sexually mature specimens had an ovary on the left side, and testis on the right of setiger 16.

Remarks.—The figure of the anal lamella in the description by Webster & Benedict has little relationship to the specimen on the lectotype slide, except that the midregion is different from the rest of the margin. The lamella of living animals (Fig. 5) is domed, and if not fully expanded projects over the fimbriae so that they may appear to be absent medially for a variable extent of the margin (Fig. 4). A fold in the middle of the dorsal surface of the anal lamella on the lectotype may have been interpreted by Webster & Benedict as corresponding to the anal lamella of the "half grown" specimens.

Pettibone (1963) described the general appearance of the notopodial simple setae on the adult slide of the type specimen of *M. abberans* but did not report observations on notopodial setation of other specimens which she identified as that species (some of which were mature). The simple notosetae of preserved specimens of *M. fragilis* Bobretzky, 1870 are thin and sharply pointed; some are slightly bent toward the apex; those of *M. urofimbriatus* Alikunhi, 1948 were reported to be straight. [Hartmann-Schröder (1960) stated that the setae of *M.* c.f. *urofimbritta* (sic) from the Red Sea were too delicate to allow for characterization. The clusters of notopodial simple setae present in *M. aberrans* (Fig. 1), *M. fragilis,* and *M. urofimbriatus* are so apparent that it is more likely that her worms belong to the *M. similis* group of species.] The apex of the pectinate seta of *M. fragilis* is long and slender beyond the denticulated portion of the blade.

The species has not been routinely encountered nor in significant numbers. The single specimen obtained from the subtidal of Nahant Bay was associated with *Ophryotrocha* cf. *gracilis* Huth 1934, *Parougia caeca* (Webster & Benedict, 1884) and an eyeless species of *Protodorvillea,* all subtidal species in Nahant Bay but routinely



Figs 1–10. 1–6; *Microphthalmus aberrans,* living specimens. 1. Optical section of foregut region. 2. Notopodial setal bundle in situ. 3. Paired simple neuropodial seta in situ. 4. Anal lamella, anal cirri detached, dorsal view. 5. Anal lamella second specimen, anal cirri detached, ventral view. 6. Blade of pectinate seta, dissociated preparation. 7–9; *M. aggregatus,* 7. Optical section of foregut region. Living specimen. 8. Anal lamella and anal cirri, living specimen. 9. Penis stylet and papilla, living specimen. 10; *M. pettiboneae.* 19 μm falciger blades, slightly oblique. Fixed specimen.

present in the intertidal of the coast of Maine.

Microphthalmus aggregatus, new species
Figs. 7–9, 11–15

?*Podarke aberrans* Webster & Benedict, 1887:713 p.p., "same form at Provincetown, Massachusetts."

?*Microphthalmus* c.f. *similis* Westheide & Rieger, 1978; Westheide, 1979.

Diagnosis.—Transparent except for opaque white gonads. Individuals with gonads 3.2–7.1 mm long; with 31–43 setigers. Paired and median prostomial antennae approximately same length; palps extend about same distance beyond prostomium as paired tentacles. Blackish brown ocellus about mid-way between bases of paired prostomial antennae and 1st tentacular cirrus on each side. Dorsal cirri about four times length of neuropodium. Notopodium of first setiger with aciculum, following setigers with notopodial aciculum and pectinate seta. Neuropodium with bidentate falcigers and one or more simple setae. Pharynx bipartite; ventriculus oval to round, occupying 3rd setiger. Testes bilobed, in setigers 9 through 16; ovaries in subsequent setigers to penultimate. Penis digitiform with eight stylets and dorsal sensory papilla (Fig. 9); anterior to parapodia of third setiger on each side. Anal lamella with digitiform fimbriae.

Holotype.—USNM 186534. Massachusetts; Ellisville, intertidal coarse sand.

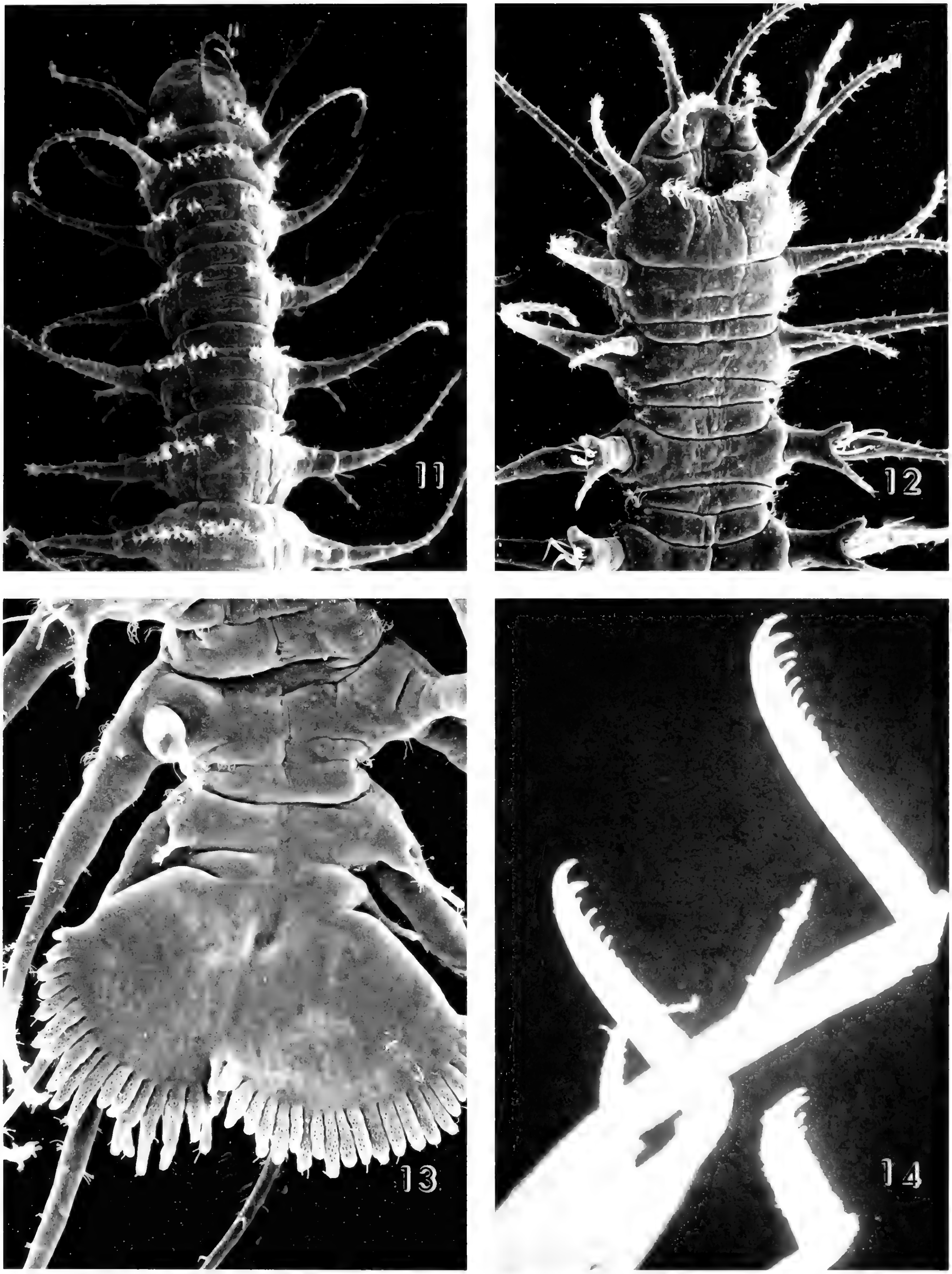
Paratypes.—USNM 186535, 12 specimens in alcohol. Peabody Museum of Natural History, Yale University, New Haven, Connecticut: YPM 24000, YPM 24001, stained whole mounts.

Etymology.—Latin *aggregatus,* clustered; referring to the tendency to occur in large concentrations, and to aggregate when isolated in vitro.

Material examined.—More than two hundred specimens from Ellisville, Massachusetts have been collected. Morphological data were obtained from 84. Additional data were recorded from specimens collected on Manomet Beach, Massachusetts (about 1 km North of Ellisville).

Morphological notes.—The body tapers from the anterior end to the female region, but the interparapodial width is about constant. Bands of refringent granules in the dorsal epidermis are colorless and do not produce opacity. Pigment is restricted to black granules in the epithelial cells of the rectum. The setigers containing ovaries are inflated and have a larger diameter than the anterior setigers. The prostomial antennae and palps range from 0.13–0.15 mm in length; the median antenna is thinner and is occasionally forked. The palpophore is small, accounting for very little of the extent of the palp. The dorsal tentacular cirri are longer than the ventral, viz., 1st 0.20–0.22:0.13–0.16, 2nd 0.27:0.14–0.16, 3rd 0.27–0.30:0.05–0.07 mm. Dorsal cirri of parapodia 0.24–0.27 mm long, except setiger 1 which are shorter, rarely exceeding 0.17 mm. Frequently, apparently as the result of regeneration, individual tentacular and dorsal cirri are shorter than these measurements. The pleura of all setigers expand laterally and the cirrophores are elongate, capped distally with a lobe above the base of the cirrus (Fig. 11). This lobe contains numerous mucous cells. The pair of anal cirri to either side of the anus attain lengths up to 0.4 mm. (Fig. 8). The fully expanded anal lamella is about 0.25 mm broad with as many as 42 digitate fimbriae 0.03 mm long. Shorter fimbriae as well as those that are forked probably indicate injury.

Ciliation on the prostomium is restricted to the nuchal organs (Fig. 11), each of which bears a small papilla on the anterior margin. A band of cilia extends across the dorsum between the bases of the second tentacular cirri but is interrupted medially on the subsequent four segments. Complete ciliary bands extend from the median edge of the lobe at the apex of the cirrophore (Fig. 11) across the dorsum of succeeding setigers. There is a lateral cluster of cilia anterior to each parapodium, and a lateral



Figs. 11–14. *Microphthalmus aggregatus,* SEM. 11. Dorsal view, anterior end. 12. Ventral view, anterior end. 13. Anal lamella, ventral view. 14. Medium and short falciger blades.

patch posteriad. Ventrally, a band of cilia extends along the posterior edge of the mouth (Fig. 12), constituting the only consistent ciliation on the ventral surface.

Cirrophores of the dorsal cirri are almost as long as the neuropodia. Notopodial lobes are not present. Notopodial setation consists of one or two pointed acicula 45–57 μm long and one or two pectinate setae 24–33 μm long of which the comb occupies one-fourth to one-third of the length. The presetal lobes of the neuropodia are conical, about 22 μm long and are supported by a thin pointed aciculum 57 μm long accompanied by a bidentate simple seta which moves independently, or sometimes in conjunction with the other neuropodial setae. A pointed simple or bidentate seta, or both, may be present in the neurosetal bundle, which consists of as many as nine apically bidentate falcigers (Fig. 14), most of which are 17–20 μm long and accompanied by one or more with short blades 7–8 μm long and usually one or more with blades in excess of 36 μm long. Ventral cirri of the parapodia are thin and filiform ranging between 35 and 42 μm in length.

The soft portion (cap) of the pharynx occupies the first tentacular segment and bears eight simple digitiform papillae tightly packed together around a large and expansive surface. Retractor muscles pass directly from the base of the cap to the body wall of the third tentacular segment from whence, protractors extend to the base of the pharynx. The second region occupies the second tentacular segment and is muscular (Fig. 7) with an epithelium containing granular products. The third region extends from the third tentacular segment to the third setiger. The ventriculus is firmly attached to the adjacent wall of the body.

Remarks.—In April and May, the ovaries are packed with yolky oocytes 35 μm in diameter, and the testes are primarily in early stages of spermiogenesis with few spermatids undergoing flagellar development. By August, the testes are packed with fully developed sperm; ovarian segments contain sperm in seminal receptacles; and the number of oocytes is reduced. Ovaries contain two or three degenerating oocytes in November and December, but the testes are packed with sperm. The animals have lived in the sorting bowls for up to eight months with biweekly water changes, but egg laying has not occurred in the absence of a food source, and the gonads have been resorbed. Efforts to investigate posterior regeneration, as the result of the discovery of a specimen with a bifurcated posterior end (Fig. 15), in 1977, have been futile for the same reason.

The major difference between *M. aggregatus* and *M. similis* Bobretzky, 1870, in addition to size and number of segments, is the distribution of the gonads. Ovaries of *M. similis* do not occur anterior to setiger 20. About 10% of the *M. aggregatus* individuals (7 of 92) had the ovary on the right side of setiger 16 and testis on the left, and the first testis on the right in setiger 8 instead of 9. One specimen was encountered with a mixed gonad in the right antimere of setiger 17 and ovary on the left. Some specimens of *M. aggregatus* have lacked pigmented ocelli, while others have lacked them on one side, or have had two (one dorsal and one ventral) on one or both sides. Variation, as well as absence of ocelli in *M. fragilis,* was noted as an intraspecific variation by Bobretzky (1870).

The divided pharynx of *M. fragilis* figured by La Greca (1950:fig. 1) was not apparent in any of the three specimens from the Black Sea which I examined, but the pharynx of *M. similis* from there was all divided as in *M. aggregatus.*

Microphthalmus pettiboneae, new species
Fig. 10

Podarke aberrans Webster & Benedict, 1887: 713–715, p.p. "juvenile form", figs. 16, 17, 19, 20.

Microphthalmus aberrans Southern, 1914: 46, fig. 7.–Pettibone, 1963:104, p.p., figs. 27a–b.—Clausen, 1986:184–186, figs.

Figs. 15,16. 15. *Microphthalmus aggregatus,* with posterior bud, living specimen. Scale equals 0.09 mm. 16. Anal lamella of living *Microphthalmus nahantensis* Westheide & Rieger, 1987. Scale equals 0.045 mm.

14, 19 (for additional synonymy see Hartmann-Schröder 1971).

Diagnosis.—Variable intensity of brown pigmentation; mature individuals less than 10 mm in length with 30–35 setigers; pair of ocelli present; dorsal cirri only slightly longer than neuropodial lobes; unpaired sucker-like penis; single pectinate and simple seta with an aciculum in notopodium; testes in setigers 6 through 9; bilobed (medially indented) anal lamella.

Syntypes.—USNM (447), slides 137, 138, 501, and two in alcohol deposited by Webster & Benedict.

Additional material deposited.—USNM (186536) from Beacon Point, Blacks Harbour, New Brunswick, Canada: ARC 9953141; 995314, from Pagan Point, St. Andrews, New Brunswick, Canada.

Etymology.—The species is named for Dr. Marian Pettibone, who in 1953, was responsible for my initial efforts to resolve the problem.

Material examined.—Observations have been recorded from numerous living individuals collected in intertidal coarse sand beaches between Beacon Point, Blacks Harbour, New Brunswick, Canada and East Point, Nahant, Massachusetts, USA. Specimens identified by Pettibone as *M. aberrans* (USNM 28413) from Southport Island, Maine; (USNM 32498) from Rye Beach, New Hampshire, and from Halifax, Nova Scotia, Canada (USNM 49180) were examined and found to be *M. pettiboneae,* as were specimens from the subtidal (ARC 9661230) of Lime Kiln Bay, Letang Estuary, New Brunswick, and (ARC 9953146) "off" Navy Island, St. Andrews, New Brunswick in the Atlantic Reference Centre collection.

Morphological notes.—The simple notopodial seta tapers to a point, and is strongly developed, approximately 51 μm long and slightly more than 2 μm maximum diameter. The cutting edge of the pectinate seta is reinforced by 8–12 strongly developed denticles, beyond which the blade is thin and serrations are not visible. Blades of the neuropodial falcigers are bidentate with serrated margins; one or two with fine denticulations are long and spiniger-like, measuring 75–85 µm in length; three to five, with strong denticulations, are about 40 µm; two with strong denticulation are small, about 12 µm long; while some (Fig. 10) approximate 20 µm in length. One or two simple neuropodial setae are present in the terminal 2–4 setigers.

Remarks.—Westheide (1967) noted that the juveniles included in the type description of *M. abberans* constituted a separate species characterized by the presence of eyes, short cirri, and a simple rounded anal lamella, features for which no ontogenetic evidence supported the possibility of change to the "adult" morphology.

Denticulation of the blades of the pectinate setae of *M. pettiboneae* is difficult to show accurately in line drawings, and while the SEM micrograph of this seta in Clausen (1986) from a North Sea specimen, is slightly rotated, denticulation is similar to that of the New England forms. The strongly developed simple notopodial seta frequently projects from the body of preserved specimens and is the primary morphological feature by which immature *M. pettiboneae* can be distinguished from *M. sczelkowii* (Table 1). Mature specimens of the two species are easily distinguished by oocyte size and number (Table 1).

Discussion

The genus *Microphthalmus* is hermaphroditic and its members are typical meiofaunal animals attaching to hard particles with a caudal adhesive organ and coiling when disturbed. Intact specimens are infrequently present in routine screenings of substrate, and pretreatment to release attached animals is essential in order to obtain complete specimens or population densities.

An investigation similar to that of Westheide & Rieger (1987), which clarified the systematics of the *M. listensis* group of species, may demonstrate that the species listed in the synonymy of *M. aberrans* by Hartmann-Schröder (1971) are *M. pettiboneae*

Table 1.—Morphological features of New England species of *Microphthalmus*.

	M. abberans	*M. aggregatus*	*M. nahantensis*	*M. pettiboneae*	*M. sczelkowii*
Ocelli	absent	present	absent	present	present
Anal lamella	fimbriate	fimbriate	spatulate	hemisphere	hemisphere
Notopodial simple setae	to 15	0	1	1	0
Dorsal cirri	>3× neuropodial cirri	>3× neuropodial cirri	>3× neuropodial cirri	<2× neuropodial cirri	<2× neuropodial cirri
Penes	paired	paired	paired	single	paired
Oocyte diameter	<100 µm	<100 µm	>200 µm	<100 µm	>200 µm
Oocyte number	many	many	<13	many	<12
M/f juncture	16/17	16/17	9/10	9/10	9/10

or that speciation has occurred and they constitute different species.

Very young individuals of *M. similis* were described by Westheide (1967) from the intertidal at Sylt and Hartmann-Schröder & Stripp (1968) recorded sexually immature individuals up to 18 mm long and consisting of more than 60 segments, characteristics which agree with those of *M. similis,* from a depth of 21 m in the North Sea. Gonad distribution and penis characteristics have not been reported for the North Sea populations. The specimens listed as *M.* cf. *similis* by Westheide & Rieger (1978) from North Carolina, U.S.A. were small and immature. The distribution of gonads in the two sexually mature specimens from the same region was not recorded by Westheide (1979). It is possible that they represent a southern distribution of *M. aggregatus* or constitute a separate species. Westheide (1977) noted that reproductive organs were significant but could not be included in a phylogenetic analysis of *Microphthalmus* because of the absence of data for many species. However, the male-female (m/f) juncture of the five New England species (Table 1) supports the possible adelphotaxa indicated in his cladogram. The occurrence of ova in one antimere and sperm in the other of setigers at the m/f juncture of *M. aggregatus* has also been recorded by Bobretzky (1880) for *M. fragilis* and *M. similis* and Clausen (1896) for *M.* cf. *pettiboneae.*

The prostomium of *Microphthalmus* species is malleable, influencing its shape and the location of the palps and antennae. Retraction of the prostomium into the peristomium may draw the median antenna back against or into the peristomial fold. The median antenna is thin, rarely visible from ventral view unless bent to one side, and is often undetectable on preserved specimens.

Ciliation has been described and figured for members of the *listensis*-group by Westheide & Rieger (1987), but other than for the present description of *M. aggregatus* has not been recorded for other species in the genus.

A pectinate notopodial seta is characteristic of members of the genus but is absent in *M. hartmanae* Westheide, 1977 and *M. simplicichaetosus* Westheide & Purschke, 1992, species with fimbriate anal lamellae, dorsal cirri slightly more than twice as long as the neuropodium and in which strongly serrated simple setae are present in the neuropodium (Westheide 1977, Westheide & Purschke 1992). The pectinate notopodial setae may be involved in stimulating the glands on the cirrophore or in spreading secretions from those glands. The role of notopodial setae in members of the genus with more than one or two simple setae in addition to the comb seta is difficult to assess.

The presence of the male copulatory organs in the third setiger is a generic character; however, the morphology and number of penes varies between species. Transmission electron microscopy (TEM) by Westheide (1979) demonstrated that the penis stylets of *M.* cf. *similis* from North Carolina are separate entities and not ridges in the wall of the penis.

The presence of an aciculum in the presetal neuropodial lobe appears to be characteristic of the Microphthalminae *sensu* Hartmann-Schröder (1971) while absent from that lobe in the Hesionidae s.str.

Westheide (1977), with "hesitation", postulated the fimbriate anal lamella as "ancestral". Dorsal cirri of the parapodia more than twice as long as the neuropodium appears to be characteristic of species in which the anal lamella is a large free fan as in the fimbriate species and *listensis*-group (Fig. 16). [The figure and description of the anal lamella of *M.* c.f. *urofimbritta* (sic) by Hartmann-Schröder (1960) is of a preserved specimen with the lamella flexed so that the anal cirri and anus are terminal, and the fimbriate posterior margin has folded back beneath the terminal setigers. Artistic license is also apparent in the figure of the anal lamella of *M. similis* in La Greca

(1950) and *M. abberans* in Webster & Benedict (1887).]

Gland openings on the anal lamella of fimbriate species are restricted to the ventral surface of the fimbrae (Fig. 13). The arrangement of these glands has not been recorded for either the *listensis*-group nor for the species with a simple hemispherical (sometimes indented) lamella, and thus is not available for assessment at present.

The ventriculus is attached by muscle fibers to the body wall, and is restrained posteriorly by the septum at the anterior end of the intestine. Telescoping of segments alters the topography as does eversion of the pharynx. Eversion in species with a bipartite pharynx (including the related genus *Hesionides*) does not significantly alter ventricular location; which is in setiger 2 in the *listensis*-group, 3 in a number of species, 5 in *aberrans,* [the pharynx was reported by Westheide & Purschke (1992) to extend to setiger 4 in *M. simplicichaetosus,* which would place the ventriculus in 5], 12 in *M. hamosus* Westheide, 1982. The location of the ventriculus, or origin of the intestine, have not been routinely recorded in descriptions of species.

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The constant advice and encouragement of Drs. Pettibone and Westheide throughout the years would have been in vain if I had not finally checked the type material of *M. aberrans* deposited in the USNM (courtesy of William Moser). The collection of *Microphthalmus* species present at the Atlantic Reference Centre was obtained through the courtesy of Dr. G. Pohle. Translations of the two papers in Russian by Bobretsky were furnished by Dr. Pettibone. Alcoholic specimens of *M. fragilis* and *M. similis* from the Black Sea were generously furnished by Dr. T. Marinov in 1979 for comparative purposes. The manuscript was greatly enhanced by the conscientious reviews of Drs. Brigitte Hilbig and Stephen Gardiner.

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Parapionosyllis cabezali, a new species of Exogoninae (Polychaeta: Syllidae) from Spain

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Abstract.—Parapionosyllis cabezali, a new species of Exogoninae (Polychaeta: Syllidae) from the Atlantic coast of Spain, is described. This new species is characterised by the shape of the simple and compound setae, small dorso-ventral gradation in the length of the blades, and by the presence along the body of two types of parapodial glands, which open dorsally separately from each other.

Campoy (1982) identified three specimens collected in Punta Endata, Guipúzcoa, NE Atlantic, Spain, as *Parapionosyllis* cf. *gestans* (Pierantoni, 1903). Subsequently, during a study of the taxonomy and ecology of the sublittoral soft bottom benthic polychaetous annelids in the Ría de Ferrol and Ría de Baiona, both located on the Atlantic coast of NW Spain, more specimens of this species were collected and reported by Parapar (1991), Parapar et al. (1994) and Moreira (1999). Examination by SEM of several specimens collected in the Ría de Baiona (NW Spain) has provided evidence that these organisms represent a new species. The specimens are characterized by the shape and dorso-ventral gradation in the length of the compound setal blades and by the presence along the body of two types of parapodial glands. In this paper, we describe and discuss this new species. The diagnosis of the genus was provided by Fauvel (1923) and San Martín (1984).

Materials and Methods

The type specimens (holotype and paratypes) were collected by the junior author (JM) in littoral soft bottom areas of the Ría de Baiona (Galicia, NW Spain) at 9–12 m depth. Additional specimens were collected in Galicia, in the Ría de Ferrol. Samples were taken both by means of a naturalist rectangular dredge and a Van Veen dredge in Dec 1995 in the case of the type series and in 1987 and 1989 in the Ría de Ferrol. Samples with the letters VD denote sampling for the vertical distribution of animals in the sediment. In this study, samples were taken by scuba diving and by pushing a 50 cm corer into the sediment. Animals taken from the sediment were fixed in 10% buffered formalin and preserved in 70% ethanol. Body and setae measurements provided in the description refer to the holotype, the width was measured across the proventriculous and excludes cirri, parapodia and setae. Observations, drawings, and measurements were obtained using a microscope with interference contrast optics (Nomarsky). Drawings were made with the aid of a drawing tube. The SEM micrographs were taken at the Servicio Interdepartamental de Investigación of the Universidad Autónoma de Madrid, Spain. The types are deposited in the Museo Nacional de Ciencias Naturales de Madrid, Spain.

Family Syllidae Grube, 1850
Subfamily Exogoninae Rioja, 1925
Genus *Parapionosyllis* Fauvel, 1923
Parapionosyllis cabezali, new species
Figs. 1, 2

Parapionosyllis cf. *gestans.*—Campoy, 1982: 267–269, fig. 18.—Parapar et al., 1994: 96–97, fig. 2.—Moreira, 1999: 319–323, fig. 26. [Not *Parapionosyllis gestans* Pierantoni, 1903].

Material examined.—Ría de Baiona (Galicia, NW Spain). Holotype and 23 paratypes. Sta. 8, Dec 1995, coarse sand, 12 m (10 specimens); Sta. 9, Dec 1995, medium sand, 10 m (10); Sta. 12, Dec 1995, coarse sand, 9 m (4).

Additional material.—Ría de Ferrol (Galicia, NW Spain), 39 specimens. Sta. 1, Jul 1987, muddy sand, 15 m (1 specimen). Sta. 3, Jun 1987, muddy sand, 11 m (1). Sta. 10, May 1987, muddy sand, 18 m (2). Sta. 11, Jul 1987, muddy sand, 20 m (1). Sta. 13, May 1987, coarse sand, 14 m (2). Sta. 15VD, Aug 1989, 20–25 cm in sediment depth, 17 m (1). Sta. 17, Jul 1987, very coarse sand, 25 m (1). Sta. 22, Oct 1987, very coarse sand, 20 m (1). Sta. 22VD, Aug 1989, 0–5 cm in sediment depth, 20 m (8). Sta. 22VD, Aug 1989, 5–10 cm in sediment depth (6). Sta. 22VD, Aug 1989, 10–15 cm in sediment depth (1). Sta. 22VD, Aug 1989, 15–20 cm in sediment depth (2). Sta. 26, Aug 1987, very coarse sand, 15 m (5). Sta. 37VD, Aug 1989, 0–5 cm in sediment depth, 15 m (7). Ensenada de Baiona (Galicia, NW Spain), 704 specimens. Sta. 8, Dec 1995, coarse sand, 12 m (327 specimens). Sta. 9, Dec 1995, medium sand, 10 m (120). Sta. 12, Dec 1995, coarse sand, 9 m (236). Sta. 13, Dec 1995, medium sand, 8 m (18). Sta. 14, Dec 1995, medium sand, 9 m (3).

Description.—Body relatively long and thin, with well marked segments. Holotype 3.36 mm long, 0.24 mm wide with 39 segments. Prostomium semicircular to pentagonal (Figs. 1A, 2A); four eyes in an open trapezoidal arrangement and two very small anterior eyespots; eyes disappear soon after fixation in alcohol. Antennae bottle or ninepin shaped, relatively long; median antenna somewhat longer than the lateral ones, approximately of the same length as the prostomium and palps together; lateral antennae inserted ahead of anterior eyes; median antenna between posterior eyes, near the posterior margin of the prostomium. Palps robust, equal to or slightly longer than the prostomium, fused at bases but separated in the anterior one-half; a slight junction suture occasionally observed. Tentacular segment distinct but shorter and narrower than the following segments; a pair of tentacular cirri similar in shape to antennae but approximately one-half the length of the lateral ones. Two ciliated nuchal organs (Fig. 2A, B) deeply imbedded between the posterior margin of the prostomium and the anterior margin of the tentacular segment.

Anterior dorsal cirri short and oval, with slightly enlarged bases (Figs. 1A, 2A); progressively more elongated and slender; slightly longer than the parapodial lobes; posterior dorsal cirri thinner and longer than anterior ones (Fig. 1B). Two types of parapodial glands (Fig. 1A, B); the smaller ones beginning in the most anterior segments, including the first setiger, with granular content, and the larger ones with fibrillar material, located near the central body line and starting from the proventricular segments. These parapodial glands open dorsally near the dorsal cirri, separate from each other; each pore is provided with a mobile, digitiform papilla which ejects the products of these glands (Fig. 2C, D). Both types of glands are dark red in colour. Parapodial lobes short and conical, ending in a small rounded papilla (Fig. 1C). Ventral cirri digitiform, long and slender, shorter than the parapodial lobes or similar in length.

Most anterior parapodia have about nine compound setae; six or seven in the re-

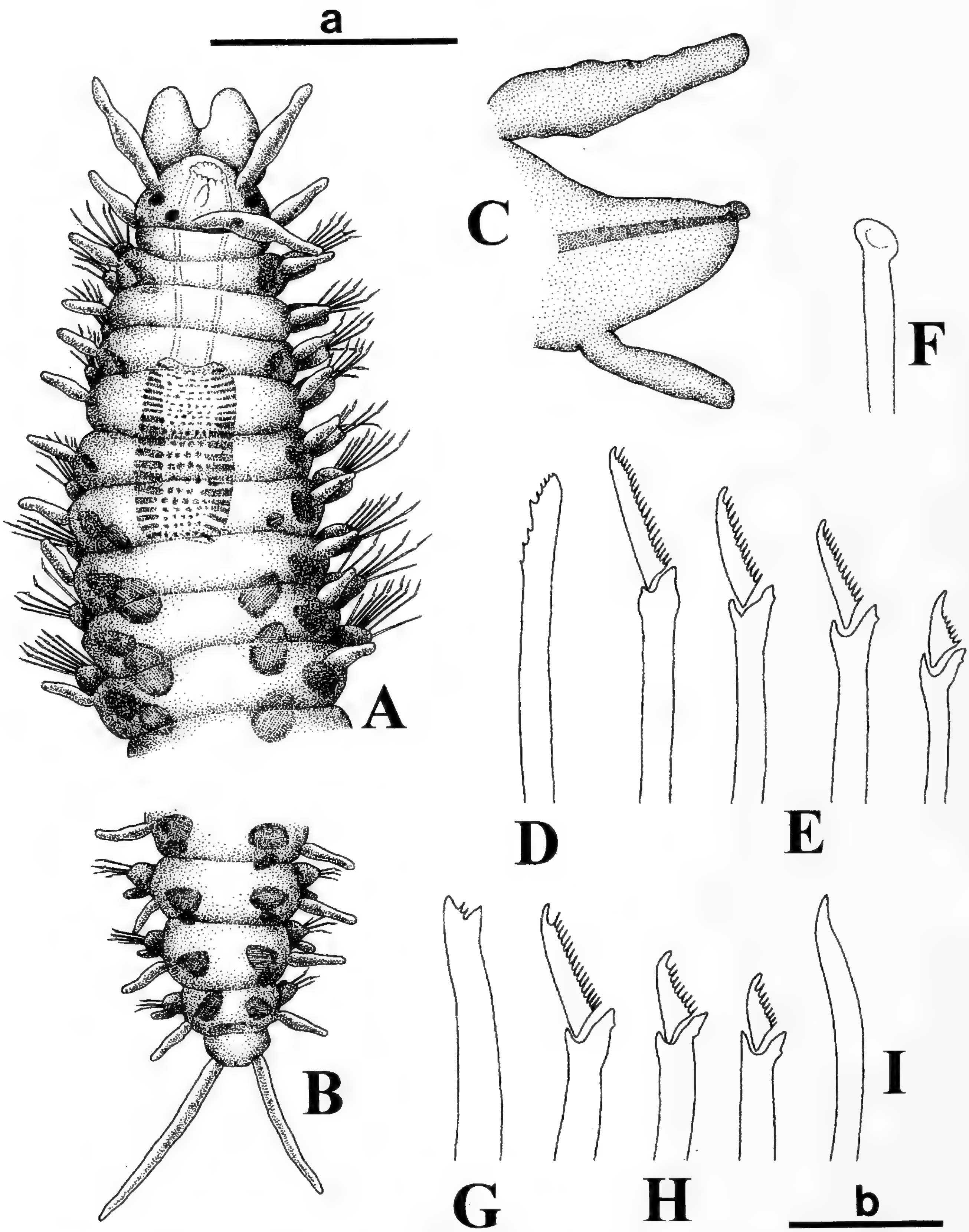

Fig. 1. *Parapionosyllis cabezali,* new species. Holotype. A, anterior end and midbody, dorsal view; B, posterior end, dorsal view; C, parapodium of midbody, posterior view; D, anterior dorsal simple seta; E, anterior compound setae; F, aciculum; G, posterior dorsal simple seta; H, posterior compound setae; I, posterior ventral simple seta. Scale bar a: 0.25 mm for A, B and 60 μm for C; scale bar b: 25 μm for D to I.

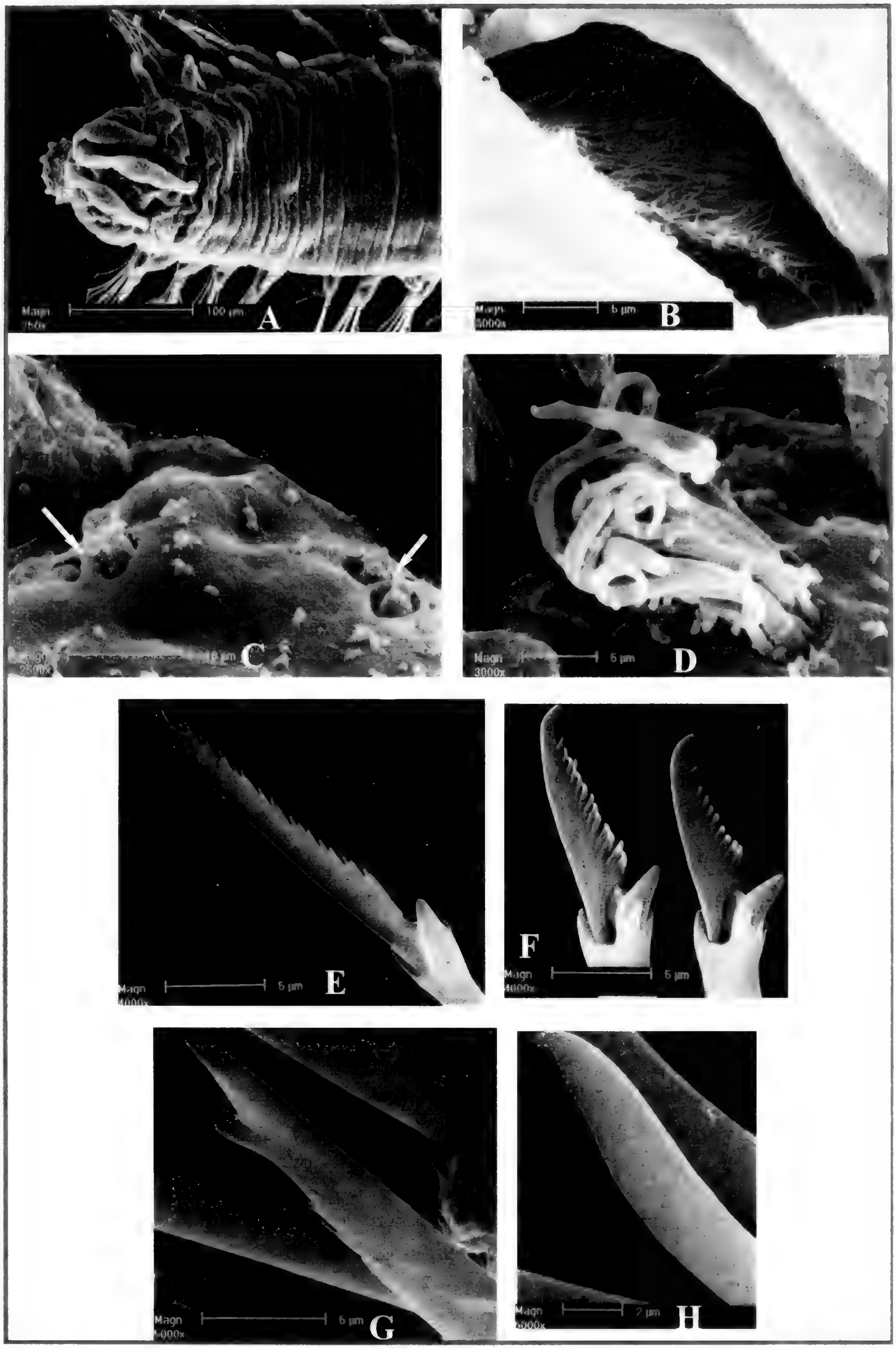

Fig. 2. *Parapionosyllis cabezali,* new species. SEM micrographs. A, anterior end, dorsal view; B, detail of a nuchal organ opening; C, parapodial glands pores and papillae (arrows); D, detail of fibrilar material protruding from a parapodial gland; E. long bladed, dorsal compound seta from anterior parapodium; F, mid-length and short compound setae from midbody; G, posterior dorsal simple seta; H, posterior ventral simple seta.

maining anterior parapodia. Anterior dorsal compound setae with thick shafts and heterogomph articulation (Fig. 1E); median and ventral shafts with hemigomph articulation (Fig. 2E, F). Shafts apparently smooth but having a few subdistal spines. Blades unidentate with spines on the margin and a longer sub-distal spine more evident on more dorsal and anterior setae. Dorso-ventral gradation in blade length; blades of the dorsal-most compound setae about 25 μm in most anterior setigers, 20 μm in the median ones and 15 μm in posterior-most ones; with moderately long spines on the margin; blades progressively shorter towards the ventral part of the parapodium (Fig. 1E, H), 10 μm in the ventral most seta with shorter spines on the margin. Solitary dorsal simple seta on each post-proventricular parapodium, slightly thicker than the shafts of compound setae, provided with various spines on the margin, one of which thicker and longer (Fig. 1D); most posterior dorsal simple setae have fewer spines on margin but are provided with a larger subdistal spine (Figs. 1G, 2G). Solitary ventral simple setae sigmoid, unidentate, apparently smooth (Fig. 1I) but provided with a few minute subdistal spines (Fig. 2H). Solitary aciculum per parapodium, relatively thick and with a rounded, enlarged and apparently hollow tip (Fig. 1F).

Pharynx relatively long and thin, extending through five or six segments (Fig. 1A); pharyngeal tooth located near the anterior margin; anterior end of pharynx surrounded by 10 papillae (Fig. 2A). Proventriculous shorter than the pharynx, extending through three or four segments, with about 22 rows of muscle cells. Pygidium small, semicircular, with two long and thin anal cirri, longer than the antennae (Fig. 1B). Mature males provided with natatory capillary setae and sperm packets in each segment between setigers 11 and 27; females carry eggs ventrally.

Ecology.—Parapionosyllis cabezali, was found in Punta Endata in sublittoral muddy sand (70 m depth), in the Ría de Ferrol in sublittoral muddy sand, coarse sand and very coarse sand (11–25 m depth) with organic matter content between 0.12% and 0.20% and reaching 20 cm depth in sediment. In the Ría de Baiona this species was found in sublittoral medium sand and coarse sand (8–12 m depth).

Remarks.—Campoy (1982) and, more recently, Parapar et al. (1994) reported this species as *Parapionosyllis* cf. *gestans* (Pierantoni, 1903), due to its similarity to *P. gestans* [as described by Fauvel (1923) and Cognetti (1965)]. A more detailed study of the specimens revealed two main differences between the species. *P. cabezali* shows a moderate dorso-ventral gradation in the length of the blades of the compound setae, while in *P. gestans* all blades are similar in length (Cognetti 1965). Unlike Campoy (1982), we consider the setae illustrated to be an accurate representation of the complete set of setae in each parapodium. In the same figure, the author provides detailed sketches of the setae of three other species (*Parapionosyllis minuta, Parapionosyllis elegans* and *Parapionosyllis labronica*), drawing the same number of setae for all of them and showing the variation in the size of the blades where it exists. Also, all specimens of *P. cabezali* had numerous and conspicuous parapodial glands, of two kinds and different in size, which are not described in the Mediterranean species. Perkins (1981) also report the presence of paired parapodial glands in specimens of *Parapionosyllis longocirrata* (Webster & Benedict 1884) from the Atlantic coast of the United States, but this species differs from *P. cabezali* in that it has much larger dorsal cirri, in the shape and spinulation of the anterior dorsal simple setae and in the length of the dorsal-most compound setae blades (15 μm in *P. longocirrata* and 25 μm in *P. cabezali*). *Parapionosyllis brevicirra* Day, 1954, a species also present in the Atlantic coast of the Iberian Peninsula (Parapar et al. 1994) and western Mediterranean Sea, occasionally shows granular and fibrillar inclusions in the dorsal part of the parapodia (San Martín 1984), but this well known species has much longer dorsal compound setae blades (45 μm) than *P. cabezali.* The type-series of *P. gestans* (Pierantoni, 1903) was apparently lost, and it was not possible to examine any type specimens of this species. San Martín (1984) recorded 12 described species of *Parapionosyllis* and provided a key for identification in which *P. gestans* (Pierantoni, 1903) was distinguished from *P.* cf. *gestans* of Campoy (1982).

Distribution.—Parapionosyllis cabezali seems to be distributed along the Iberian Atlantic coast, from Basque Country (Campoy 1982, Aguirrezabalaga 1984), Galicia (NW Spain) in the Ría de Ferrol (Parapar et al. 1994) and Ría de Baiona (Moreira 1999) to Punta Umbría (Huelva, SW Spain) (Rodríguez & Viéitez 1992), although it has not been reported in Portugal.

Etymology.—The species is named in fond memory and honour of the late Luis Cabezal Gómez, lecturer in the Escuela Politécnica Superior de Lugo (Universidade de Santiago, Spain), brother-in-law of the first author, in recognition of his love for nature and friendship.

Acknowledgments

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Paralarval gonatid squids (Cephalopoda: Oegopsida) from the Mid-North Atlantic Ocean

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Abstract.—Ninety six gonatid cephalopod specimens (Oegopsida: Gonatidae) from the University of Amsterdam Mid-North Atlantic Plankton Expeditions were analyzed and two species were identified: *Gonatus steenstrupi* (Kristensen 1981) and *Gonatus fabricii* (Lichtenstein 1818). Gonatids were collected only in spring and summer, despite sampling in autumn and winter. This paper describes aspects of their development and reports their geographical distribution in the central North Atlantic Ocean. Chromatophore patterns were the most consistently useful characters for distinguishing between the species. Among 34 measurements, Tentacle Length (TtL) relative to Dorsal Mantle Length (ML) and number of suckers on Arms I–IV were useful for distinguishing specimens >13 mm ML. Both species develop hooks from suckers on the arms and tentacular clubs at ML >20 mm. Subtle differences were noted in the morphology of the funnel pads except in the smallest specimens. Specimens of *G. steenstrupi* >20 mm ML were collected at greater depths (250 to 995 m) than the smaller specimens (found at depths <200 m). Our data suggest that 20 mm ML is the point of transition between paralarvae and juveniles of *G. steenstrupi,* because specimens larger than 20 mm ML have well defined hooks, and a juvenile vertical distribution is established.

Knowledge of early-life-history stages is required for comprehensive understanding of the ecology of squids. These stages presumably are most vulnerable to starvation and predation and they occupy a separate niche from older conspecifics (Vecchione 1987). Because of controversy about use of the term "larva" for early life history stages in cephalopods, Young & Harman (1988: 202) introduced the term "paralarva" for "a cephalopod of the first post-hatching growth stage that is pelagic in near-surface waters during the day and that has a distinctly different mode of life from that of older conspecific individuals." The paralarval concept includes both morphological and ecological features, in contrast to the definition of a "larva", which is based on morphological differences from the adults.

The University of Amsterdam, Netherlands, conducted four research expeditions in the North Atlantic Ocean between 55°N and 24°N approximately along 30°W longitude. This research was designed to "elucidate the patterns of latitudinal diversity, taxonomical variation below species level, vertical variation and interaction of climate, hydrographic features and ecology on morphological variation of marine plankton" (Van der Spoel 1981:1). The expeditions were conducted during four consecutive years (1980–1983), each during a different season (Van der Spoel 1981, 1985; Van der Spoel & Meerding 1983). Discrete-depth samples were collected using opening/closing nets. Cephalopod paralarvae sorted from the samples were donated to the National Museum of Natural History, Smithsonian Institution for systematic and ecological studies. Shea (1995) sorted the material into families in preparation for subsequent studies. The present paper reports on paralarval development and distribution of the squid family Gonatidae in these samples.

The identification of paralarval cephalopod stages is difficult because of insufficient collections which often come from inadequate sampling devices and methods, and because of poorly understood taxonomy, even in adults (Vecchione 1987). This is true for the genus *Gonatus* in the North Atlantic Ocean in which only one arctic/boreal species was recognized, *Gonatus fabricii* (Lichtenstein 1818), until Kristensen (1981) described *Gonatus steenstrupi* from boreal waters. At least five *Gonatus* species are found in the North Pacific Ocean and one in the Southern Ocean (Kristensen 1981). The primary morphological characters used to separate adults of the two North Atlantic species are (a) the presence or absence of chromatophores on the ventral surface of the head, (b) the shape of the funnel organ, and (c) the patterns of hooks and suckers on the tentacular clubs. The onset of formation of hooks from suckers both on the tentacular clubs and arms I–III seems a good character to define the differences between paralarvae and juveniles in gonatids (Young 1972, Kristensen 1977a). The presence of hooks presumably indicates a change in feeding and therefore in the squid's role in the oceanic trophic structure.

The main goals of the present study were to identify the species of paralarval gonatids in the Mid-North Atlantic collections, to analyze early-life-history features that could separate paralarvae from juveniles, and to determine the distribution of the two species in these samples.

Methods

Gonatid specimens were arranged by size and their taxonomic identification began with the largest specimens, then proceeded sequentially to the smallest specimens. We looked in particular for previously unrecognized taxonomic characters for these paralarvae, in addition to using various taxonomic guides (Kristensen 1981, Nesis 1987, Roper et al. 1984). Fifteen specimens were damaged and were excluded from some of the quantitative analysis. Characters were measured or counted on each of the 81 undamaged gonatids following Roper & Voss (1983), including:

ML (Dorsal Mantle Length); MW (Mantle Width); HL (Head Length); HW (Head Width); ED (Eye Diameter); FL (Fin Length); FW (Fin Width); TL (Total Length); TtL (Tentacle Length); CL (Club Length); AHI-IV (number of hooks on Arms I-IV); ASI-IV (Arm I-IV Sucker counts); ALI-IV (Arm I-IV Length); AWI-IV (Arm I-IV Width).

We also measured the following characters:

D (Dactylus Length); M (Manus Length); C (Carpus Length); CS (Club Sucker Length); ForgL (Funnel Organ Length); ForgW (Funnel Organ Width); ForgL1 (Funnel Organ Dorsal Pad Length); ForgW1 (Funnel Organ Dorsal Pad Width). Characters on damaged specimens were measured when their condition permitted.

Three specimens of different sizes from each of the two species were selected based on condition, and their third arms and tentacular clubs (left for *G. fabricii* and right for *G. steenstrupi,* because of specimen damage) were removed for scanning electron microscopical (SEM) analysis. The specimens had been fixed in formalin and preserved in 45% isopropanol. Tissue for SEM was transferred through a dehydration series to 100% ETOH prior to critical-point drying, which was conducted using a Denton Vacuum-1_1 Critical-Point Dryer. The arms and tentacular clubs were examined using a Leica 440 SEM to find morphological features that could separate the species.

Results

In total, 96 specimens of the family Gonatidae were collected during the spring (1980) and summer (1983) cruises. No gonatids were found in samples from the other two cruises. The presence of two chromatophores on the ventral side of the head in *G. fabricii* and their absence in *G. steenstrupi,* the shape of the funnel organ and the development and pattern of hooks and suckers on the tentacular club were the basic features that we used to distinguish these two species. The 96 gonatids were separated into 43 *G. fabricii* and 38 *G. steenstrupi,* the remaining 15 specimens were too damaged to determine species with certainty. The 81 undamaged specimens ranged in size from 1.6 to 31.6 mm ML in *G. steenstrupi,* 3.3 to 24.1 mm in *G. fabricii* and 3.0 to 10.8 mm for the damaged specimens.

Gonatus fabricii paralarvae are characterized by the presence of a pair of round or oblong chromatophores on the ventral surface of the head slightly anterior to the ocular axis (see Kristensen 1981:67, fig. 3 for specimens larger than those reported here). The dorsal pad of the funnel organ in this species has an inverted V-shape with very straight lateral sides (Fig. 1; cf. Kristensen 1981:69, fig. 5). After the largest specimen of *G. fabricii* (24.1 mm ML) was identified, published taxonomic characters could then be recognized in progressively smaller specimens. The presence of chromatophores was the primary character used to identify the smallest specimens of *G. fabricii.* The funnel organ is so small in specimens <3.6 mm ML that its shape can not be determined confidently. Scanning electron microscopy on specimens of 24.1, 14.6, and 7.2 mm ML revealed that the patterns of hooks and suckers on the tentacular clubs of the largest *G. fabricii* were similar to those described by Kristensen (1977a, 1981). The largest specimen (24.1 mm ML) had one large hook, with three small hooks and a sucker proximal to the large hook. A concentration of small suckers occurs on both dorsal and ventral sides of the club, especially on the proximal end, where the suckers form a large cluster (Fig. 2d).

The largest specimens of *G. steenstrupi* (e.g., 31.6 mm ML) were identified following the description of the holotype (Kristensen 1981). The shape of the funnel organ is characterized by a slight curve on the lateral edges of the dorsal pad (Kristensen 1981: 83, fig. 20). This character can be seen in our largest specimens (Fig. 3). The absence of chromatophores on the ventral surface of the head is the primary distinguishing character of the smallest *G. steenstrupi* paralarvae available, which could not be identified based on funnel-organ morphology. Scanning electron microscopy was used to examine specimens of 31.6, 19.2 and 9.6 mm ML. The tentacular club of the largest specimen under SEM had the pattern of hooks and suckers described by Kristensen (1981) in which one large hook is preceded proximally with four small hooks and no suckers (Fig. 2c). At <20 mm ML the hooks are not yet well developed (Fig. 2a, b). *Gonatus steenstrupi* and *G. fabricii* smaller than 20 mm ML have similar sucker patterns in this central series on their tentacular clubs.

The scatterplot of the relation between TtL and ML for all the undamaged specimens indicates a growth curve for *G. steenstrupi* that diverges from that of *G. fabricii* at ML >13 mm (Fig. 4). The relation between TtL and ML is more linear for *G. fabricii* than for *G. steenstrupi,* perhaps because of the lack of large *G. fabricii* specimens. However, all *G. steenstrupi* >13 mm ML had tentacles that were longer than those of similar-sized *G. fabricii.* Extension of a quadratic function line fitted to the *G. fabricii* data indicates that the difference in TtL between species likely continues at larger sizes, although a shift in growth pa-

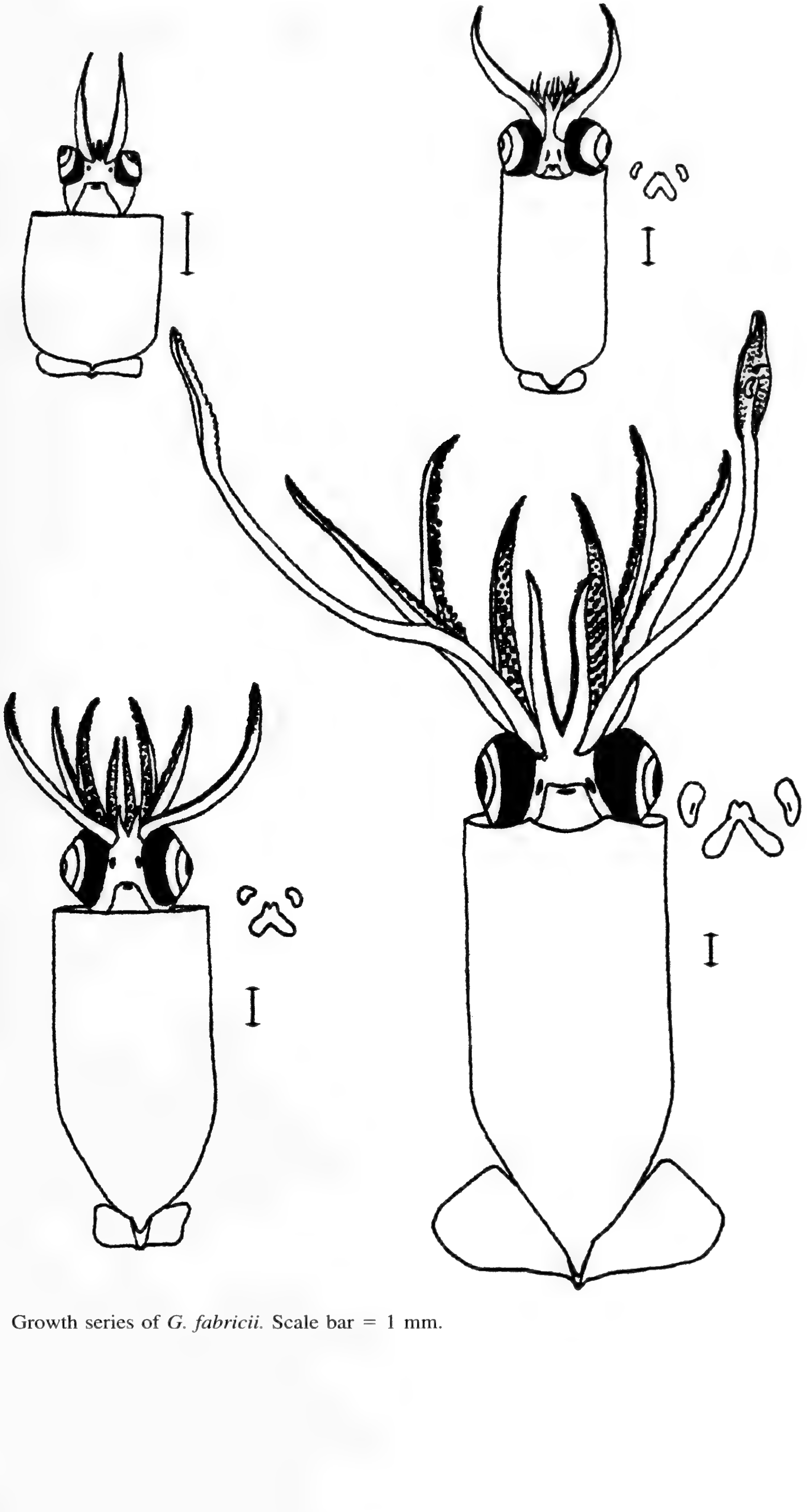

Fig. 1. Growth series of *G. fabricii.* Scale bar = 1 mm.

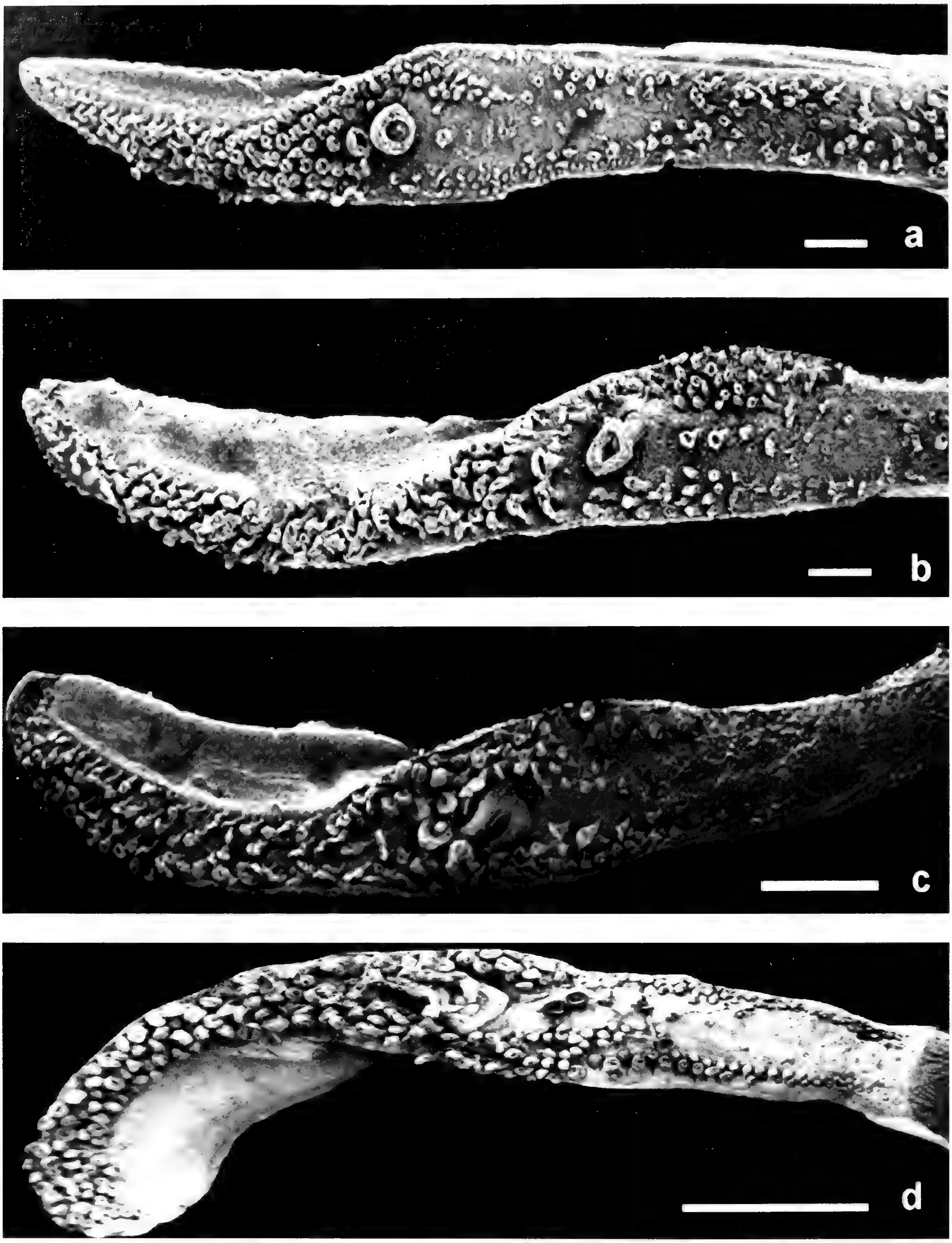

Fig. 2. Tentacular clubs. a–c) *G. steenstrupi,* 9.6, 19.2, and 31.6 mm ML respectively, d) *G. fabricii,* 24.1 mm ML. Scale bars: a) 200 μm, b) 300 μm, c) 1 mm, d) 1 mm.

rameters at the transition between paralarvae and juveniles (Shea 1995) could either reduce or increase interspecific differences.

Well-developed hooks on arms and tentacular clubs and well-differentiated tentacular clubs are found in specimens of both species larger than 20 mm ML. Kristensen (1981) described major differences between these species on specimens larger than 37 mm gladius length, which is equivalent to

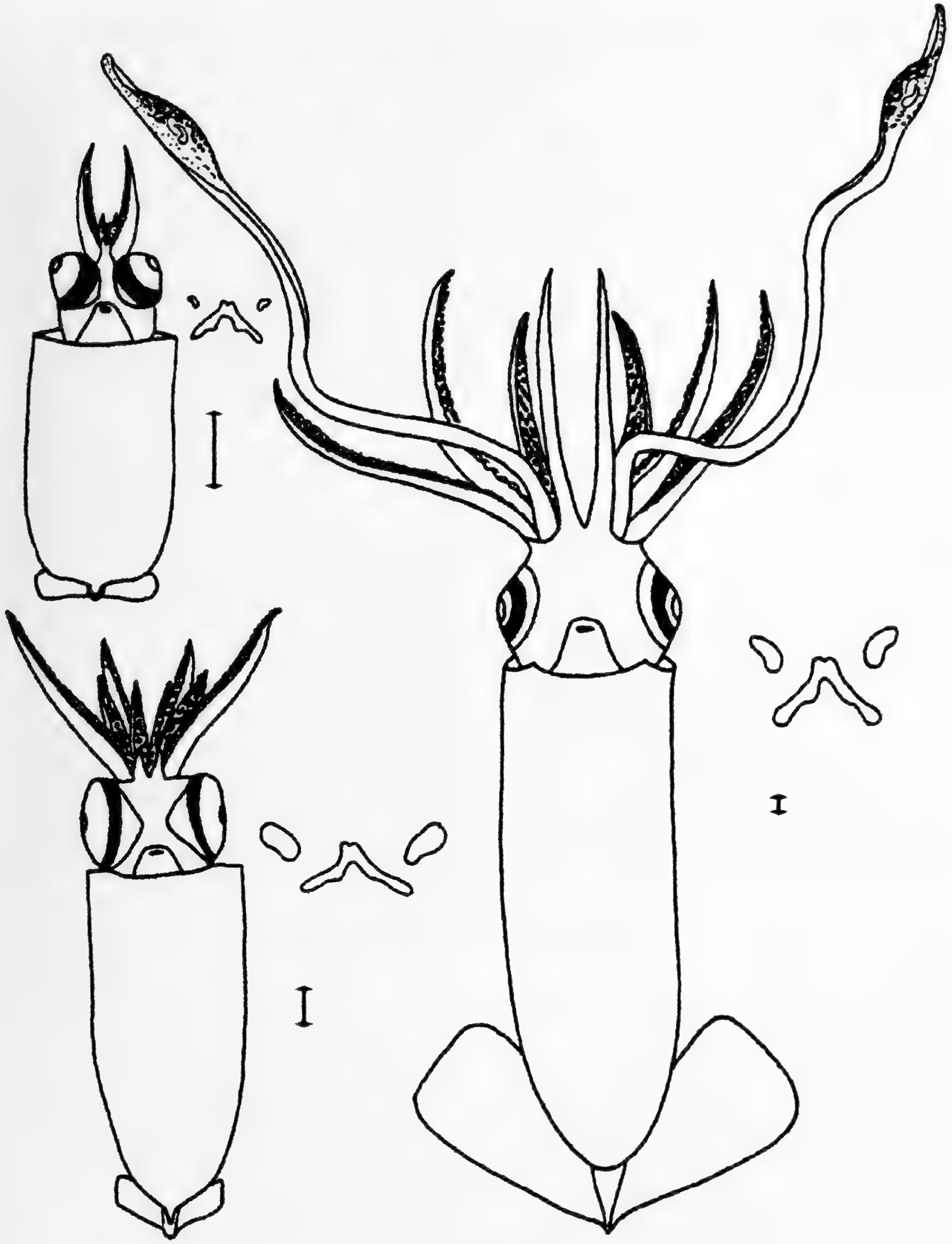

Fig. 3. Growth series of *G. steenstrupi.* Scale bar = 1 mm.

ML in gonatids. Our SEM analysis of arm III suckers for *G. steenstrupi* of 31.6 mm ML (Fig. 5a) and *G. fabricii* of 24.1 mm ML (Fig. 5c) shows that no obvious differences occur, although the chitinous teeth of the internal ring of the suckers are sharper in *G. steenstrupi.* There is no difference between species in this character on smaller specimens (Fig. 5b, d).

The vertical distribution of the paralar-

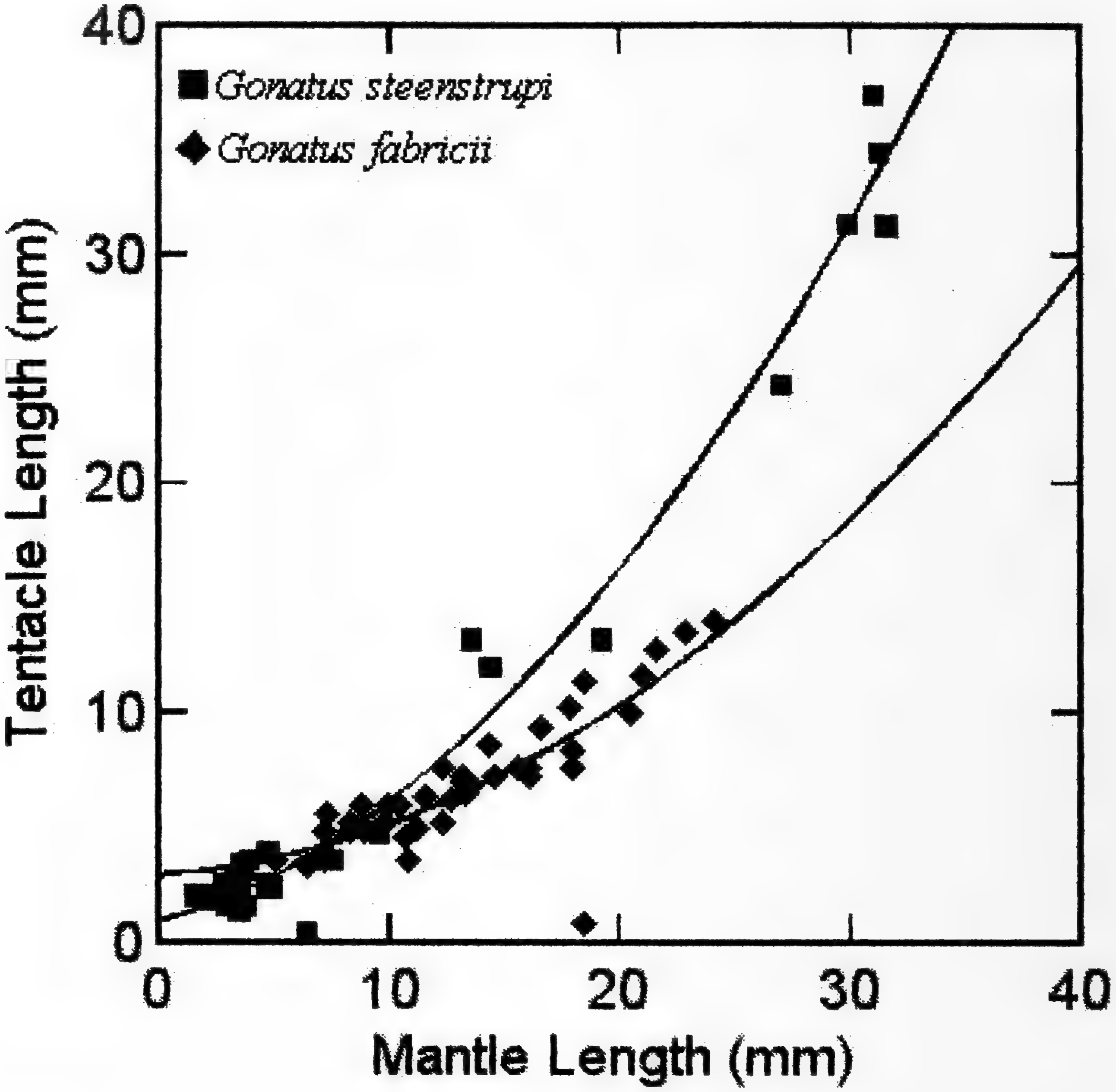

Fig. 4. Dorsal Mantle Length (ML) vs. Tentacle Length (TtL). Quadratic function lines are fitted to the scatterplots of the two species simply to identify trends in the data, rather than to test hypotheses of differences.

vae was analyzed for each cruise (Fig. 6). During the spring cruise (1980), *G. steenstrupi* larger than 20 mm ML were captured at the deepest sampling stations (250 to 995 m). The specimens smaller than 20 mm ML were collected in the upper 200 m, although one specimen of 2.8 mm ML was caught between 390 and 510 m. *Gonatus fabricii* differed in spring vertical distribution, exhibiting greater variability in depths for all sizes. All *G. fabricii* specimens were captured shallower than 400 m although samples were collected from depths as great as 1750 m. The summer cruise (1983) showed a similar distribution for *G. steenstrupi* where specimens larger than 20 mm ML were caught between 490 and 995 m and those smaller than 20 mm ML were found in the upper 50 m. *Gonatus fabricii* were again found with greater variability in their vertical distribution, as specimens with 7.2 mm and 15.6 mm ML were collected at the deepest stations (1750 to 1000 m), while the rest of the sampled population was found in the upper 100 m.

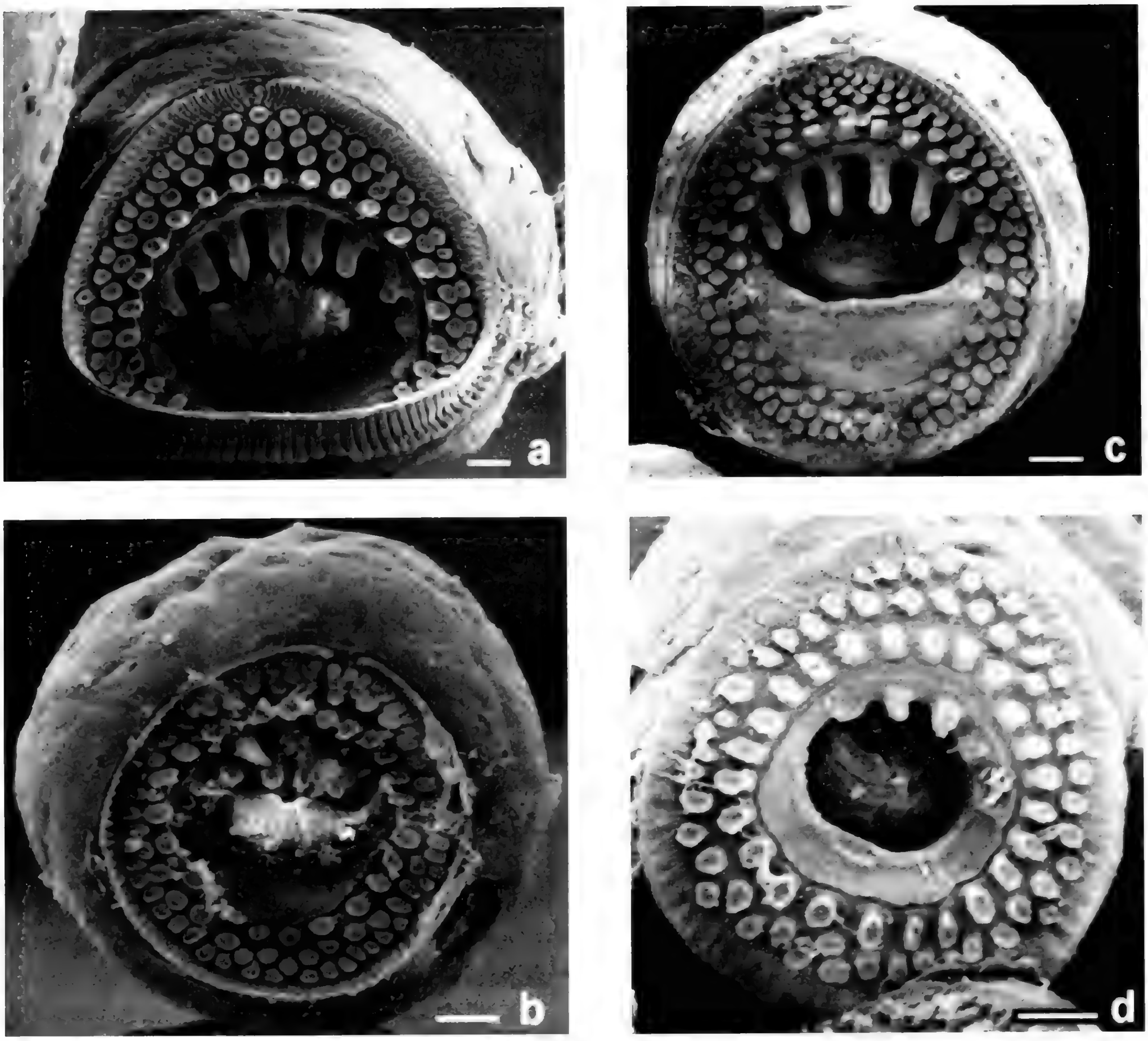

Fig. 5. Suckers in Arm III. a) *G. steenstrupi,* 31.6 mm ML, b) *G. steenstrupi,* 19.2 mm ML, c) *G. fabricii,* 24.1 mm ML, d) *G. fabricii,* 14.6 mm ML. Scale bars: a) 20 μm, b) 20 μm, c) 30 μm, d) 10 μm.

Discussion

Van der Spoel (1981) reported that during the 1980 spring cruise subarctic polar water was present at depths greater than 500 m north of 50°N. The 1983 summer cruise also may have sampled subarctic water north of 53°N, as well as an isothermal layer above the thermocline at depths greater than 90 m near 55°N. Both the spring (1980) and summer (1983) cruises found a well marked northern branch of the North Atlantic Drift, although the southern branch was much more marked in 1983 (Van der Spoel 1985). The presence of *Gonatus* in these samples likely resulted from the presence of cold subarctic water in the area.

Both *Gonatus fabricii* and *Gonatus steenstrupi,* occurred in a previously unreported distribution (54°53′54″N 029°55′48″W to 48°58′54″N 030°01′18″W). Earlier reports (Kristensen 1977b, 1981: 62, fig. 1) listed their distribution as nearer to the coast and much more northerly, especially *G. fabricii.* This new distribution extends the known occurrence of both species far offshore towards the Central North Atlantic Ocean and more southerly.

The change in vertical distribution by *G. steenstrupi* larger than 20 mm ML and the coincident presence above that size of well-developed hooks on the arms and tentacular clubs of both species may define the tran-

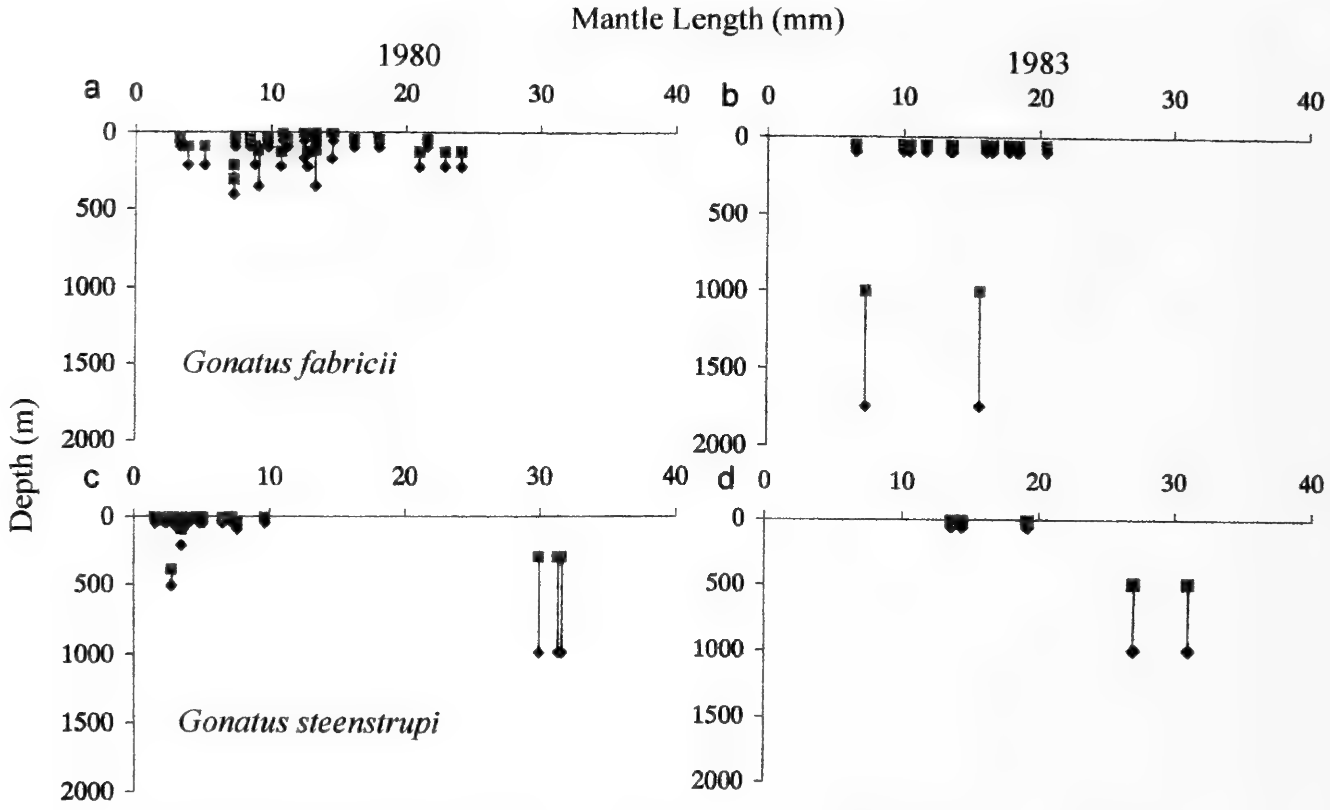

Fig. 6. Depth of capture vs Dorsal Mantle Length (ML). a) *G. fabricii* in spring 1980, b) *G. fabricii* in summer 1983, c) *G. steenstrupi* in spring 1980, b) *G. steenstrupi* in summer 1983. Diamonds indicate depth at opening of net, squares depth at closing of net, vertical lines, depth range sampled.

sition between paralarvae and juveniles. Differences between the species on specimens larger than 20 mm ML include the pattern of hook development from suckers both on the tentacular clubs and the arms. Additional specimens are needed to confirm the apparent transition point between early-life-history stages for *G. steenstrupi* and to delineate such stages for *G. fabricii.* The results reported here, however, do indicate changes in both the morphological and ecological characteristics at sizes about 20 mm ML, particularly for *G. steenstrupi.*

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Parabuccinum, a new genus of Magellanic buccinulid (Gastropoda: Neogastropoda), with a description of a new species

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Abstract.—A new genus, *Parabuccinum,* is established for four bathyal Magellanic species, of which one, *Parabuccinum rauscherti,* is described as new. The remaining three species were originally described in the Antarctic genus *Chlanidota,* from which they differ in the morphology of their protoconch, operculum, radula, stomach, and male reproductive system. *Parabuccinum* appears to be most closely related to the monotypic circumAntarctic genus *Neobuccinum,* but may be distinguished on the basis of shell and penis morphology, as well as by the size and shape of the gland of Leiblein. *Parabuccinum* is endemic to the Magellanic Province, and is the first record of the subfamily Bucinulinae in the malacofauna of this region.

The genus *Chlanidota* Martens, 1878 had been considered to be one of the more diverse and wide-ranging members of the antiboreal buccinoidean radiation. Dell (1990) included 13 species within this genus, some tentatively, among them four species that he described as new. A more recent revision (Harasewych & Kantor, 1999) divided the genus *Chlanidota* into two subgenera, *Chlanidota sensu stricto,* with five species, and *Chlanidota* (*Pfefferia*) containing three species. Five species were excluded from *Chlanidota* on the basis of newly obtained anatomical data as well as radular and opercular morphology.

Three of the species described by Dell (1990) (i.e., *Chlanidota bisculpta, C. eltanini,* and *C. polyspeira*), all from the Magellanic Province, differ substantially from all species of *Chlanidota.* In this publication, we propose a new genus to include these species, as well as an additional species more recently collected by R/V *Polarstern* and R/V *Vidal Gomaz* and described herein. A review of each of the species included in this new genus is provided.

Materials and Methods

This report is based primarily on material collected by the United States Antarctic Program (USAP), housed at the National Museum of Natural History, Smithsonian Institution (USNM), and consisting mostly of the type material for the three species described by Dell (1990). Additional samples, including alcohol preserved anatomical material, were collected at two stations of the R/V *Polarstern* and one station of the R/V *Vidal Gomaz.* These samples are maintained in the collections of the Zoologisches Institut und Zoologisches Museum der Universität Hamburg (ZMH).

In the material examined sections, "specimen" denotes live collected material, while "shell" refers to records containing only the dead collected shells.

Shell and operculum measurements were obtained for representative specimens of each species (*n* = 10, when available), as detailed in Harasewych & Kantor (1999: fig. 1). Anatomical descriptions are based on gross dissections of preserved material. Radulae were removed by dissection, cleaned using diluted bleach (NaClO), coated with carbon and gold, and examined using a Hitachi S570 Scanning Electron Microscope (SEM).

Photographs were obtained using a Leaf Lumina Digital Scanning Camera. Optical and SEM images were processed using Photoshop Version 5.02 (Adobe).

The following abbreviations are used in the text: SL—shell length, AL—aperture length, BWL–body whorl length, SW—shell width.

Systematics

Order Neogastropoda Wenz, 1938

Superfamily Buccinoidea Rafinesque, 1815

Harasewych & Kantor (1999:256) provided a brief overview of the current state of buccinoidean systematics and summarized several of the more prevalent classifications. Until the phylogenetic relationships of the higher taxa of Buccinoidea are reassessed on a global scale, we provisionally continue to use the family Buccinulidae and its subdivisions, as defined by Powell (1951), to include the many distinctive austral buccinoidean taxa.

Family Buccinulidae Finlay, 1928

According to Powell's (1951:151) concept of Buccinulidae, the chief characteristics of the group are tricuspid rachidian teeth and an operculum with a terminal or subterminal nucleus. In our ongoing studies on Buccinoidea, we were able to identify several anatomical characters, among them the prevalance of fused salivary glands, and a simple stomach that lacks a posterior mixing area, that will likely serve to distinguish Buccinulidae from Buccinidae and other buccinoidean families.

Subfamily Buccinulinae Finlay, 1928

Powell (1951) subdivided the family into three subfamilies, the Cominellinae, Buccinulinae and Prosiphiinae based on the morphology of the lateral teeth of the radula. Cominellinae were characterized as having bicuspid lateral teeth, Buccinulinae were diagnosed by their tricuspid lateral teeth, while Prosiphiinae were recognized by their lateral teeth with a long basal projection. However, taxa included in Prosiphiinae vary considerably in their radular morphology, suggesting that resolution on a fine scale may be possible within this group.

The radular teeth of the four species included in the new genus *Parabuccinum* all have tricuspid lateral teeth, indicating that this genus is referable to the subfamily Buccinulinae.

The geographic range of the subfamily Buccinulinae spans Australia, New Zealand, Antarctica, and the eastern Pacific coast as far north as California (based on Powell's (1951) inclusion of the genus *Kelletia* in Buccinulidae). *Parabuccinum* extends that range into the Magellanic Province.

Genus *Parabuccinum,* new genus

Type species.—Chlanidota bisculpta Dell, 1990.

Description.—Shell small for family, reaching 10.2–16.4 mm, depending on species. Shell relatively thick, solid, elongate or elongate-ovate in outline, spire high (about 0.33 to 0.5 SL). Spiral sculpture of thin to prominent low cords. Axial sculpture ranges from fine growth lines to prominent, sigmoidal, weakly prosocline ribs, depending on species. Aperture narrowly oval. Siphonal notch broad, slightly recurved dorsally, abaxial margin may form ridge along fasciole. Periostracum thin, smooth or finely hirsute, covering most of shell. Operculum large (0.53–0.60 AL), ovate, paucispiral, with nucleus rotated clockwise, nearly 180° along long axis of operculum. Proboscis of moderate length. Radular ribbon long, triserial. Rachidian tooth with 3 large cusps (central cusp largest) emerging from shallowly arched, straight-sided basal plate. Lateral teeth with 3 cusps, outer cusp longest, middle cusp shortest, closely adjacent to innermost cusp. Salivary glands small, fused. Valve of Leiblein well defined. Gland of Leiblein very small, tubular. Stomach broadly U-shaped, without caecum. Penis long, with flattened distal surface, bordered by thickened edge. Papilla long, cylindrical, situated in middle of distal surface, surrounded by very narrow circular fold at its base.

Remarks.—Conchologically, species of *Parabuccinum* somewhat resemble juvenile specimens of *Chlanidota,* but differ in having shells that are more slender and have a large, invariably well preserved protoconch, a relatively tall spire, and a very thin periostracum. In contrast, the protoconch of *Chlanidota* remains unknown, despite the large number of specimens (including juveniles <10 mm SL) that were studied (Harasewych & Kantor, 1999). Anatomically, *Parabuccinum* differs from *Chlanidota* in having a proportionally larger, paucispiral operculum, a very long and thin-walled siphon, a very small gland of Leiblein, a penis with a flattened distal surface with a thickened edge, and a stomach that overlies a portion of the esophagus.

There are some conchological similarities between this new genus and *Buccinella jucunda* (Thiele, 1912), which differs in having a prosiphiine radula (Thiele 1912: pl. 16, fig. 13) and an operculum with a terminal nucleus (pl. 13, fig. 20). *Parabuccinum,* especially *P. eltanini,* also resembles *Neobuccinum eatoni* (Smith, 1875) in general shell outline, operculum and protoconch morphology.

Parabuccinum is endemic to the Magellanic Province, and has a bathymetric range of 247 to 2165 m.

Parabuccinum bisculptum (Dell, 1990)
Figs. 1, 2A–E, 3, 4, 7A–B, Table 1.

Chlanidota bisculpta Dell, 1990:185, figs. 291, 294, 295, 312.

Description.—Shell (Fig. 1) large for genus (to 14.8 mm), solid, white, elongate, with angulated shoulder. Protoconch (Fig. 7 A–B) large (diameter 1.33–1.67 mm), of about 2.25 smooth, glossy, convex, slightly flattened whorls. Protoconch diameter/protoconch height = 1.02–1.09. Transition from protoconch to teleoconch well marked by onset of axial and spiral sculpture. Teleoconch of up to 3.25 convex whorls. Suture impressed. Spiral sculpture of raised, distinct, narrow cords (12–16 on body whorl, 5–7 on penultimate whorl), half the width of intervening spaces. Axial sculpture of raised, narrow, weakly sinuate, opisthocline ribs (18–22 on first teleoconch whorl, 16–24 on subsequent whorls) that form nodules at intersections with spiral cords. Aperture large (0.51–0.65 SL), narrow, ovate, deflected from shell axis by 15–19°. Outer lip, simple, rounded anteriorly, shouldered posteriorly. Columella ≈0.5 to 0.67 AL, weakly concave, with strong siphonal fold. Callus of thick glaze overlying parietal region, siphonal fasciole. Siphonal notch narrow, slightly dorsally recurved, with nearly straight columellar and rounded apertural margins that define borders of fasciole. Ridge margin of fasciole formed by apertural margin of siphonal notch. Shell color chalky white, aperture weakly glazed. Periostracum thin, transluscent, light yellowish, thinly lallemose, with fine periostracal hairs produced at intersections of spiral threads with axial growth lines. Operculum (Fig. 1E) medium-sized (0.53 AL), elongate ovate, strongly coiled, with nucleus rotated clockwise, nearly 180° to long axis of operculum.

Anatomical data based on single immature, male specimen (Fig. 1 I, R/V *Polarstern,* Sta. 10–109), from which only a portion of the animal was recovered.

External anatomy.—(Fig. 2 A–B). Man-

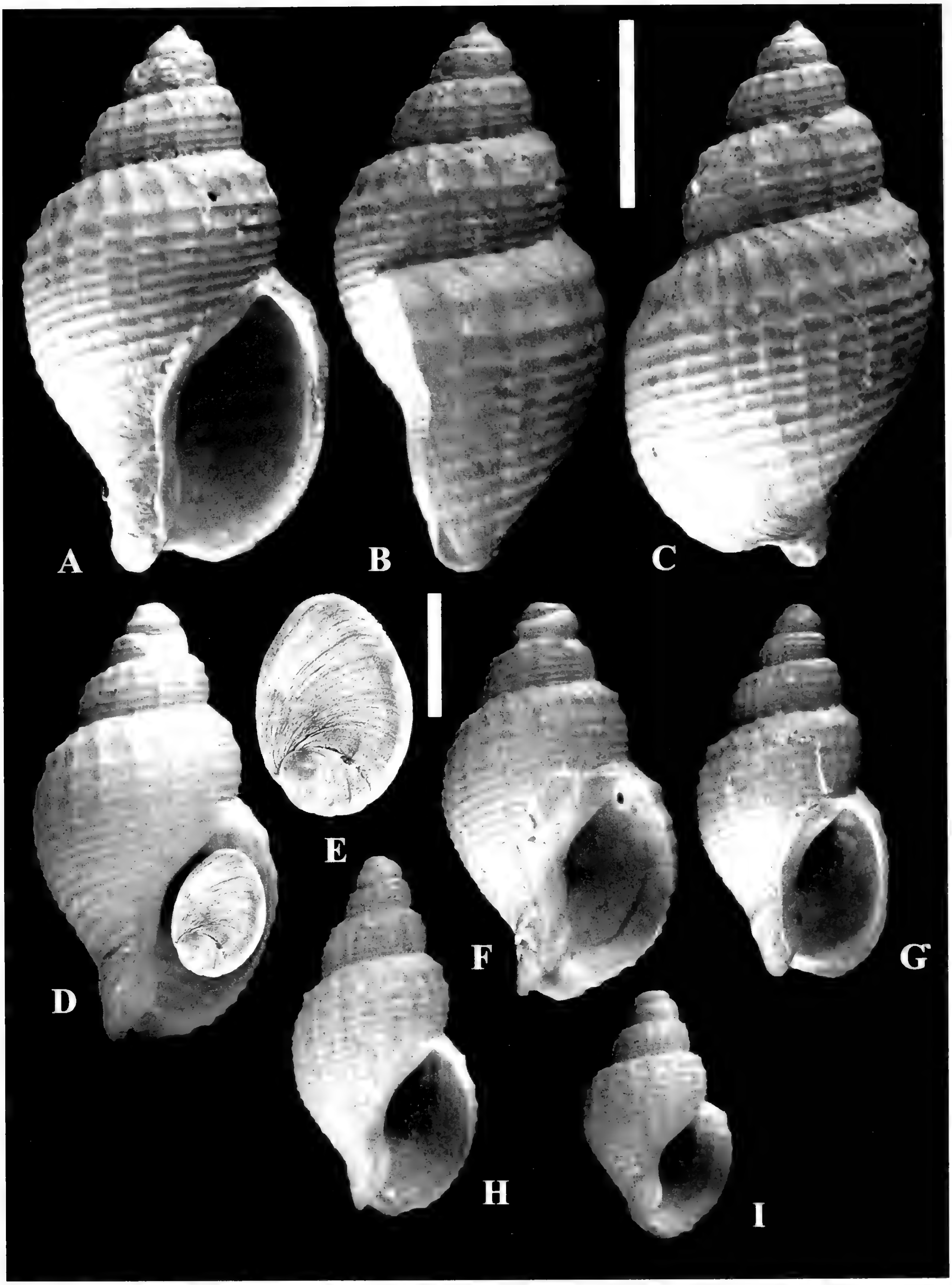

Fig. 1. *Parabuccinum bisculptum* (Dell, 1990). A–C. Holotype, USNM 860128, off Burdwood Bank, 53°08′S, 59°23′W, in 567–578 m (R/V *Eltanin,* Sta. 340). D–E. Paratype 1, USNM 860129, off Falkland (Malvinas) Islands, 51°56′S, 56°39′W, 855–866 m (R/V *Eltanin,* Sta. 557). D. Apertural view of shell. E. Operculum (coated with ammonium chloride). F. Paratype 2, USNM 860129. Same locality as paratype 1. G–I. Off Cape Horn, 55°44.0′S, 66°14.5′W, 430–397 m (R/V *Polarstern,* Sta. 40–109; G, H. ZMH, I. USNM 892150). Scale bar = 5 mm for shells, 2 mm for operculum.

tle cavity spans just over 0.5 whorl, kidney (Fig. 2A, k) ⅓ whorl. Upper whorls of visceral mass unknown. Columellar muscle comprises 1.5 whorl, thick and narrow, attaching to shell at rear of mantle cavity. Foot large, oval, broader anteriorly. Body color very light yellow, nearly white, without pigmentation. Head small, tentacles (Fig. 2 A, B, ten) very long, narrow, widely separated, gradually tapering. Eyes absent. Siphon (Fig. 2 A, B, s) very long (0.75 AL), thin-walled, open.

Alimentary system.—Proboscis (Fig. 2 C–D, pr) of moderate length when contracted (0.44 SL, 0.73 AL), smooth, unpigmented. Proboscis sheath thin-walled, transparent. Mouth (Fig. 2 C, m) triangular slit. Proboscis retractors (Fig. 2 C, D, prr) broad, extremely thin, attached to middle part of rhynchodaeum on left side, to its base on right side. Buccal mass spans ≈0.67 proboscis length. Radular ribbon (Fig. 3) 1.55 mm long (0.39 AL), ~100–140 μm wide (~0.015 SL, 0.025 AL), triserial, consisting of about 60 rows of teeth. Rachidian teeth with 3 closely spaced cusps (central cusp slightly longer, wider than lateral cusps) on posterior portion of basal plate. Anterior margin of basal plate not thickened, overlaid by adjacent tooth. Lateral teeth usually with 3 cusps. Outer cusp roughly twice as long, half as wide as inner cusp. Intermediate cusp very thin, adjacent to, equal in length to inner cusp. In one specimen (Fig. 3 A–B) intermediate cusp split into two separate cusps of equal size along portion of radular ribbon. Salivary glands (Fig. 2 D, sg) small, fused, situated above nerve ring along left side of proboscis. Valve of Leiblein (Fig. 2 C, vL) well defined, although not large, pyriform. Gland of Leiblein (Fig. 2 C, D, gL) very small, short, tubular, uncoiled, whitish, opening into oesophagus without constriction, just posterior to nerve ring (Fig. 2 C, nr). Oesophagus narrow, thin-walled, broader posteriorly. Stomach (Fig. 2 E, st) broad, simple, U-shaped, without caecum. Stomach simple, broad, overlies posteriormost oesophagus. Internal structures of stomach not well-preserved.

Male reproductive system.—Specimen immature male, with very short, dorso-ventrally flattened penis (Fig. 2B, p) lacking defined papilla.

Type locality.—Off Burdwood Bank, 53°08′S, 59°23′W, in 567–578 m (R/V *Eltanin,* Sta. 340).

Type material.—Holotype (Fig. 1 A–C), USNM 860128, from the type locality; Paratypes 1–6, USNM 860129, Paratype 7, NMNZ MF .56615, off Falkland (Malvinas) Islands, 51°56′S, 56°39′W, 855–866 m (R/V *Eltanin,* Sta. 557); Paratypes 8–9 (Paratype 9 is a specimen of *Parabuccinum rauscherti,* new species, see below), USNM 860130, Paratype 10, NMNZ MF .56616, off Cape Horn, 56°06′S, 66°19′W, 384–349 m (R/V *Eltanin,* Sta. 740).

Material examined.—Type material in USNM. 1 specimen + 1 shell, USNM 892150, 5 shells ZMH, off Cape Horn, 55°44.0′S, 66°14.5′W, 430–397 m, 16 May, 1996 (R/V *Polarstern* ANT XIII/4. Sta. 40–109).

Distribution.—Off the Falkland (Malvinas) Islands and Cape Horn at depths ranging from 349 to 866 m (Fig. 4).

Remarks.—This species most closely resembles *Parabuccinum polyspeirum* and *P. rauscherti,* new species. *Parabuccinum bisculptum* may be distinguished from *P. polyspeirum* by its slightly smaller protoconch (1.33–1.67 vs. 1.52–1.84 mm diameter), its strongly shouldered rather than rounded whorl profile, as well as by the presence of fewer, stronger spiral cords and more pronounced axial sculpture in the former (compare Tables 1, 4). Characters that may be used to differentiate *P. bisculptum* from *P. rauscherti,* new species, are discussed in the description of the new species.

Parabuccinum polyspeirum (Dell, 1990)
Figs. 4, 5, 7 E–F, Table 2.

Chlanidota polyspeira Dell, 1990:186, figs. 292, 293, 313.

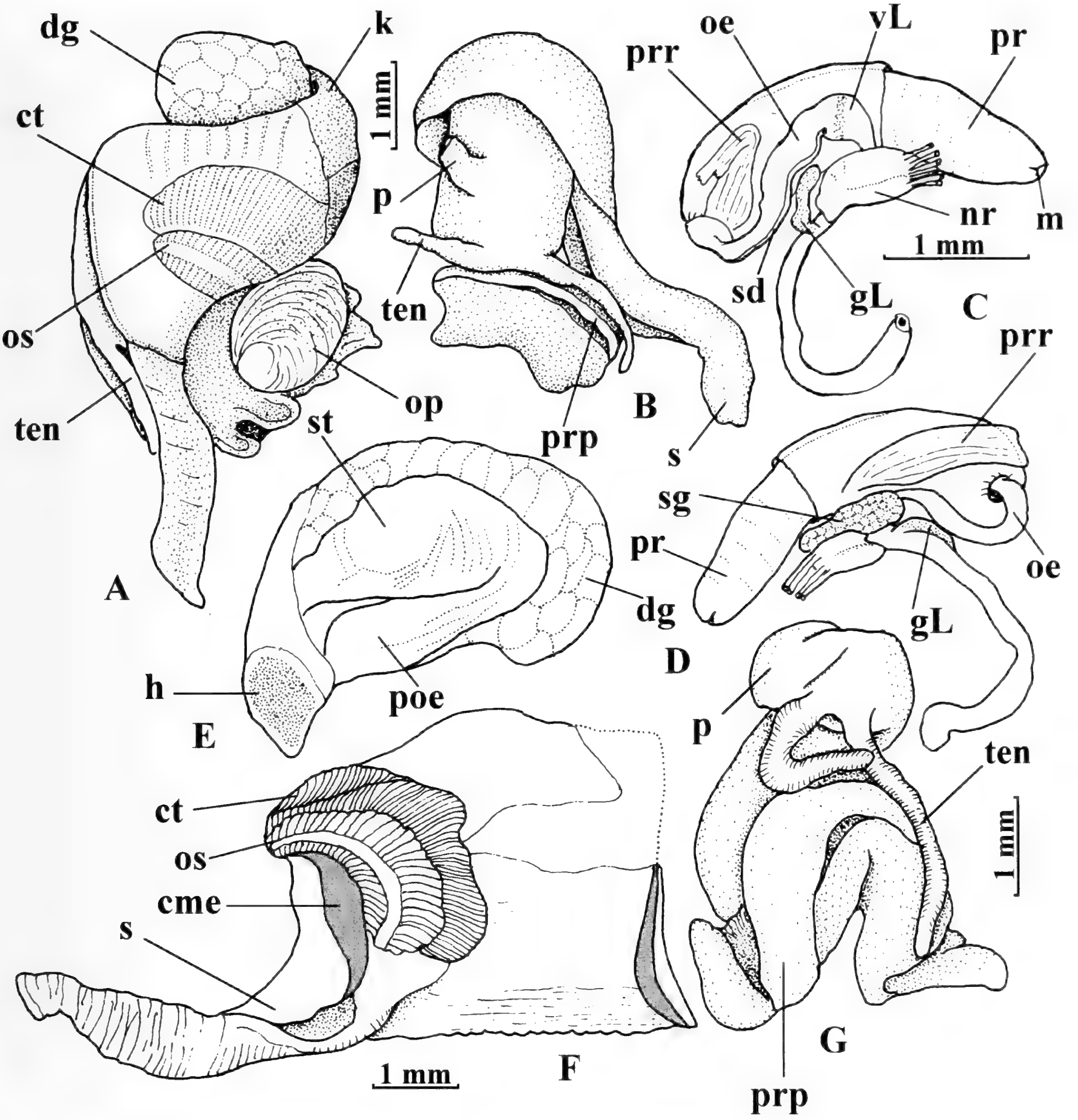

Fig. 2. Anatomy of *Parabuccinum bisculptum* (A–E, USNM 892150) and *P. rauscherti* (F–G, USNM 880616). A, B. Body removed from the shell. A. Right view. B. Anterior view of foot-head. C. Right lateral D. Left lateral, views of anterior alimentary system (salivary glands removed to show valve of Leiblein in C). E. Lateral view of stomach. F. Mantle complex of organs (partially preserved, missing part is indicated by dotted line). G. Anterior view of the body, mantle removed. Abbreviations: cme, cut mantle edge; ct, ctenidium; dg, digestive gland; gL, gland of Leiblein; h, heart; k, kidney; m, mouth; nr, circumoesophageal nerve ring; oe, oesophagus; op, operculum; os, osphradium; p, proboscis; poe, posterior oesophagus; prp, propodium; prr, proboscis retractors; s, siphon; sd, salivary duct; sg, salivary gland; st, stomach; ten, cephalic tentacles; vL, valve of Leiblein.

Description.—Shell (Fig. 5) large for genus (to 15.4 mm) solid, white, glossy, elongate, with rounded shoulder. Protoconch (Figs. 7 E–F) large (diameter 1.52–1.84 mm), consists of ≈2.5 smooth, glossy, convex, raised whorls. Protoconch diameter/protoconch height = 1.12–1.28. Traces of weak spiral cords may be present in final 0.25 whorl of protoconch. Transition from protoconch to teleoconch abrupt, marked by

Table 1.— *Parabuccinum bisculptum* (Dell, 1990). Measurements of shell characters. Linear measurements in mm ($n = 9$, including holotype).

Character	Mean	σ	Range	Holotype
Shell Length (SL)	9.9	1.56	6.6–14.8	14.8
Body Whorl Length (BWL)	7.6	1.33	5.0–11.6	11.6
Aperture Length (AL)	5.6	1.08	4.0–8.9	8.9
Shell Width (SW)	5.4	0.83	3.9–8.2	8.2
Protoconch diameter	1.53	0.12	1.33–1.67	1.53
BWL/SL	0.76	0.03	0.74–0.81	0.78
AL/SL	0.56	0.05	0.51–0.65	0.60
SW/SL	0.54	0.03	0.51–0.59	0.55
Number of axial ribs on 1st teleoconch whorl	19.5	1.52	18–22	—
Number of axial ribs on 2nd teleoconch whorl	19.7	2.53	16–24	19
Number of axial ribs on body whorl	20.4	3.26	16–24	23
Number of spiral cords on body whorl	13.7	1.27	12–16	13
Number of spiral cords on penultimate whorl	6	0.53	5–7	6

onset of pronounced spiral cords, followed within 0.5 whorl by first, weak axial ribs. Teleoconch of up to 3.25 convex whorls. Suture impressed. Spiral sculpture of numerous (19–26 on body whorl, 8–14 on penultimate whorl) closely-spaced, raised cords. Axial sculpture of raised, narrow, sinuate, weakly prosocline ribs (16–18 on first teleoconch whorl, increasing to 19–21 on body whorl) that form faintly cancellate sculpture at intersection with spiral cords. Aperture large (0.53–0.63 SL), narrow, ovate, deflected from shell axis by 13–17°. Outer lip thin, evenly rounded. Columella ≈0.5 AL, weakly concave, with strong siphonal fold. Callus of thin glaze (very thin in smaller specimens) overlying parietal region, siphonal fasciole. Siphonal notch narrow, slightly dorsally recurved, with nearly straight columellar and rounded apertural margins that form borders of fasciole. Apertural margin of siphonal notch demarcates ridge margin of fasciole. Shell color chalky white, aperture weakly glazed. Periostracum very thin, smooth, translucent, tightly adherent to shell surface. Operculum unknown.

Type locality.—Patagonian Shelf, NE of Islas de los Estados (Staten Island), 54°04′S, 63°35′W, in 247–293 m (R/V *Eltanin,* Sta. 369).

Type material.—Holotype (Figs. 5, A–C), USNM 860131, 3 paratypes, USNM 860132, 1 paratype NMNZ MF.56617, all from the type locality.

Material examined.—Type material in USNM.

Distribution.—Known only from the type locality (Fig. 4).

Remarks.—The species is known from five shells. Dell (1990) regarded this taxon to be very similar to *P. bisculptum,* but distinguished it on the basis of its narrower shell, larger protoconch, more numerous spiral cords and axial sculpture that is weaker, and becomes obsolete on the anteriormost part of the body whorl.

Parabuccinum polyspeirum is known from a single station that represents the shallowest record for any species of *Parabuccinum.*

Parabuccinum eltanini (Dell, 1990)

Figs. 6, 8, 12, Table 3.

Chlanidota eltanini Dell, 1990:184-5, figs. 290, 292, 297, 314.

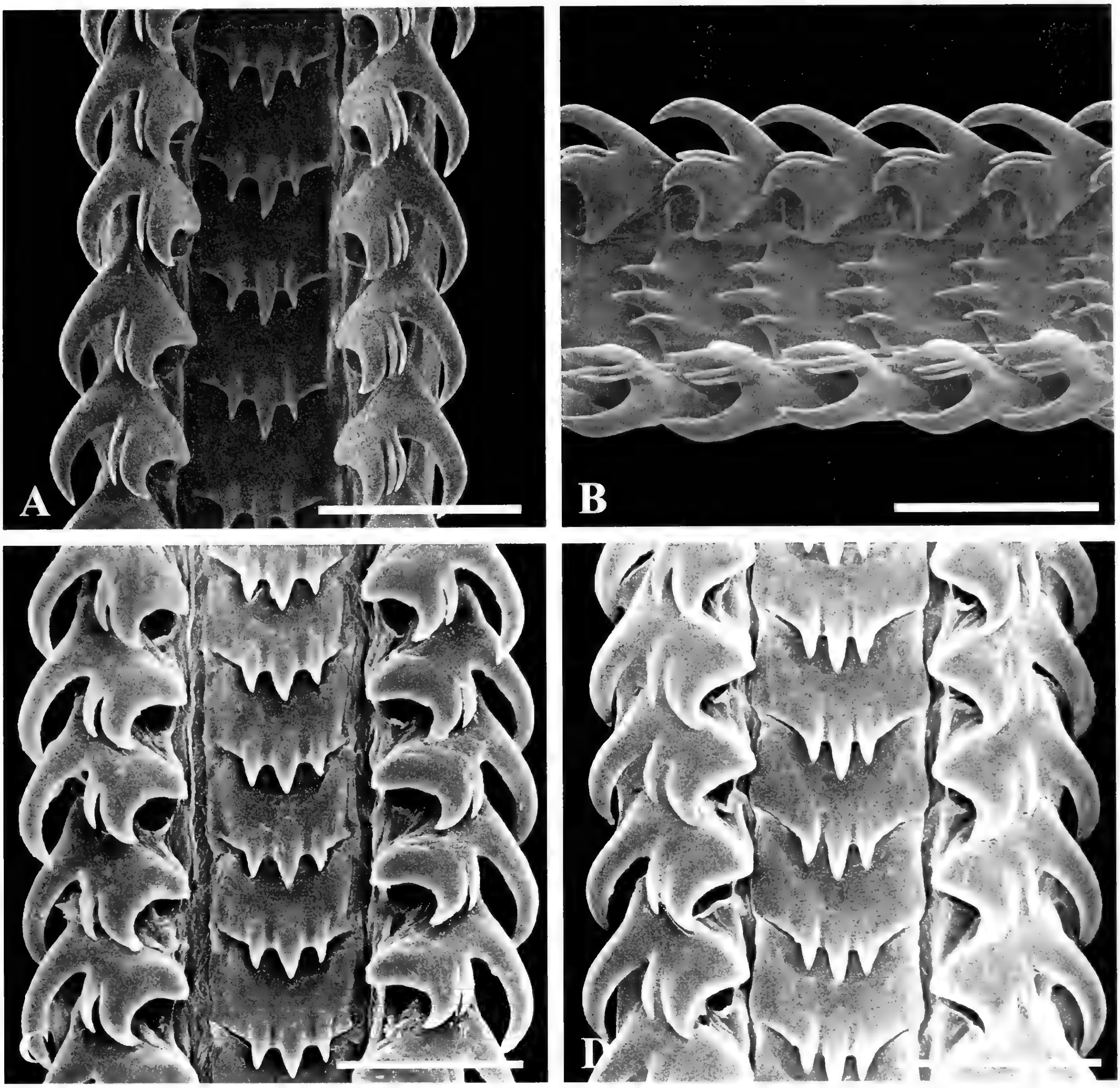

Fig. 3. Radulae of *Parabuccinum bisculptum* (Dell, 1990). A. Dorsal, and B. right lateral (45°) views of the central portion of the radular ribbon taken from animal in Fig. 1I (USNM 892150). C, D. Dorsal views of the radulae of two specimens from R/V *Polarstern,* Sta. 40–109. Scale bars = 50 μm.

Description.—Shell (Fig. 6) largest of genus (to 16.4 mm), solid, white, ovate, with lower spire, rounded shoulder. Protoconch (Fig. 8) very large (diameter 2.06–2.94 mm), dome-shaped, of about ≈2.25 smooth, low, whorls. Protoconch diameter/protoconch height = 1.30–1.52. Border between protoconch and teleoconch whorls well demarcated, protoconch well preserved, teleoconch eroded. Teleoconch of up to 2.75 broadly convex whorls. Suture deeply impressed, with narrow, nearly flattened rim. Spiral sculpture of numerous (32–53 on body whorl, 17–24 on penultimate whorl), adjacent, very low, fine, narrow, sometimes sinuous threads, covering entire shell surface. Axial sculpture limited to fine prosocline growth lines. Aperture large (0.65 SL), ovate to broadly ovate, deflected from shell axis by 10–14°. Outer lip simple, evenly rounded. Columella <0.5 AL, weakly concave, with broad siphonal fold. Callus consisting of thick glaze narrowly overlying parietal region, siphonal

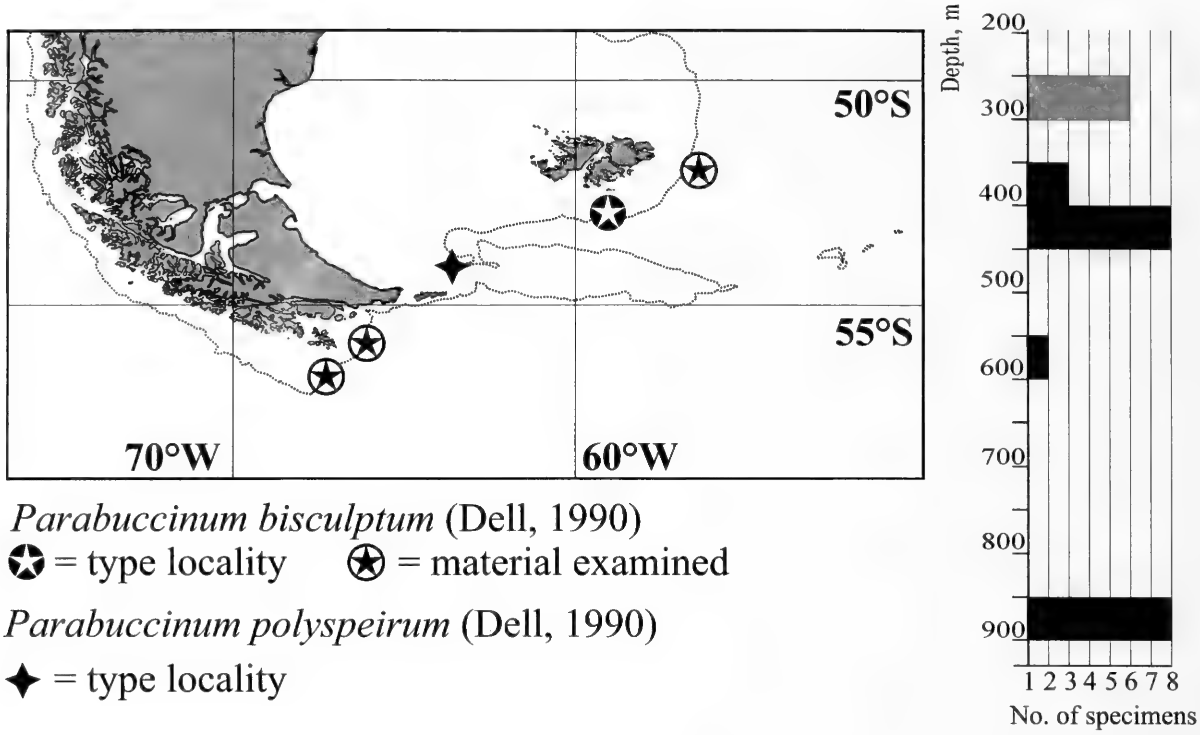

Fig. 4. Geographical distribution and bathymetric ranges of *Parabuccinum bisculptum* (Dell, 1990) and *Parabuccinum polyspeirum* (Dell, 1990). Dashed line indicate 500 m isobath. The bathymetric range of *P. bisculptum* is shown in black, that of *P. polyspeirum* in gray.

fasciole. Siphonal notch narrow, shallow, slightly dorsally recurved, its margins defining weak fasciole. Ridge margin of fasciole runs from apertural margin of siphonal notch. Shell color chalky white, aperture glazed. Periostracum thin, yellowish, tightly adhering to the shell surface, bearing irregularly spaced very short hairs. Operculum (Fig. 6H) large (0.60 AL), broadly ovate, strongly coiled, with nucleus rotated clockwise, nearly 180° to long axis of operculum. Radula illustrated by Dell (1990:fig. 297).

Type locality.—East of Falkland (Malvinas) Islands, 51°58′S, 56°38′W, in 845–646 m (R/V *Eltanin,* Sta. 558).

Type material.—Holotype (Fig. 6, A–C), USNM 860124, paratypes 1–2, USNM 860125, paratype 3, NMNZ MF.56613,

Table 2.—*Parabuccinum polyspeirum* (Dell, 1990). Measurements of shell characters. Linear measurements in mm.

Character	Holotype	Paratype 1	Paratype 2	Paratype 3
Shell Length (SL)	13.2	15.4	9.1	8.1
Body Whorl Length (BWL)	10.3	11.5	7.3	6.4
Aperture Length (AL)	7.2	8.2	5.7	5.0
Shell Width (SW)	6.9	7.7	4.8	4.7
Protoconch diameter	1.84	1.84	1.75	1.52
BWL/SL	0.78	0.75	0.80	0.79
AL/SL	0.55	0.53	0.63	0.62
SW/SL	0.52	0.50	0.53	0.58
Number of axial ribs on 1st teleoconch whorl	16	16	17	18
Number of axial ribs on 2nd teleoconch whorl	22	18	24	21
Number of axial ribs on body whorl	21	20	19	19
Number of spiral cords on body whorl	26	24	22	19
Number of spiral cords on penultimate whorl	14	11	8	8

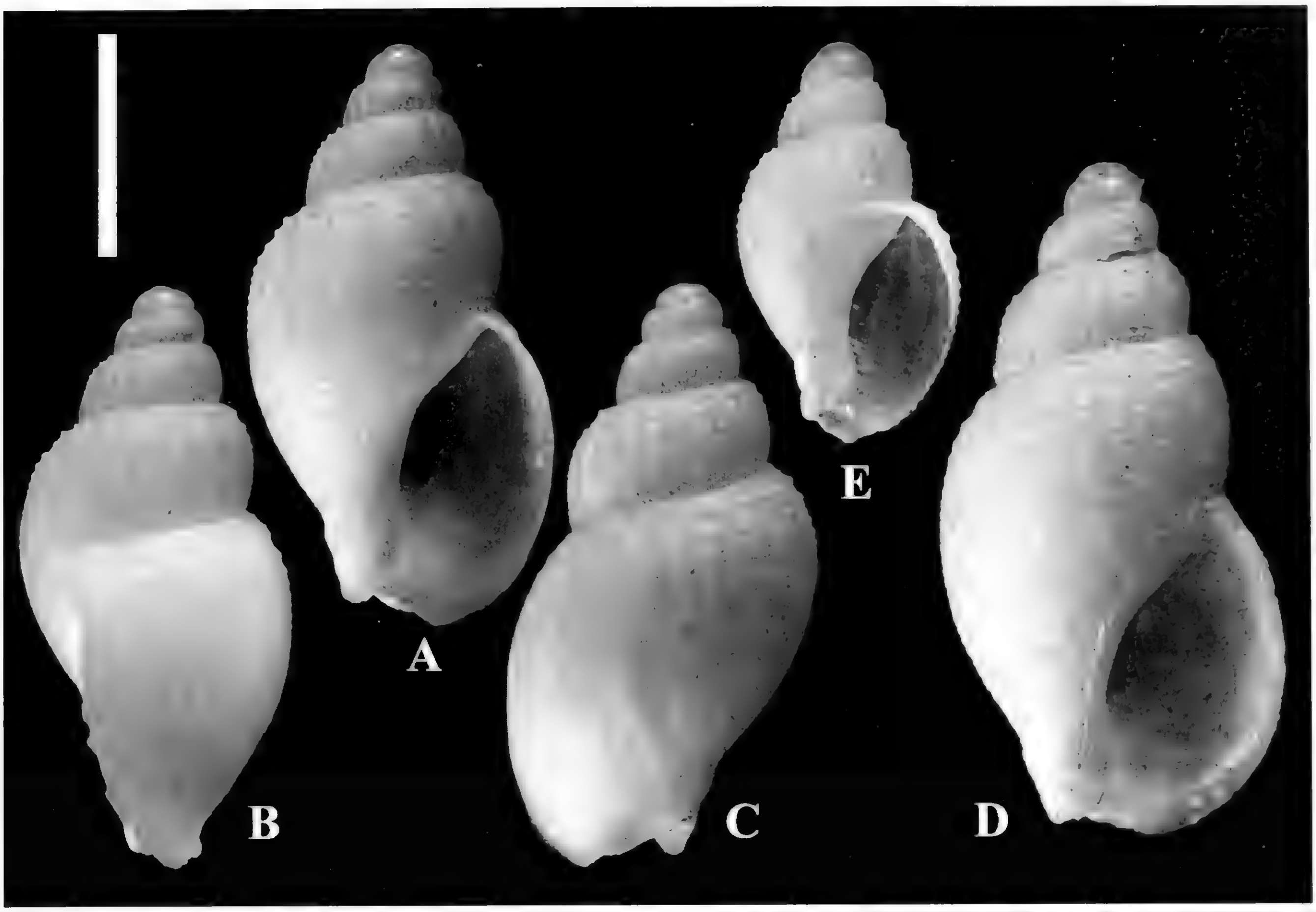

Fig. 5. *Parabuccinum polyspeirum* (Dell, 1990). A–C. Holotype, USNM 860131, R/V *Eltanin*, Sta. 369, Patagonian Shelf, NE of Islas de los Estados (Staten Island), 54°04′S, 63°35′W, in 247–293 m D. Paratype 1. E. Paratype 2. Both from type locality. Scale bar = 5 mm.

from the type locality. Paratypes 4–5 [paratype 5 (SL 4.8 mm) is not a buccinoidean, but belongs in the family Cancellariidae (Admetinae)] USNM 860126, E off Falkland (Malvinas) Islands, 51°56′S, 56°39′W, 855–866 m (R/V *Eltanin*, Sta. 557). Paratypes 6–7, USNM 860127, paratype 8, NMNZ MF.56614, E off Falkland (Malvinas) Islands, 54°09′S, 52°08′W, 419–483 m (R/V *Eltanin*, Sta. 1521).

Material examined.—Type material in USNM.

Table 3.—*Parabuccinum eltanini* (Dell, 1990). Measurements of shell characters of intact specimens. Linear measurements in mm. * = heavily eroded.

Character	Holotype USNM 860124	Paratype USNM 860127	Paratype USNM 860125
Shell Length (SL)	13.5	16.4	15.8
Body Whorl Length (BWL)	11.3	13.6	13.0
Aperture Length (AL)	8.8	10.3	9.9
Shell Width (SW)	8.8	10.0	9.6
Protoconch diameter	2.06*	2.94	2.24*
BWL/SL	0.84	0.83	0.80
AL/SL	0.65	0.63	0.63
SW/SL	0.65	0.61	0.61
Number of spiral cords on body whorl	37	53	38
Number of spiral cords on penultimate whorl	17	24	20

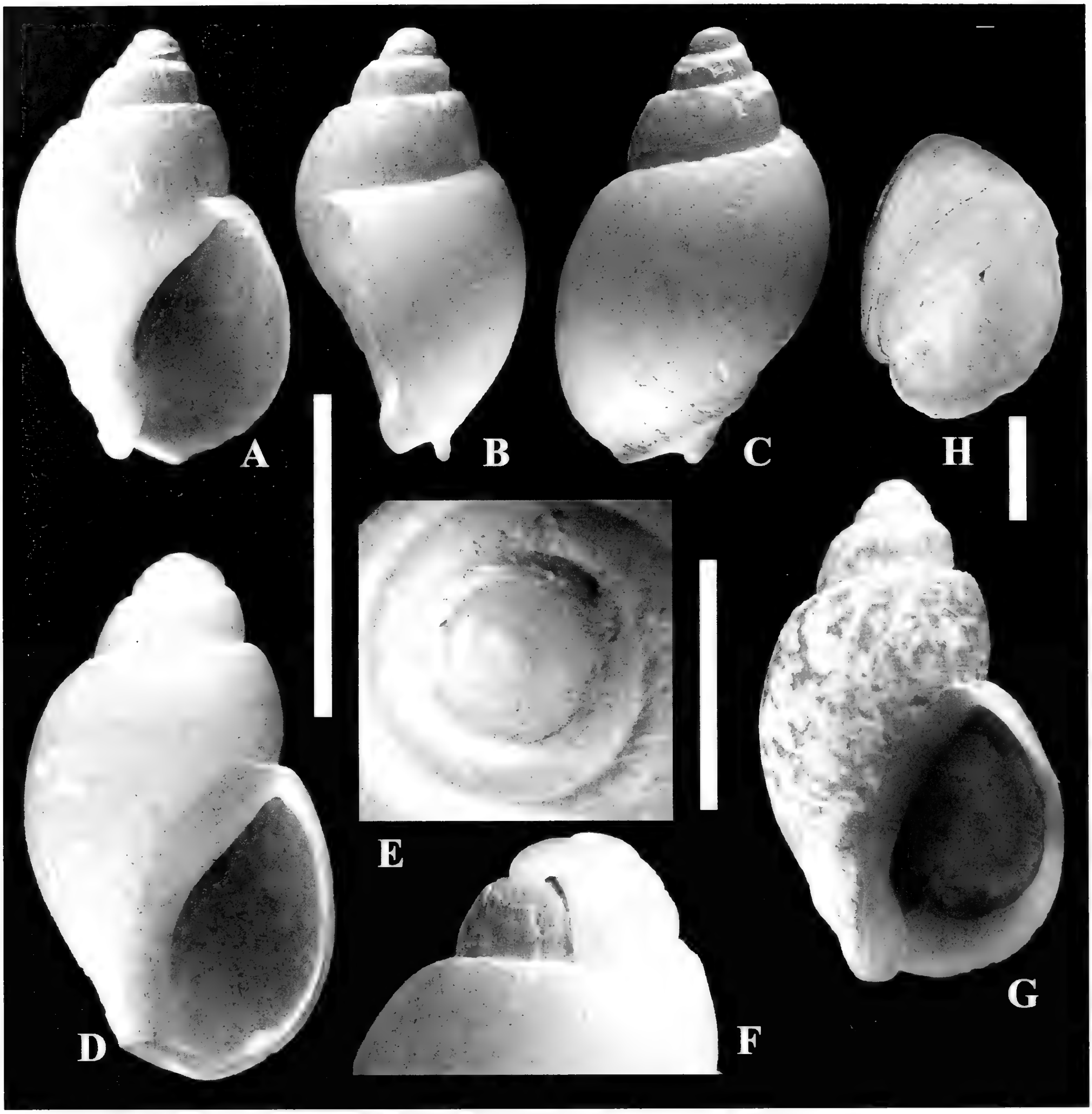

Fig. 6. *Parabuccinum eltanini* (Dell, 1990). A–C. Holotype, USNM 860124. D–F. Paratype, USNM 860127, E of Falkland (Malvinas) Islands, 54°09′S, 52°08′W, 419–483 m (R/V *Eltanin,* Sta. 1521). D. Apertural view. E. Dorsal view of the protoconch. F. Lateral view of the protoconch showing transition between protoconch and teleoconch whorls. G–H. Paratype, USNM 860125, type locality, E off Falkland (Malvinas) Islands, 51°58′S, 56°38′W, 845–646 m (R/V *Eltanin,* Sta. 558). G. Apertural view. H. Operculum (coated with ammonium chloride). Scale bars = 1 cm for shells, 5 mm for protoconch, 2 mm for operculum.

Distribution.—Off Falkland (Malvinas) Islands. Specimens collected at depths from 419 to 866 m. (Fig. 12).

Remarks.—This species differs from all congeners in having a smoothly ovate shell with a tall body whorl, a strongly prosocline outer lip, an extremely large, dome-shaped protoconch, and by the absence of axial sculpture. Dell's (1990:fig. 297) line drawing of the radula of *P. eltanini* shows a lateral tooth with a narrow basal plate and inner cusp, which differs from those of other *Parabuccinum* (Figs. 3, 10) and somewhat resembles those of *Chlanidota* (see, eg., Harasewych & Kantor, 1999 figs. 10 A, C). Although we were unable to study the anatomy of *P. eltanini,* we assign it to the genus *Parabuccinum* on the basis of the morphology of its shell, especially the characteristic protoconch, and operculum.

Paratype 5, the smaller (SL = 4.8 mm) of the two paratypes from R/V *Eltanin* station 557 (USNM 860126), is not conspecific with the rest of the type series, but is a species referable to the cancellariid subfamily Admetinae.

Parabuccinum rauscherti, new species
Figs. 2F–G, 7C–D, 9–12, Table 4.

Chlanidota bisculpta Dell, 1990 (partim):185.

Description.—Shell (Fig. 9) small for genus (to 10.2 mm), solid, white, broadly ovate to elongate, with flattened, shallow subsutural rim, pronounced, rounded to angulated shoulder. Protoconch (Fig. 7 C–D) small (diameter 1.07–1.2 mm), of about 1.75 glossy, convex, inflated whorls. Protoconch diameter/protoconch height = 1.10–1.31. Transition from protoconch to teleoconch well marked by onset of spiral followed immediately by axial sculpture. First teleoconch whorl thinner than protoconch. Teleoconch of up to 3.25 convex whorls. Suture strongly impressed. Spiral sculpture of closely spaced cords varying in strength from strongly pronounced to nearly smooth (16–40 on body whorl, 10–16 on penultimate whorl), generally broader than intervening spaces. Axial sculpture of strong, broad, slightly sinuous, orthocline ribs (13–17 on first teleoconch whorl, 15–20 on subsequent whorls). Nodules formed at intersections with spiral cords evident in early whorls, abbraded on body whorl. Aperture large (0.51–0.65 SL), narrow to moderately ovate, deflected from shell axis by 12–15°. Outer lip evenly rounded, usually slightly thickened. Columella <0.5 AL, weakly concave, with strong, sharply deflected siphonal fold. Callus of thin to thick glaze narrowly overlying parietal region and siphonal fasciole. Siphonal notch moderately broad, very slightly dorsally recurved, with straight columellar, rounded apertural margins defining borders of fasciole. Ridge margin of fasciole formed by apertural margin of siphonal notch. Shell color chalky white, aperture weakly glazed. Periostracum very thin, tightly adherant, yellowish, weakly hirsute. Operculum (Fig. 9D, G) medium-sized (0.49–0.53 AL), elongate ovate, strongly coiled, with nucleus rotated clockwise, nearly 180° to long axis of operculum.

Anatomical data based on single, poorly preserved male specimen (Fig. 9 E–F, Paratype 1) from which only a portion of the animal was recovered.

External anatomy.—(Fig. 2F–G). Foot long (L/W ~2.5), oval, broad anteriorly, tapering posteriorly, with thickened propodium. Body color uniformly yellowish-white. Head small short, tentacles (Fig. 3G, ten) long, left longer than right, tapering distally. Eyes absent. Mantle cavity (Fig. 3F) as wide as long. Mantle edge thickened, with scalloped edge. Siphon (Fig. 3F) very long (0.9 AL), thin walled, wide. Osphradium ≈0.67 mantle length, wide, with curved axis. Ctenidium slighter longer, 0.67 as wide as osphradium, spans about 0.75 of mantle length, formed of tall triangular lamellae that become narrower toward mantle edge.

Alimentary system.—Proboscis of moderate length in contracted position (0.35 SL, 0.6 AL), smooth, unpigmented. Proboscis sheath very thin-walled, transparent. Mouth opening triangular. Proboscis retractors broad, extremely thin, asymmetrically attached to proboscis sheath. Buccal mass occupies ≈0.63 length of retracted proboscis. Radula (Fig. 10) 1.54 mm long (0.33 AL), ~120–140 μm wide (~0.015–0.017 SL, 0.026–0.030 AL), of 65 rows of teeth, posteriormost 3 nascent. Rachidian teeth tricuspid (central cusp slightly longer, as wide as lateral cusps). Lateral teeth usually with 3 cusps. Outer cusp nearly twice as long, half as wide as inner cusp. Intermediate cusp thin, equal in length to inner cusp. In one specimen (Fig. 10 C) intermediate cusp

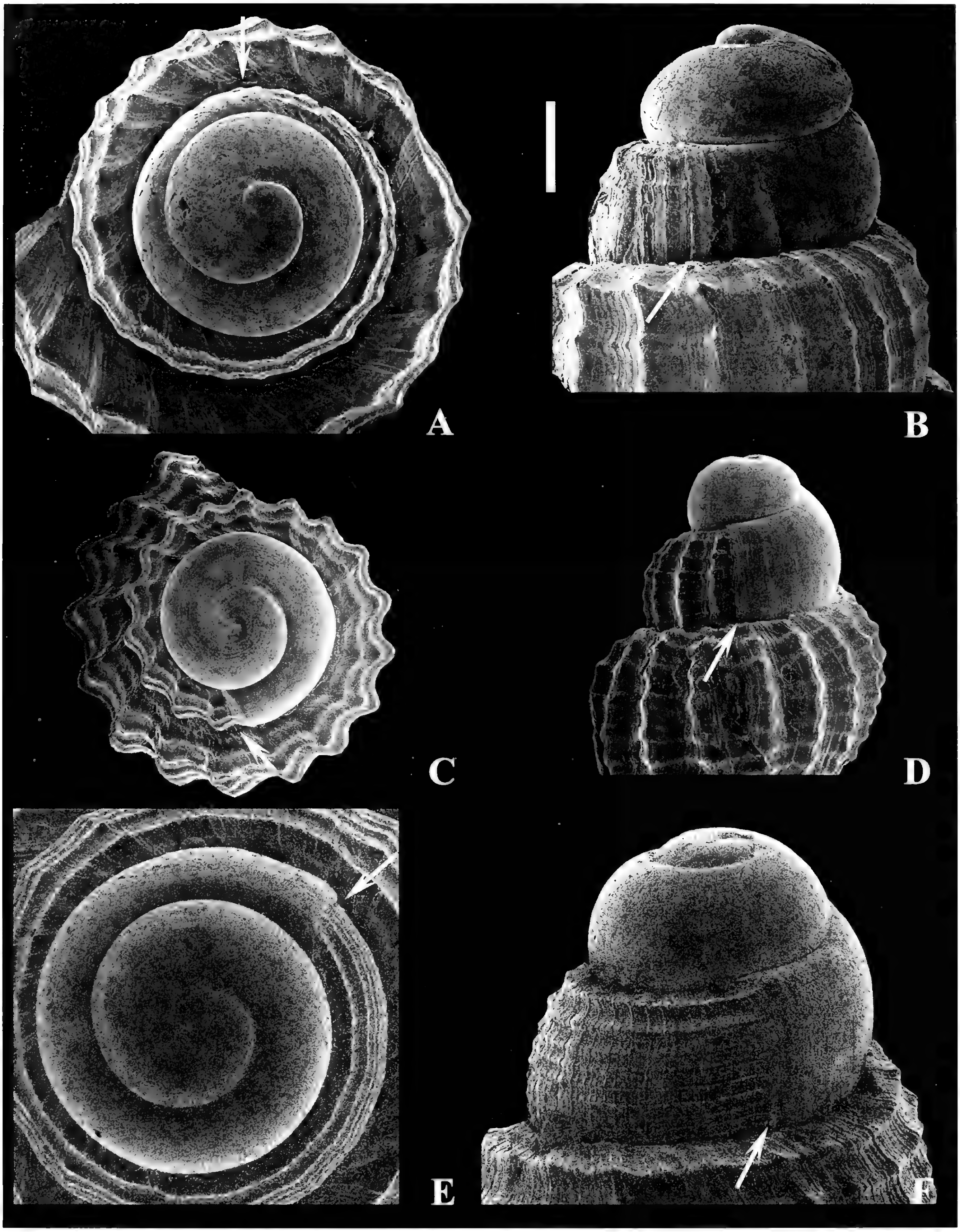

Fig. 7. Protoconchs of *Parabuccinum*. A–B. *P. bisculptum* (Dell, 1990), ZMH. C–D. *P. rauscherti*, new species. Paratype, ZMH 2813. E–F. *P. polyspeirum* (Dell, 1990) Paratype in fig. 5 E. Arrows indicate transition from protoconch to teleoconch. Scale bar = 500 μm for all figures.

Table 4.—*Parabuccinum rauscherti,* new species. Measurements of shell characters. Linear measurements in mm (n = 12, including types).

Character	Mean	σ	Range	Holotype	Paratype 1	Paratype 4
Shell Length (SL)	8.4	0.67	7.6–9.6	7.7	8.1	8.1
Body Whorl Length (BWL)	6.5	0.63	5.4–7.4	6.1	6.3	6.2
Aperture Length (AL)	4.7	0.49	4.2–5.5	4.2	4.7	4.6
Shell Width (SW)	5.0	0.44	4.1–5.8	4.6	4.7	4.9
Protoconch diameter	1.15	0.05	1.07–1.20	1.07	1.18	1.13
BWL/SL	0.76	0.03	0.71–0.80	0.79	0.78	0.77
AL/SL	0.56	0.05	0.51–0.65	0.55	0.58	0.57
SW/SL	0.60	0.04	0.54–0.67	0.59	0.58	0.60
Number of axial ribs on 1st teleoconch whorl	15.0	1.15	13–17	13	15	14
Number of axial ribs on 2nd teleoconch whorl	16.5	1.76	15–20	16	17	16
Number of axial ribs on body whorl	17.7	1.95	15–20	16	17	17
Number of spiral cords on body whorl	25.8	6.88	16–40	25	17	20
Number of spiral cords on penultimate whorl	12.1	2.28	10–16	12	10	10

fused with inner cusp along portion of radular ribbon. Valve of Leiblein well defined, medium-sized, pyriform. Salivary ducts join oesophagus just anterior to the valve. Remainder of alimentary system poorly preserved.

Male reproductive system.—Specimen mature male, with long, broad penis (Fig. 11) extending length of mantle length. Distal end of penis transversely flattened, bordered by thickened edge. Penial papilla (Fig. 11B, pap) long, cylindrical, surrounded by narrow circular fold at the base.

Type locality.—Off Cape Horn, 55°44.0′S, 66°14.5′W, in 430–397 m. (R/V *Polarstern,* ANT XIII/4. Sta. 40–109).

Type material.—Holotype (ZMH 2811), paratypes 1–3 (USNM 880616), paratype 4 (ZMH 2812), paratypes 5–20 (ZMH 2813), paratypes 21–30 (ZMH 28134), from the type locality.

Material examined.—Type material. R/V *Eltanin.* Sta. 339: Falkland (Malvinas) Islands, Beauchene Island, 53°05′S, 59°31′W, 512–586 m, 1 shell, USNM 870141; Sta. 740, off Cape Horn, 56°06′S, 66°19′W,

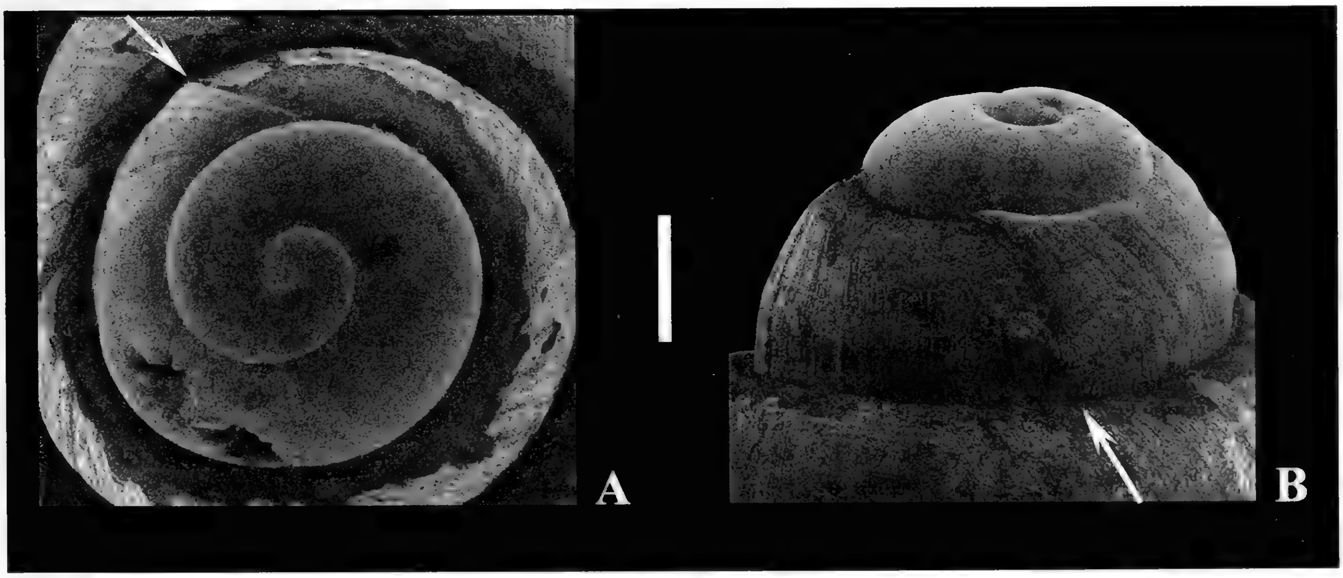

Fig. 8. Protoconch of *Parabuccinum eltanini* (Dell, 1990) at half the magnification of figure 7. Paratype, USNM 860127, E of Falkland (Malvinas) Islands, 54°09′S, 52°08′W, 419–483 m (R/V *Eltanin,* Sta. 1521). See also Fig. 6 E–F. Arrows indicate transition from protoconch to teleoconch. Scale bar = 1 mm.

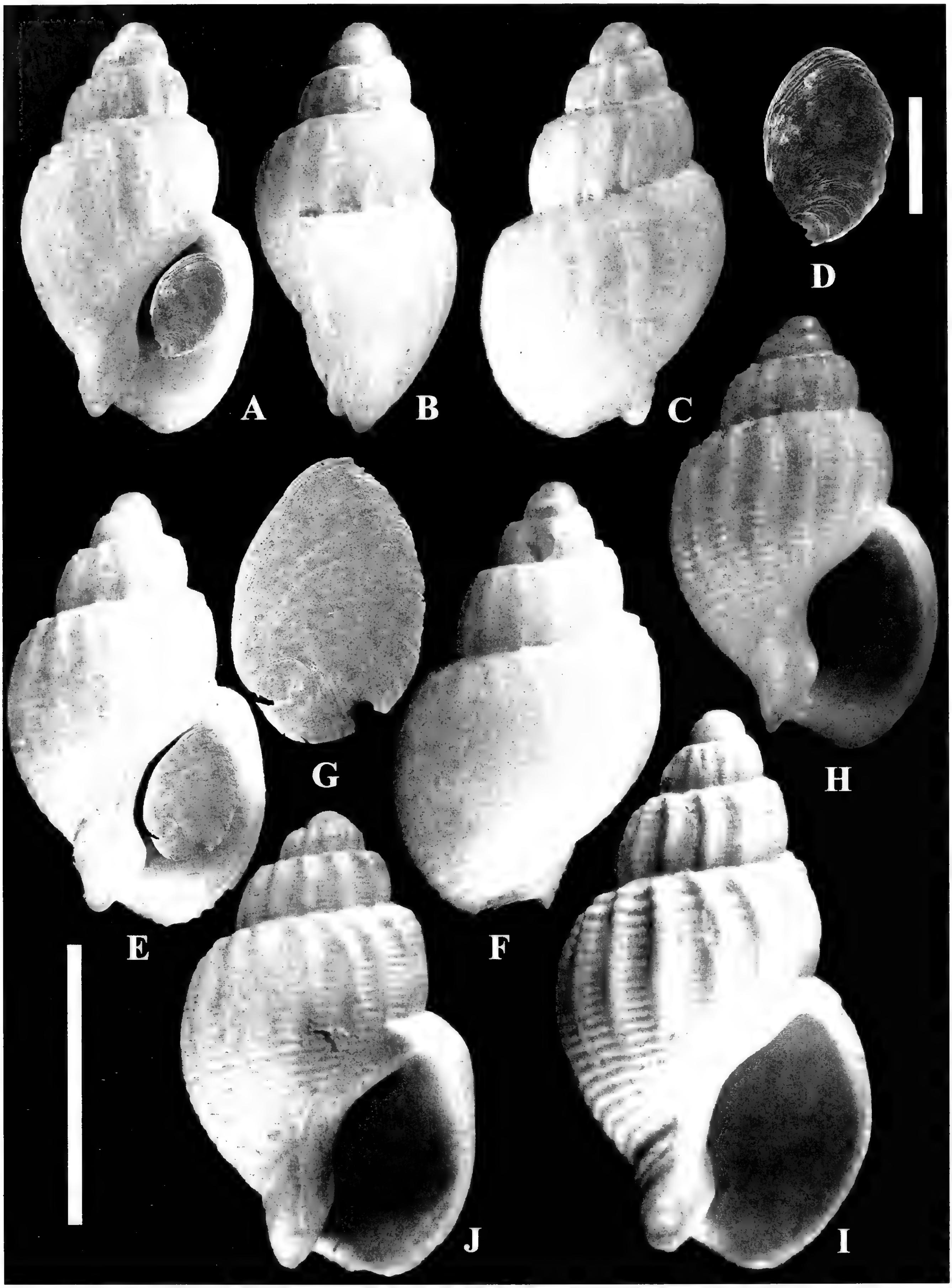

Fig. 9. *Parabuccinum rauscherti,* new species. A–D. Holotype, ZMH 2811, R/V *Polarstern* ANT XIII/4, Sta. 40–109, off Cape Horn, 55°44.0′S, 66°14.5′W, in 430–397 m. A–C. Shell. D. Operculum. E–G. Paratype 1, type locality, USNM 880616. E–F. Shell. G. Operculum. H. Paratype 4, ZMH 2812, type locality. I–J. R/V *Polarstern* Sta. 40–114, off Cape Horn, 55°31.6′S, 65°56.8′W, 2165–2008 m, ZMH. Scale bar = 5 mm for shells, 2 mm for operculum.

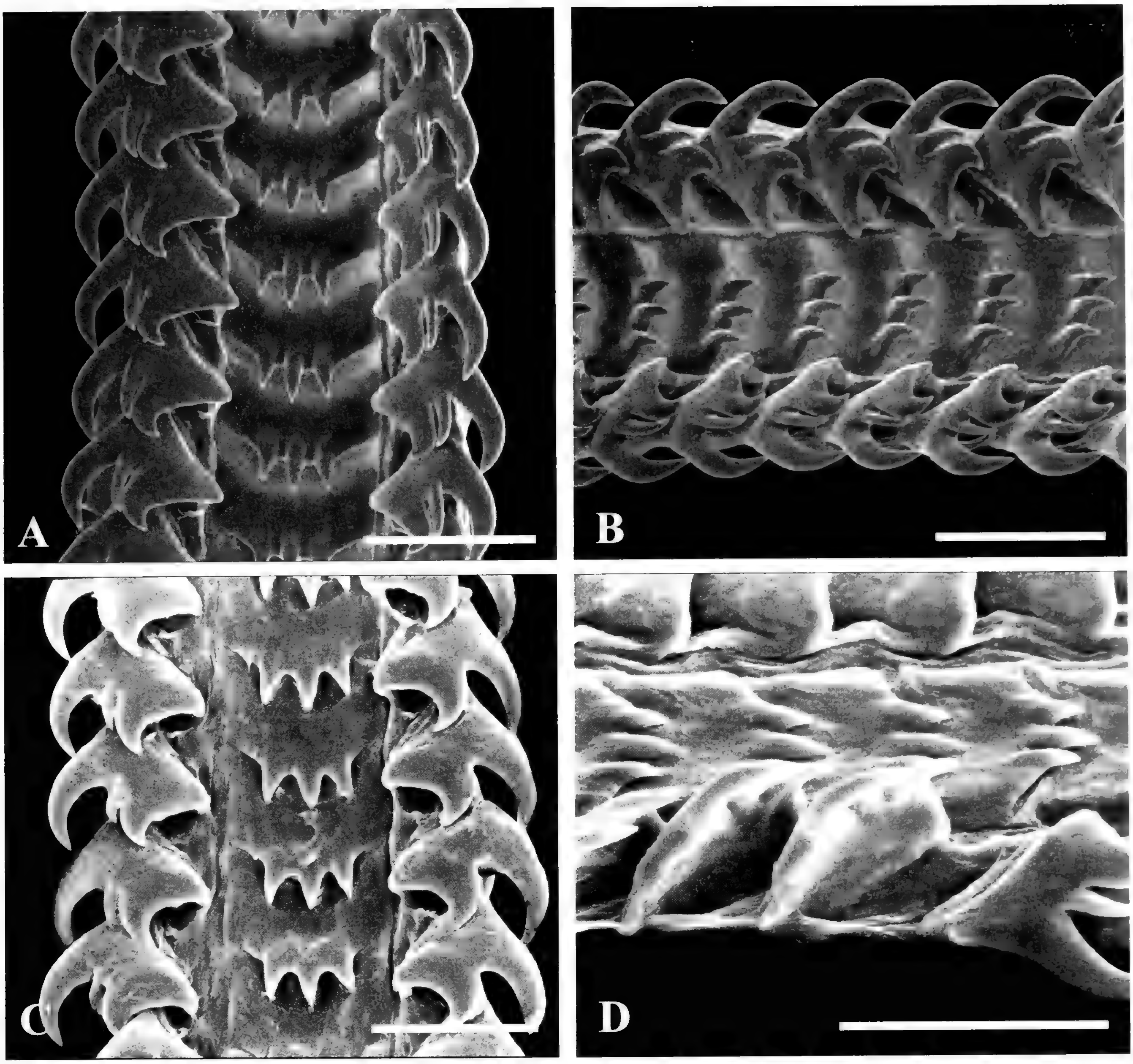

Fig. 10. Radula of *Parabuccinum rauscherti,* new species. A. Dorsal, and B. left lateral (45°) views of the central portion of the radular ribbon taken from paratype 1, USNM 880616 (Figs. 9, E–F). C. Dorsal and D. left lateral (45°) views of the central portion of the radular ribbon taken from paratype 4, ZMH 2812 (Figs. 9 G). Scale bars = 50 μm.

384–349 m, 1 shell (paratype of *Chlanidota bisculpta*), USNM 860130. R/V *Polarstern* ANT XIII/4: Sta. 40–114, off Cape Horn, 55°31.6′S, 65°56.8′W, 2165–2008 m, 18 May, 1996, ZMH, 29 shells. R/V *Vidal Gomaz:* Sta. 42, Canal Concepcion, 50°35.7′S, 75°04.5′W, 250 m, 25 Oct 1996, ZMH, 5 specimens.

Distribution.—Off the Falkland (Malvinas) Islands, Cape Horn and northward along western coast of Chile to Canal Concepcion. Shells were trawled at depths ranging from 349 to 2165 m. Live animals were collected from 349 to 532 m (Fig. 12).

Etymology.—This new species is named after Martin Rauschert who developed the small dredge used to collect this species. Dr. Rauschert is an amphipod taxonomist who has worked for several years in the Antarctic and Magellanic regions.

Remarks.—*Parabuccinum rauscherti* is most similar in shell sculpture structure to *P. bisculptum* from which it differs in having a smaller, slightly broader shell (SW/SL

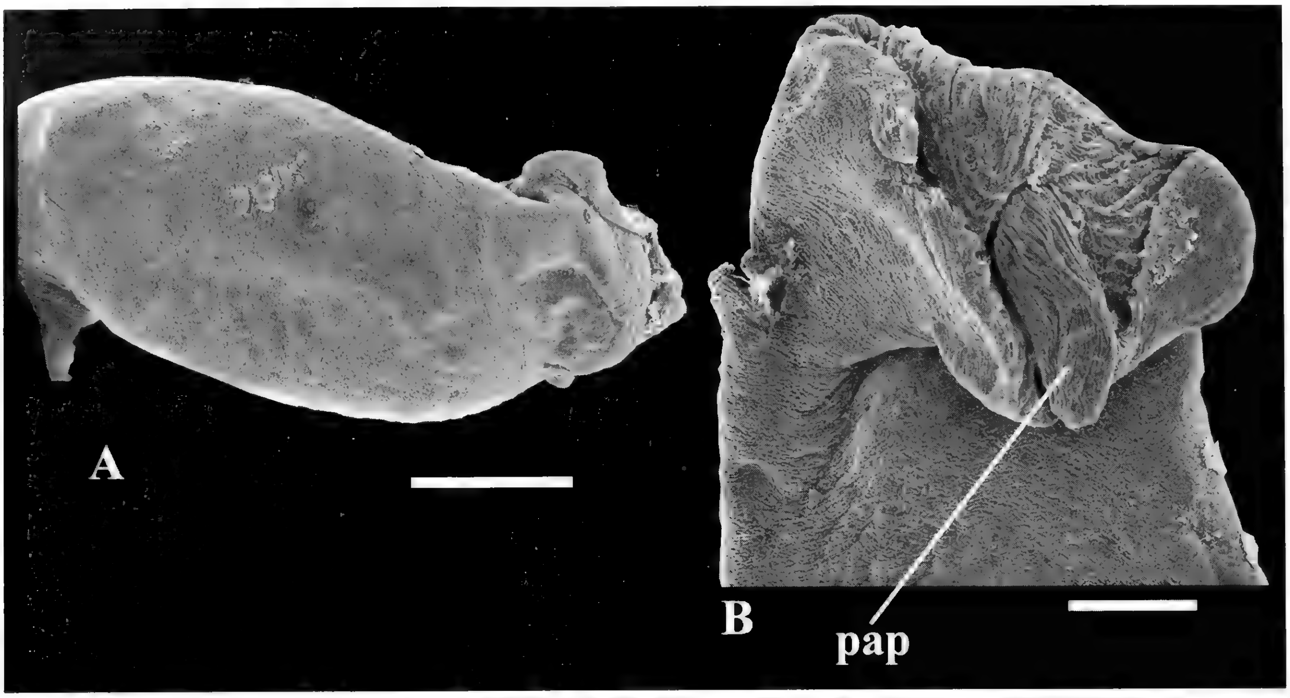

Fig. 11. *Parabuccinum rauscherti,* new species. Critical point dried penis of paratype 1, USNM 880616 (Figs. 9, E–F). A. Dorsal surface. Scale bar = 500 μm. B. Distal tip showing papilla. Scale bar = 200 μm.

≈0.60 in *P. rauscherti,* 0.54 in *P. bisculptum*), a smaller protoconch (average diameter = 1.16 mm in *P. rauscherti,* 1.53 in *P. bisculptum*) (compare Fig. 7A, B and 7C, D). *Parabuccinum rauscherti* also has more numerous and closely spaced spiral cords (average = 25.9 on body whorl, 12.1 on penultimate whorl) than *P. bisculptum* (average = 13.8 on body whorl, 6.0 on penultimate whorl) and less numerous (16.5 vs. 19.8) but wider axial ribs. *Parabuccinum rauscherti* and *P. bisculptum* were taken to-

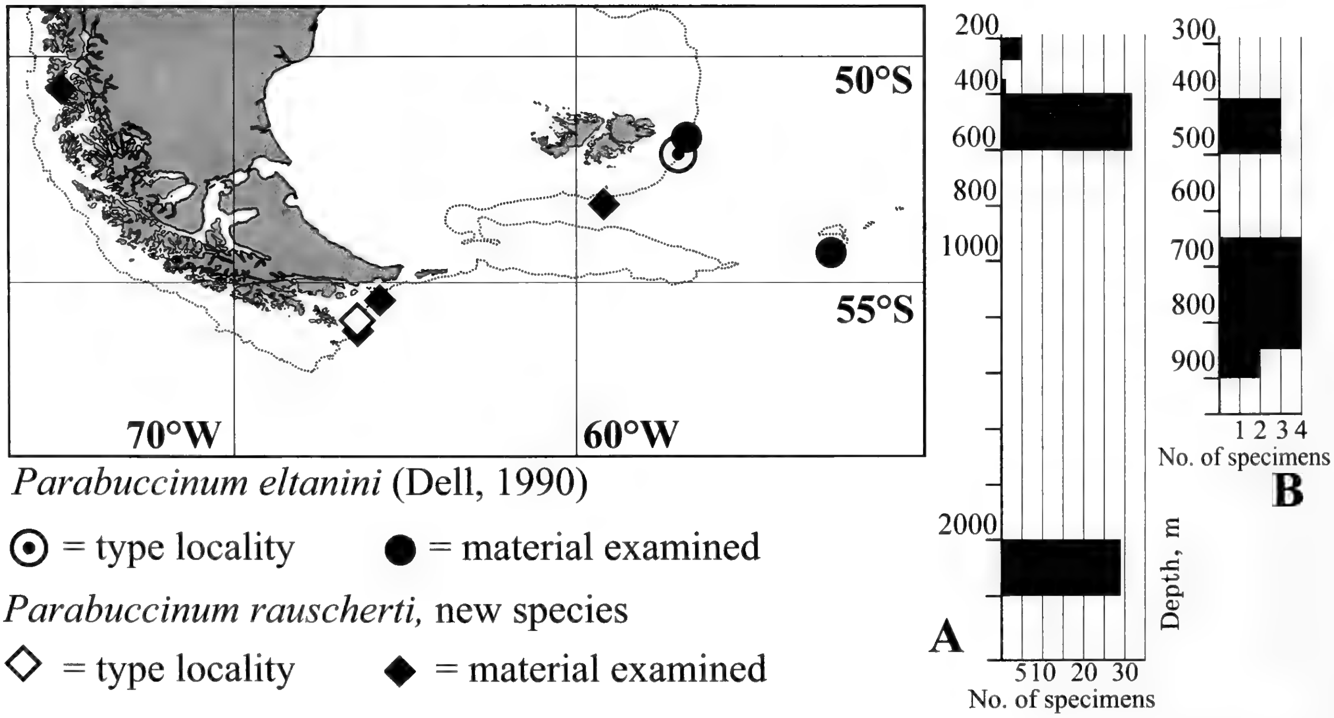

Fig. 12. Geographical distribution and bathymetric ranges of *Parabuccinum eltanini* (Dell, 1990) and *Parabuccinum rauscherti,* new species. Dashed line indicates 500 m isobath. A. Bathymetric range of *P. rauscherti.* B. Bathymetric range of *P. eltanini.*

gether at two stations off Cape Horn (R/V *Polarstern* Sta. 10–109 and R/V *Eltanin* Sta. 740).

Parabuccinum rauscherti may be most readily distinguished from either *P. polyspeirum* or *P. eltanini* by its much smaller protoconch and pronounced axial sculpture. *Parabuccinum rauscherti* exhibits some variation in shell outline and the number of spiral cords.

The smaller of the two paratypes of *Chlanidota bisculpta,* from R/V *Eltanin.* Sta. 740 (USNM 860130, SL = 6.9 mm) is actually a specimen of *Parabuccinum rauscherti.*

Discussion

Despite the limited availability of the anatomical data for *Parabuccinum,* it clearly shares anatomical features with other Buccinulinae, such as *Chlanidota, Cavineptunea* and several yet to be named genera. These similarities include proboscis morphology, tricuspid rachidian and lateral radular teeth, a well defined valve of Leiblein, fused salivary glands, a characteristic crop-like structure of the posterior oesophagus, and a broadly U-shaped stomach, lacking a caecum (posterior mixing area). This stomach morphology was found in all antiboreal Buccinoidea studied thus far. Among northern hemisphere buccinoideans, a stomach lacking a caecum was recorded only in the northern Atlantic buccinid *Colus gracilis* (DaCosta, 1778) (see Smith 1967) and deep-water Arctic species *Mohnia* (*Tacita*) *danielsseni* (Friele, 1879) (see Lus 1981).

Parabuccinum has a number of unusual features, among them a very long mantle siphon, a very small, nearly vestigial gland of Leiblein, and characteristic penis morphology previously unrecorded in Buccinoidea.

With the exception of *Parabuccinum,* the Magellanic buccinoidean fauna is comprised of genera attributed to the buccinulid subfamily Cominellinae (e.g., *Pareuthria, Falsitromina, Parficulina*). As there are no closely related South American or Magellanic Buccinoidea, *Parabuccinum* is likely derived from the Antarctic Buccinulinae.

Powell (1951) attributed the following Antarctic genera to the subfamily Buccinulinae: *Chlanidota, Pfefferia* (a subgenus of *Chlanidota,* as demonstrated by Harasewych & Kantor 1999), *Neobuccinum, Probuccinum, Cavineptunea* and *Bathydomus.*

The differences between *Parabuccinum* and *Chlanidota* have been discussed above. Of the remaining Antarctic buccinuline taxa, only one—the monotypic genus *Neobuccinum,* has a similar paucispiral operculum. The shell morphology of *Neobuccinum eatoni* (Smith, 1907) is similar to that of *Parabuccinum,* especially to that of *P. eltanini.* Both *Neobuccinum* and *Parabuccinum* have large, dome-shaped protoconchs that appear to be more resistant to errosion that their teleoconchs. The radula of *N. eatoni* (illustrated by Numanami, 1996:fig. 94C) resembles that of *P. eltanini* more that those of the other species of *Parabuccinum* in that the central cusps of the lateral teeth are larger and more distant from the inner cusps. *Parabuccinum* and *Neobuccinum* may be distinguished anatomically, particularly on the basis of penis morphology and the size and shape of gland of Leiblein. The penis of *Neobuccinum* has a broadly rounded distal end with a very small, blunt seminal papilla, while the gland of Leiblein in this species is large and well developed (unpublished observations).

Neobuccinum eatoni has a circumantarctic distribution extending along the Scotia Arc, and to Kerguelen Island, as well as a broad bathymetric range (5 to 2350 m). Despite the anatomical differences, we consider *Neobuccinum* to be the most promising candidate for sister group of *Parabuccinum* among the presently known Antarctic buccinoidean fauna. *Parabuccinum* thus represents an Antarctic component in the Magellanic malacofauna.

The distinctive paucispiral opercula of *Parabuccinum* and *Neobuccinum* differ from those of other austral Buccinoidea, yet resemble opercula of the deep-water boreal genus *Mohnia* (termed *Mohnia* type operculum by Bouchet and Warén 1985:171). Several species of *Mohnia* also have tricuspid rachidian and lateral teeth (Bouchet & Warén 1985:178–179) while at least one species [*Mohnia* (*Tacita*) *danielsseni,* see above] has a stomach lacking a caecum. *Mohnia* is readily distinguished from *Parabuccinum* and *Neobuccinum* by numerous conchological (e.g., presence of siphonal canal) and radular (rachidian teeth with squarish basal plate and lateral cusps lost or closely juxtaposed to prominent central cusp) characters. It is, as yet, unclear whether these similarities are indicative of a close relationship between these antipodal taxa, or represent plesiomorphic characters within the Buccinoidea.

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Porites arnaudi, a new species of stony coral (Anthozoa: Scleractinia: Poritidae) from oceanic islands of the eastern Pacific Ocean

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Abstract.—A new species of *Porites* (*P. arnaudi*) was found at depths of 7 to 37 m at Clipperton Atoll, France, and the Revillagigedo Islands, México, oceanic islands located west of the American mainland (eastern Pacific). Colonies are uncommon but very distinctive because of the presence of tiered plates, or laminae, expanding from a single base, smooth and concave surfaces, and a lack of living tissue on the inferior part of the plates, except on its growing edge. Calices are 0.8 to 1.4 mm in diameter, with wide walls. Corallites have a free triplet with all three septa about the same size. Lateral septa are fused in pairs and better developed than the rest. There are six to eight pali, and one or two denticles per septum, and the color of tissue is greenish-gray to dark brown. With this new species, the current total number of species in the genus *Porites* in the eastern Pacific reaches nine, with most species restricted to oceanic islands of the region.

In the last 20 years, taxonomic studies on the scleractinian zooxanthellate fauna of the eastern Pacific have noticeably increased in number and quality (Wells 1983, Guzmán & Cortés 1993, Hodgson 1995) and as a consequence, there is now fairly good agreement on coral identities since some key taxonomic problems have been resolved (Squires 1959, Wells 1983, Veron 1986). New research also has shown that the actual richness of coral species from the eastern Pacific is much higher than once thought [e.g., originally less than 20 species according to Veron (1993) and Paulay (1997)]. For example, México, Costa Rica and Panamá have 20 to 25 species each and almost 40 are known to inhabit western America (Holst & Guzmán 1993, Cortés & Guzmán 1998, Reyes-Bonilla & López-Pérez 1998). This perceived increase in richness comes from new records for particular localities or areas (e.g., Reyes-Bonilla 1992, Cortés & Guzmán 1998) and by descriptions of new species (Budd & Guzmán 1994, Glynn 1999).

Members of the genus *Porites* Link, 1807 are widely distributed in the eastern Pacific, and they are one of the dominant corals in this region, both in abundance and species richness (Glynn 1997). To date, eight species have been reported: *P. australiensis* Vaughan, 1918, *P. baueri* Squires, 1959, *P. lichen* Dana, 1846, *P. lobata* Dana, 1846, *P. lutea* Milne Edwards, 1860, *P. panamensis* Verrill, 1866, *P. rus* Forskaal, 1775, and *P. sverdrupi* Durham, 1947 (Guzmán & Cortés 1993, Glynn 1997, Reyes-Bonilla 1999). Both *P. panamensis* and *P. lobata* are present in coral communities from the Galápagos Islands, or the Ecuadorian mainland, to México (Reyes-Bonilla 1993, Glynn 1997), while *P. sverdrupi* and *P. baueri* are endemic to the Gulf of California and the Marías Islands, México, respectively (Squires 1959, Reyes-Bonilla & López-Pérez 1998). *Porites rus* is an

Indo Pacific species that was reported from Costa Rica in the early 1980's, but its population may be extinct now (Glynn 1997, Cortés & Guzmán 1998). The remaining three species are Indo Pacific also, but they have been observed in the Revillagigedo Archipelago, México, a group of four oceanic islands located about 300 km southwest of the Baja California peninsula, or at Clipperton Island, the only true atoll of the eastern Pacific, 1300 km SW of the Mexican mainland (Glynn et al. 1996, Ketchum & Reyes-Bonilla 1997).

In this paper, a new species of *Porites* is described. This coral is distinctive because its colonies have been found exclusively in the oceanic Clipperton and Revillagigedo Islands, eastern Pacific. This finding increases the known number of species of the genus *Porites* to nine, a number even greater than that reported for the Atlantic-Caribbean area (Weil 1992, Veron 1993).

Abbreviations of repository institutions.—USNM: United States National Museum of Natural History, Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560, U.S.A.; MHNUABCS: Museo de Historia Natural de la Universidad Autónoma de Baja California Sur. Departamento de Biología Marina. La Paz, B.C.S., 23080, México; ECOCHBC: Colección de Corales de El Colegio de la Frontera Sur, Grupo de Ecología Bentónica. Apartado postal 424, Chetumal, Q. Roo, 77000, México. UMML: University of Miami Marine Laboratory. Rosenstiel School of Marine and Atmospheric Sciences. 4600 Rickenbacker Causeway, Miami, FL 33149, U.S.A.

Order Scleractinia Bourne, 1900
Suborder Fungiina Verrill, 1865
Superfamily Poritoidea Gray, 1842
Family Poritidae Gray, 1842
Genus *Porites* Link, 1807

Type species.—*Porites polymorphus* Link, 1807 = *Madrepora porites* Pallas, 1766 (in part).

Diagnosis.—Massive, ramose or encrusting cerioid coralla. Corallites with calices smaller than 2 mm in width, with two cycles of septa. Septa commonly bear spines and are formed by three or four trabeculae that in their innermost portions are differentiated as pali. A single trabecular columella, absent in certain species. Colony formation by extratentacular budding. Coenosteum poorly developed (Wells 1956).

Distribution.—The genus is circumtropical, recorded in the Pacific, Indian and Atlantic oceans, as well as in the Caribbean Sea (Veron 1993). Fossil records are known from the Cretaceous (?), Eocene to Recent, but are more abundant and dominant in reef communities since the Miocene (Wells 1956, Veron 1995). In the eastern Pacific the genus is distributed from the Galápagos Islands (0°N), Ecuador, to the northern Gulf of California (31°N), México, including all adjacent oceanic islands (Wells 1983, Reyes-Bonilla 1993).

Porites arnaudi, new species
Figs. 1–6

Etymology.—Named after Gustavo Arnaud Vignon, the last Commander in Chief of the Mexican Navy garrison on Clipperton Island, who died tragically while on duty on 1916.

Diagnosis.—(Terminology after Veron & Pichon 1982 and Veron 1986) Oval shaped colonies composed of tiered, thick platelike laminae (at least 10 mm in width). Corallum originates from a single wide pedicel, with smooth, concave and undulated surfaces, with no living tissue on the inferior parts, except on its growing edges. Corallites distinct, calices 0.8 to 1.4 mm wide, with walls less than 1 mm wide. Septa rarely bifurcated. Free triplet, although the ventral directive and one lateral can be joined. Lateral septa fused in pairs and better developed than the rest. One or two conspicuous denticles in the inner part of each septum. Six to eight pali which do not reach the level of the wall; the palus of the triplet

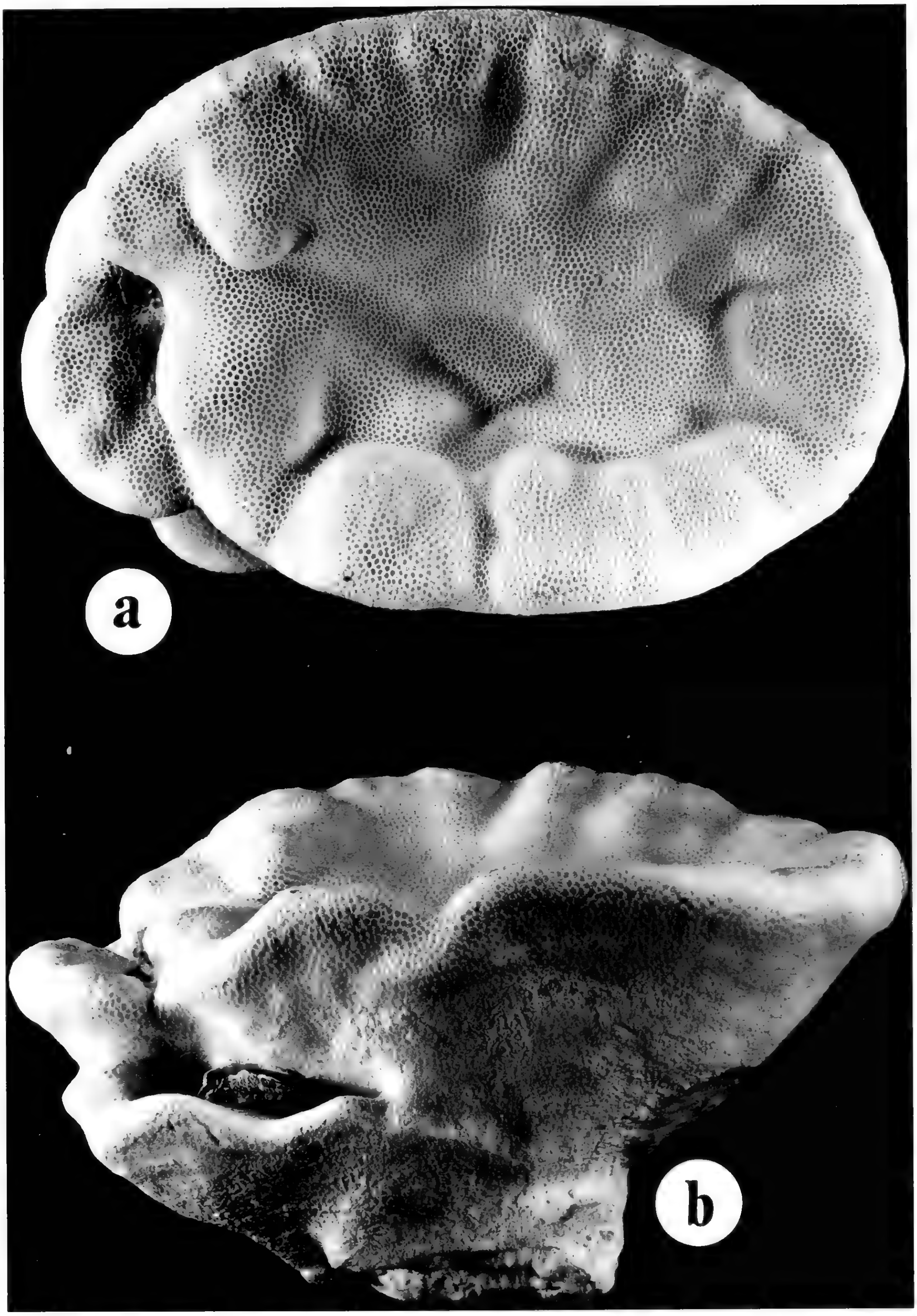

Fig. 1. *Porites arnaudi,* holotype, USNM 100261. Recent, 30 m depth, Clipperton Atoll, France. a, top view; b, side view. Both ×0.49.

and dorsal directive less developed than those of the lateral pairs. Two synapticular rings, the external more defined. Living tissue color greenish-gray to dark brown, with pale margins.

Holotype.—USNM 100261 (Figs. 1a, b; 4a, b; 5a, b): length 213 mm, width 148 mm, height 111 mm, thickness of peripherical edge of folia 19 to 21 mm; collected 25 Nov 1997 by Juan P. Carricart-Ganivet.

Paratypes.—ECOCHBC 0107 (Fig. 2a, b), MHNUABCS 1044, 1076, 1092, 1100, 1103, 1581 (Fig. 3c, d), 1582 (Fig. 3a, b), 1583, UMML 8.1475 (Fig. 6a, b).

Type locality.—Northeast seaward slope (sensu Glynn et al. 1996), off Clipperton

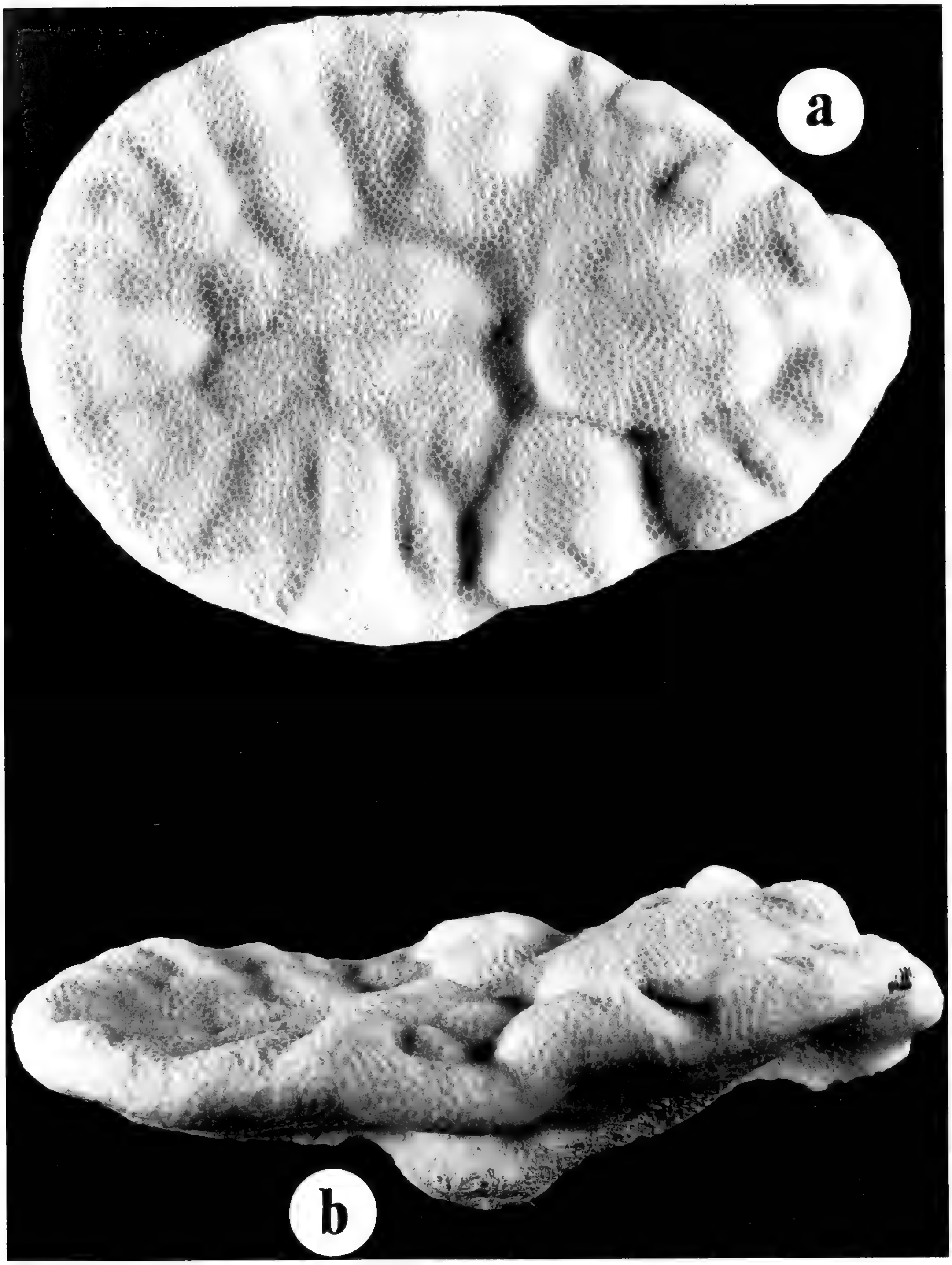

Fig. 2. *Porites arnaudi,* paratype, ECOCHBC 0107. Recent, 30 m depth, Clipperton Atoll, France. a, top view; b, side view. Both ×0.79.

Atoll, France (10°18′N, 109°13′W), at 30 m depth.

Description.—Colonies submassive, forming conspicuous tiered plates growing outwards from a central base (discoidal morphology; Figs. 1a, b; 2a, b); coralla can attain more than 40 cm in diameter and about 30 cm in height, being firmly attached to the substrate. Smooth, concave, and undulated upper surfaces, with thick folia at least 10 mm in width (Fig. 3a–d). Inferior surfaces devoid of living tissue except in their growing edges. Corallites 0.8 to 1.4 mm diameter, conspicuous, with deep, polygonal calices (normally five to six sides) having six to eight deep-set pali, which do not reach the level of the wall. Intercalicular distances 0.8 to 1.7 mm (Figs. 4a, b). Corallite walls less than 1 mm thick and composed of three rows of denticles.

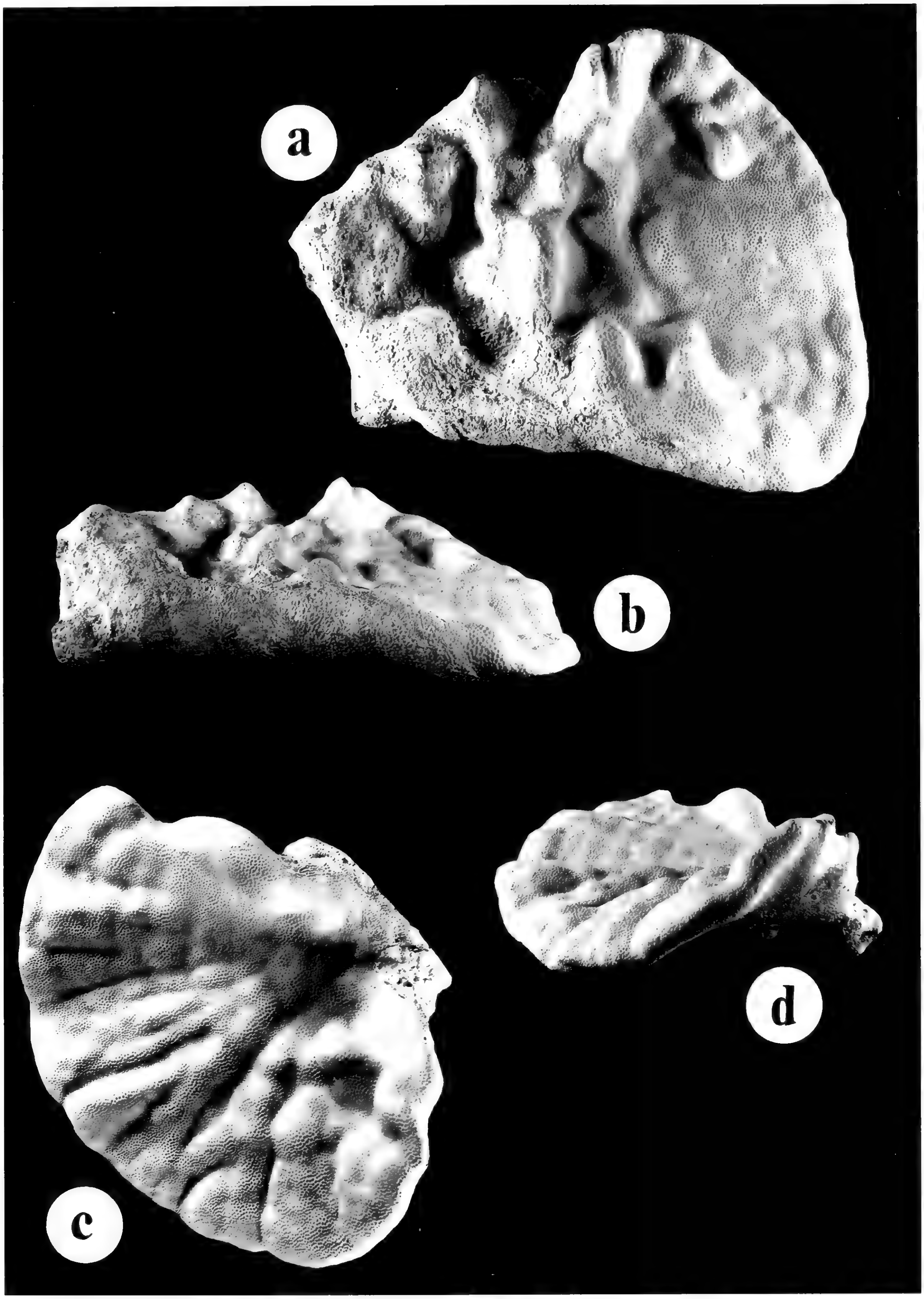

Fig. 3. *Porites arnaudi,* paratypes, top and side views of laminae from the edge of larger colonies: a, b, MHNUABCS 1582; c, d, MHNUABCS 1581. Both recent, 21 m depth, Clipperton Atoll, France. All figures ×0.30.

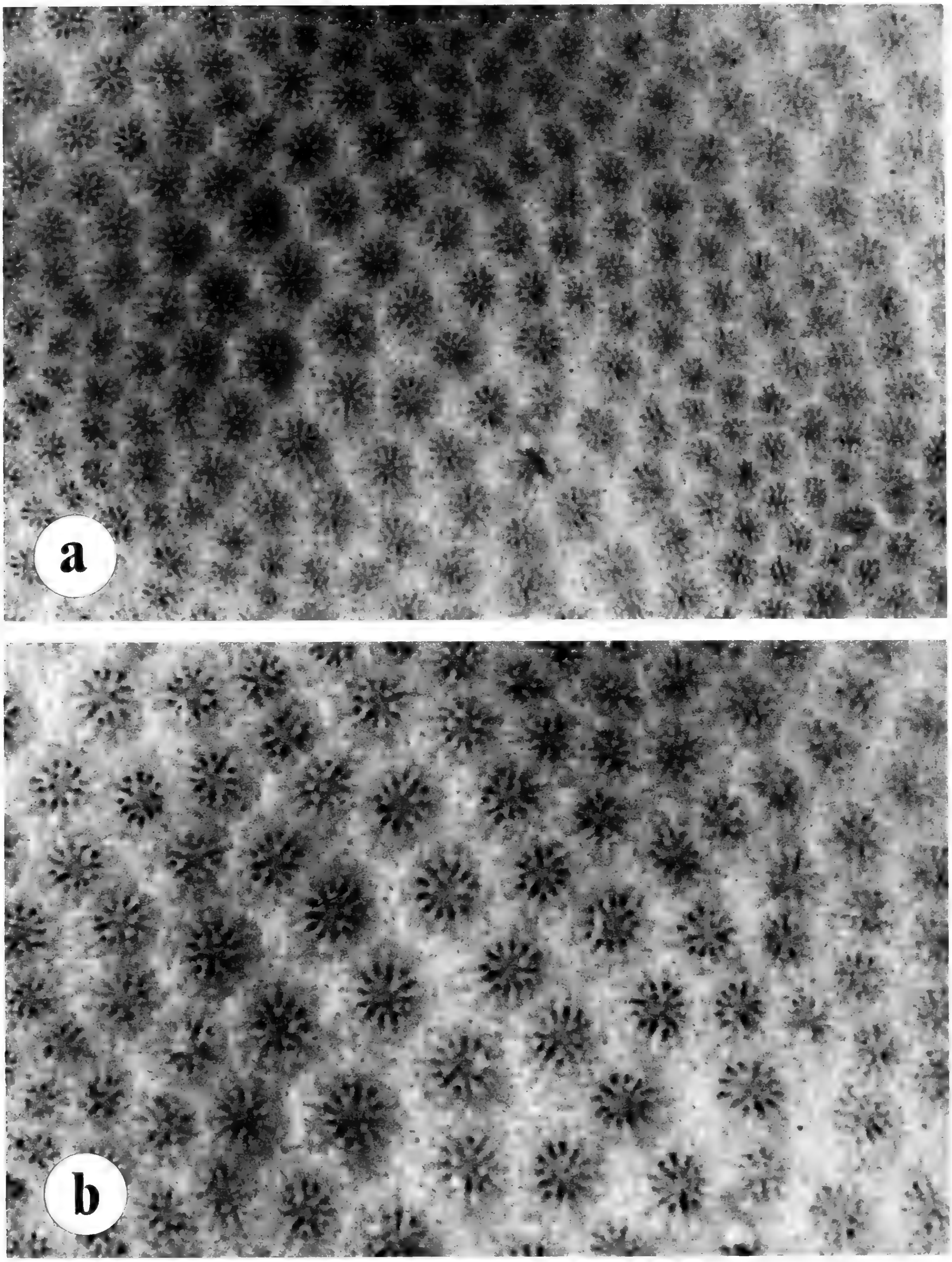

Fig. 4. *Porites arnaudi,* variation of skeletal structure in the holotype USNM 100261. Notice diagnostic characters such as polygonal calices and wide walls. a, ×6; b, ×9.

Twelve septa rarely bifurcated (Figs. 5a, b; 6a, b). The triplet normally has free margins, although it can also have the directive and a lateral septum (generally that of the right side) fused in the inner section. Lateral septa arranged in four fused pairs, better developed and longer than the rest, and in its innermost portion presents conspicuous pali that rarely reach the level of the corallite wall. Pali of the triplet and the dorsal directive septa less developed than those of lateral pairs, or may be absent (Fig. 6a, b). One or two denticles per septum, which can resemble small pali because of extensive

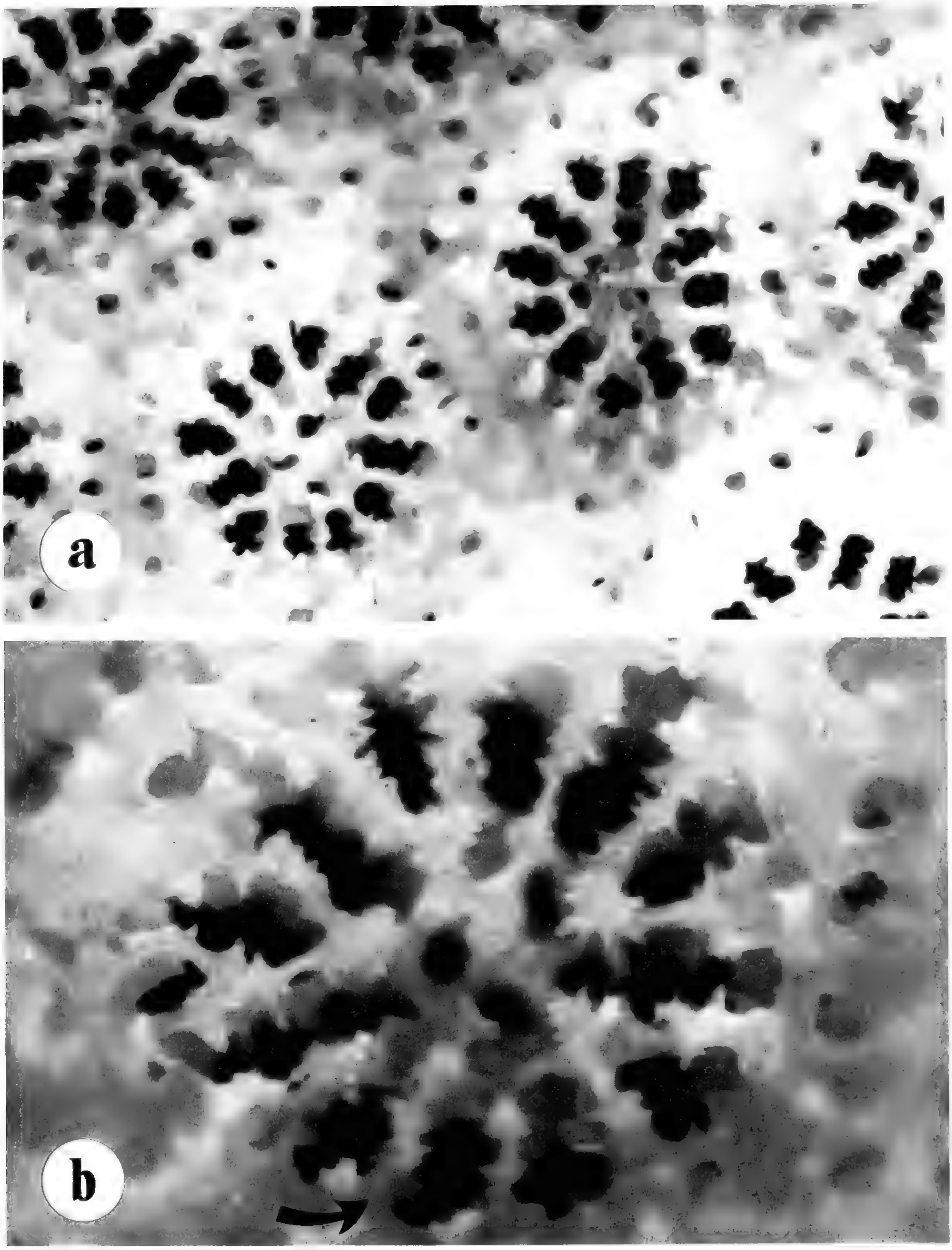

Fig. 5. *Porites arnaudi,* variation of skeletal structure in the holotype USNM 100261. Notice diagnostic characters such as prominent pali, inconspicuous columella, one denticle per septum and free triplet (arrow). a, ×34; b, ×66.

development and their position near the calicular center. Columella quite variable, sometimes appearing as a small column or stylet, may be compressed dorsoventrally, or may be absent. In some, a second prominent protuberance about the same size as the columella may be present near the inner margin of the dorsal directive. Two synapticular rings, the external more defined than the inner palar. Tissue color from greenish-gray to dark brown, with pale margins.

Distribution.—This species was first recorded by Glynn et al. (1996) at Clipperton Atoll (southeast, northeast and southwest

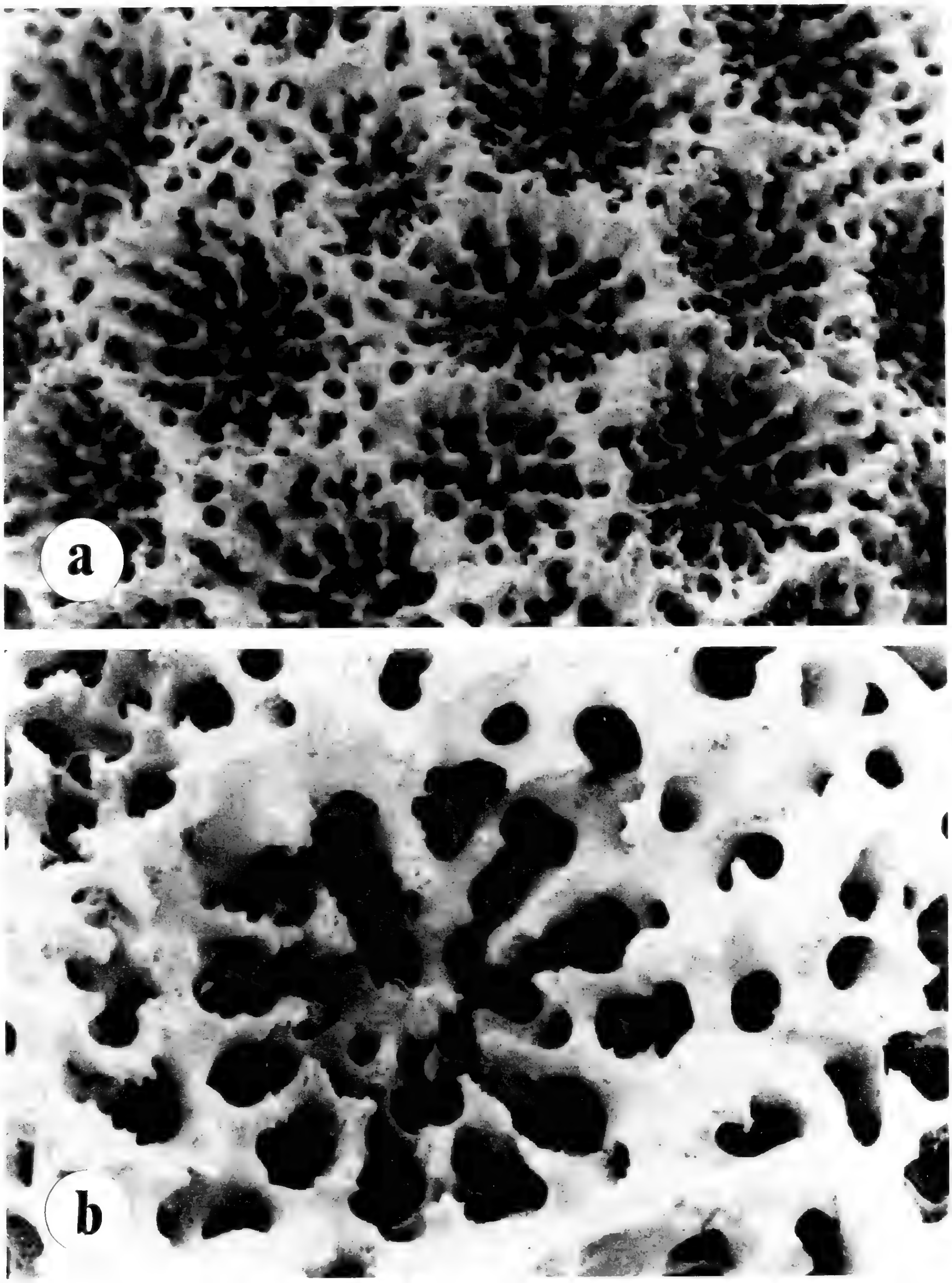

Fig. 6. *Porites arnaudi,* SEM photos of the paratype UMML 8.1475. Recent, 18 m depth, Clipperton Atoll, France. a, group of calices ×16. b, single calice ×38.

sites) and at San Benedicto (19°18′N, 110°48′W) and Clarión islands (18°20′N, 114°44′W), Revillagigedo Archipelago, under the name *Porites* sp. Later, Ketchum & Reyes-Bonilla (1997) confirmed its presence in San Benedicto and Clarión, and also at Socorro Island (18°45′N; 111°00′W), calling it *Porites* sp. 1. However, no exact locations of collection or observation sites were presented in those papers. The holotype (USNM 100261, collected by J. P. Carricart-Ganivet at 30 m depth, 25 Nov 1997) and six other specimens on which the current description is based (UMML 8.1475, collected by P. W. Glynn at 18 m depth, 14–26 Apr 1994; ECOCHBC 0107 collected by A. Medina-Cárcamo at 30 m depth, 25 Nov 1997; MHNUABCS 1581, 1582, 1583 collected by H. Reyes-Bonilla at 21 m depth, 26 Nov 1997) were found in the "Poritid zone" (sensu Glynn et al. 1996), at the northeast seaward slope, Clipperton Atoll. Other coralla of the same species were sampled at Playa Norte and Punta Tosca (Socorro Island; 18°47′25″N, 111°01′15″W, MHNUABCS 1044, collected by J. F. Castellanos-Avila at 14 m depth, 30 Nov 1991), Bahía Azufre (Clarión Island; 18°20′47″N, 114°44′00″W, MHNUABCS 1092, 1100, 1103, collected by J. Ketchum at 7, 7 and 10 m depth, 15 Dec 1994) and Roca Trinidad (San Benedicto Island; 19°18′59″N, 110°49′00″W, MHNUABCS 1076, collected by H. Reyes-Bonilla at 15 m depth, 20 May 1995). As *Porites arnaudi* has not been observed elsewhere in the central Pacific or off American mainland, it is considered to be endemic of the oceanic Revillagigedos and Clipperton islands.

Ecology.—This newly described coral is distributed at depths from 7 to 37 m, especially in steep rocky slopes, and often overgrows adjacent coralla, mostly *Porites lobata* and *Pavona varians* Verrill, 1864 in Clipperton (Glynn et al. 1996) and *P. lobata* and *Psammocora superficialis* Gardiner, 1898 in the Revillagigedos. It is not abundant; Glynn et al. (1996) mentioned that percent live cover was up to 7.4% in the southeast side of Clipperton, while in the Revillagigedos it is seldom found, although it is locally abundant at Playa Norte (Socorro Island), Bahía Azufre (Clarión Island) and Roca Trinidad (San Benedicto Island). Coralla commonly shows bite marks in the outer edges of the plates, most likely produced by *Arothron meleagris* (Bloch & Schneider, 1801) or *Melichthys niger* (Bloch, 1786), both fishes that frequent localities where *Porites arnaudi* has been found (Allen & Robertson 1994, Robertson & Allen 1996). Bioeroders and serpulid polychaetes were rare in colonies of this species observed at Clipperton and practically absent in those collected for this paper. In contrast, they were much more abundant in the Revillagigedos, in particular the bivalves *Lithophaga* spp., which commonly bore the bases of the plates.

Comparison.—Because *Porites arnaudi* has been found in Clipperton and at the Revillagigedo Archipelago, it must first be differentiated from all other conspecifics present in those localities: *P. lobata, P. lutea, P. lichen, P. australiensis* and *P. panamensis* (Ketchum & Reyes-Bonilla 1997, Reyes-Bonilla 1999). The coral here described is similar to *P. lobata,* as noted by Glynn et al. (1996), because both species have thick ledges with an inconspicuous columella, well developed dorsal directive septa and lateral pairs, palus of the dorsal directive septum smaller than those of the laterals, and septa of the triplet always free (Veron & Pichon 1982, Veron 1986; Figs. 5a, b; 6a, b). Notwithstanding, the former can be identified by its plate-like tiered colonies (Figs. 1a, b, 2a, b, 3a–d) which are not massive or hemispherical as in *P. lobata.* Also, it presents a well-defined synapticular ring and different tissue color (gray or brown in *P. arnaudi* and blue, purple or green in *P. lobata*). A third difference is that *P. lobata* has two denticles on each septum, whereas *P. arnaudi* normally has only one (Fig. 6b). *Porites arnaudi* and *P. lutea* differ noticeably because the latter is massive and has columniform lobes, shallow corallites and thin walls. In addition, in *P. lutea,* pali reach the level of the walls, all septa of the triplet are fused by a transverse rod or in their margins (in a "trident"), bifurcate septa often appear and columella is well developed. *Porites arnaudi* can be easily separated from *P. australiensis* because the latter has a large and well-developed columella and pali that reach the level of the wall denticles. Also, in the triplet, the former species has lateral septa about the same size as those of the ventral directive (Figs. 5a, b, 6a, b), while in *P. australiensis* the lateral septa are smaller than those of the ventral directive, and occasionally have fused triplets instead of free ones. The morphology of the corallum is quite different also, as *P. australiensis* (like *P. lobata*) has massive, almost spherical colonies (Veron & Pichon 1982, Veron 1986). *Porites panamensis* can be distinguished from *P. arnaudi* principally because its colonies are very small (never larger than 40 cm height and diameter), encrusting, massive or columnar, and its color is bright green instead of gray or brown. Other differences are that *P. panamensis* has fewer pali (normally five) and thin walls (Squires 1959). *Porites lichen* is another species quite similar to *P. arnaudi,* having six to eight pali and wide walls, one denticle per septum, thick ledges around colony bases, or appearing as laminar plates (Veron & Pichon 1982, Veron 1986). Nevertheless, they can be differentiated on the basis of the corallites of *P. lichen* which have septa of the triplet commonly fused in their margins, while directive dorsal septa of the same structure are shorter than laterals. Also, coralla of this species appear as columnar colonies, and when they occur as laminae, these are thin and develop only in the base of the coralla, a character never presented in *P. arnaudi* (Figs. 1a, b, 2a, b, 3a–d).

Acknowledgments

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A new species of *Heterotella* (Porifera: Hexactinellida: Euplectellidae) from the West Indies

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Abstract.—*Heterotella pomponae,* a new species, is reported from near S. Caicos Is., West Indies. This is only the second described species of the genus and the first from the Atlantic Basin. *Heterotella* was erected by Gray to accommodate *Alcyoncellum corbicula* Bowerbank from Isle de Bourbon (Reunion), southwest Indian Ocean. The genus is distinguished from other Corbitellinae by a microsclere which has controversial interpretation, as either a oxyhexactin with long spines or an oxyhexaster with irregularly originating terminal rays. The two species are distinguished by presence of sigmatocomes in *H. pomponae* and their absence in *H. corbicula.*

The first taxonomically acceptable reference to a sponge now included in the genus *Heterotella* was made by Bowerbank (1867:358), where he clearly referred the earlier published figure of a distinctive microsclere (Bowerbank 1858, 1864) to a specimen labelled *Alcyoncellum corbicula* from Isle de Bourbon in the Paris Museum. The genus *Alcyoncellum* had a very convoluted early history, originally attributed to a calcareous sponge and later considered to be an uncertain synonym of the hexactinellid genera *Euplectella* and *Corbitella.* The status of many of these previously confounded generic names was clarified by Gray (1967), where he erected the genus *Heterotella* to contain only Bowerbank's *A. corbicula.* The two closely related genera, *Corbitella* and *Heterotella,* were later reviewed by Ijima (1902), who described the three then existing specimens of *H. corbicula* from Isle de Bourbon (Reunion) in the Museum National d'Histoire Naturelle, Paris. The earlier figured and still diagnostic microsclere of the genus was considered in some detail. Ijima interpreted the oxy-tipped spicule to be a hexactin with long, irregular spines, but noted that this could alternately be accepted as a oxyhexaster with irregularly arising terminal rays. Kirkpatrick (1910) reviewed the spicule in his attempt to systematize spicule nomenclature, and decided that it was an oxyhexaster since the axial canal did not extend to the ray tip. These distinctions remain arbitrary since there is no method of objectively differentiating spines from terminal rays.

No other *Heterotella* specimens have been added to that type series collected from Reunion in 1819 and 1857. Here I describe the first recent specimen of this genus, collected in 1994 from S. Caicos Island, West Indies. The specimen represents a new species of *Heterotella* and the first member of the genus from a location other than Reunion, Indian Ocean.

Materials and Methods

The specimen of an unidentified lyssacine hexactinellid (the new species described herein) was obtained on loan from Harbor Branch Oceanographic Museum, Fort Pierce, Florida (HBOM). The type series of *H. corbicula* was reviewed during a 1997 visit to the Museum National d'Histoire Naturelle, Paris (MNHN). Fragments of two of the MNHN specimens were returned to Montreal where skeletal preparations were made. Small pieces of dermal and gastral surfaces were either whole-mounted in balsam for light microscopy (LM) or digested in hot nitric acid. Large spicules in the resulting spicule suspensions were rinsed, spread on microscope slides and mounted in balsam. Smaller spicules were dispersed on 25 mm diameter, 0.2 μm pore-size, nitrocellulose filters by filtration; the filters were rinsed, dried and mounted in balsam. Spicules were measured by computer via a microscope-coupled digitizer. Data are reported as: mean ± st. dev.$_{(\text{number})}$ (range). Spicule drawings were prepared from video-captured microscope images imported into a computer drawing program and traced on-screen. Samples for scanning electron microscopy (SEM) were nitric-acid-cleaned and mounted on stubs with epoxy. Following gold-palladium coating, specimens were viewed and photographed with a JEOL JSM-840 SEM.

Systematics

Subphylum Symplasma Reiswig & Mackie, 1983
Class Hexactinellida Schmidt, 1870
Subclass Hexasterophora Schulze, 1886
Order Lyssacinosa Zittel, 1877
Family Euplectellidae Gray, 1867
Subfamily Corbitellinae Ijima, 1902
Genus Heterotella Gray, 1867

Type species.—*Heterotella corbicula* (Bowerbank, 1867).

Diagnosis.—(from Ijima 1902:32 for *H. corbicula,* emended here). Corbitellinae of saccular shape, the lateral walls constricting distally to the margins of a terminal sieve-plate. With numerous, round, irregularly arranged parietal oscula. Skeletal beams unfused or totally fused by synapticula. Principalia parenchymalia as diactins; accessoria as diactins and hexactins. With distinctive microxyhexasters in which the slender terminal rays are irregularly undulating and do not all originate from a single point (often interpreted as microxyhexactins with irregular spines). Floricome and graphiocome present, with or without sigmatocome; discohexaster lacking.

Remarks.—A holotype has not been designated for *H. corbicula* from among the original three specimens in the collections at MNHN. A lectotype is here designated as MNHN HX 23, Ijima's specimen A, the specimen upon which he based his extensive spicule description. The specimen can be identified as consisting of only the top portion of a sponge from Isle de Bourbon donated by Mr. Leschinault, 1819. The two remaining specimens, MNHN HX 24 & 25, Ijima's B and C, thus become paralectotypes. Lectotype designations are made here with the purpose of clarifying the application of the name to a taxon.

Heterotella pomponae, new species
Figs. 1–10, Table 1

Material examined.—Holotype: HBOM 002:00019; 1 km S of S. Caicos Is., 21°28.84′N, 71°29.985′W, 467 m; col. A. Wright via RMS *Johnson SeaLink I,* dive 3788, 31 Oct 1994; in alcohol.

Shape.—Entire specimen with basal disc retrieved; broken during handling. Thin-wall, sac-shaped sponge (Fig. 1), 13 cm tall by 5.5 cm diam, attached to hard substrata by short basal disk supporting a short, rigid basal cup. Wall, 2.3 mm in maximum thickness, perforated by numerous primary parietal oscula passing directly through the wall, diameter 1.7 ± 0.3$_{25}$ mm (1.1–2.1 mm), spaced at 6.4 ± 1.4$_{25}$ mm (3.1–9.0 mm); smaller openings passing obliquely or tortuously through the wall (secondary parietal oscula) have diameter on the dermal side of 1.5 ± 0.7$_{30}$ mm (0.4–2.7 mm, Fig. 2) and on the atrial side 1.0 ± 0.3$_{76}$ mm (0.5–2.0 mm, Fig. 3). Parietal oscula are arranged without apparent pattern. The terminal osculum, 2.3 cm diam is covered by a sieve plate and bordered by a vertical marginal collar.

Surface texture.—Dermal tissue is delicate and subject to detachment by gentle

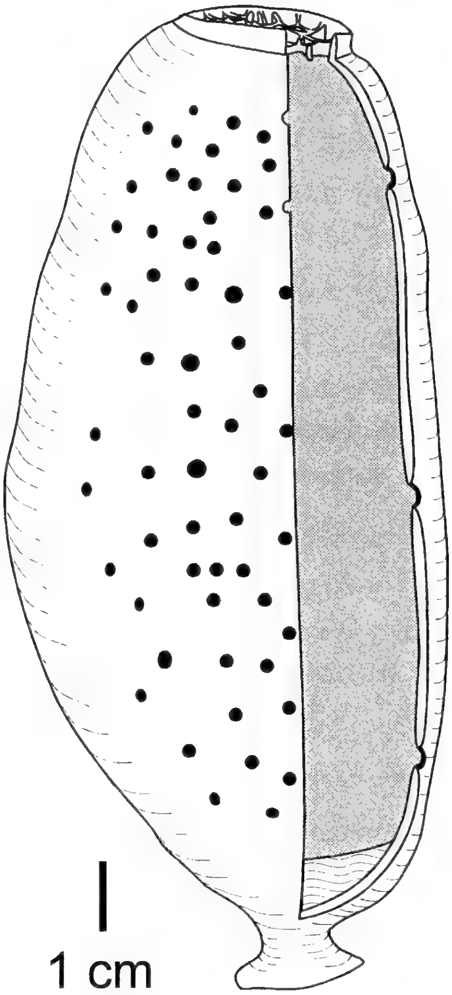


Fig. 1. *Heterotella pomponae* n. sp. (holotype) cut-away diagram reconstructed from photographs, showing distribution of main parietal oscula, terminal sieve plate and location of sinuous diactins in the base of the atrium (wavy filled area).

water currents; gastral tissue is firmer and more adherent to the skeletal framework. Both surfaces are smooth to eye but irregularly lumpy under a dissecting microscope. Prostalia are lacking; the fine tips of sword hexactins projecting from the cushion-like white tissues can be perceived only with aid of a microscope; no regular grid arrangement is detectable on either surface. Living tissues with spicules are not present in the sieve plate or marginal collar; marginalia absent, but may have existed in younger stage.

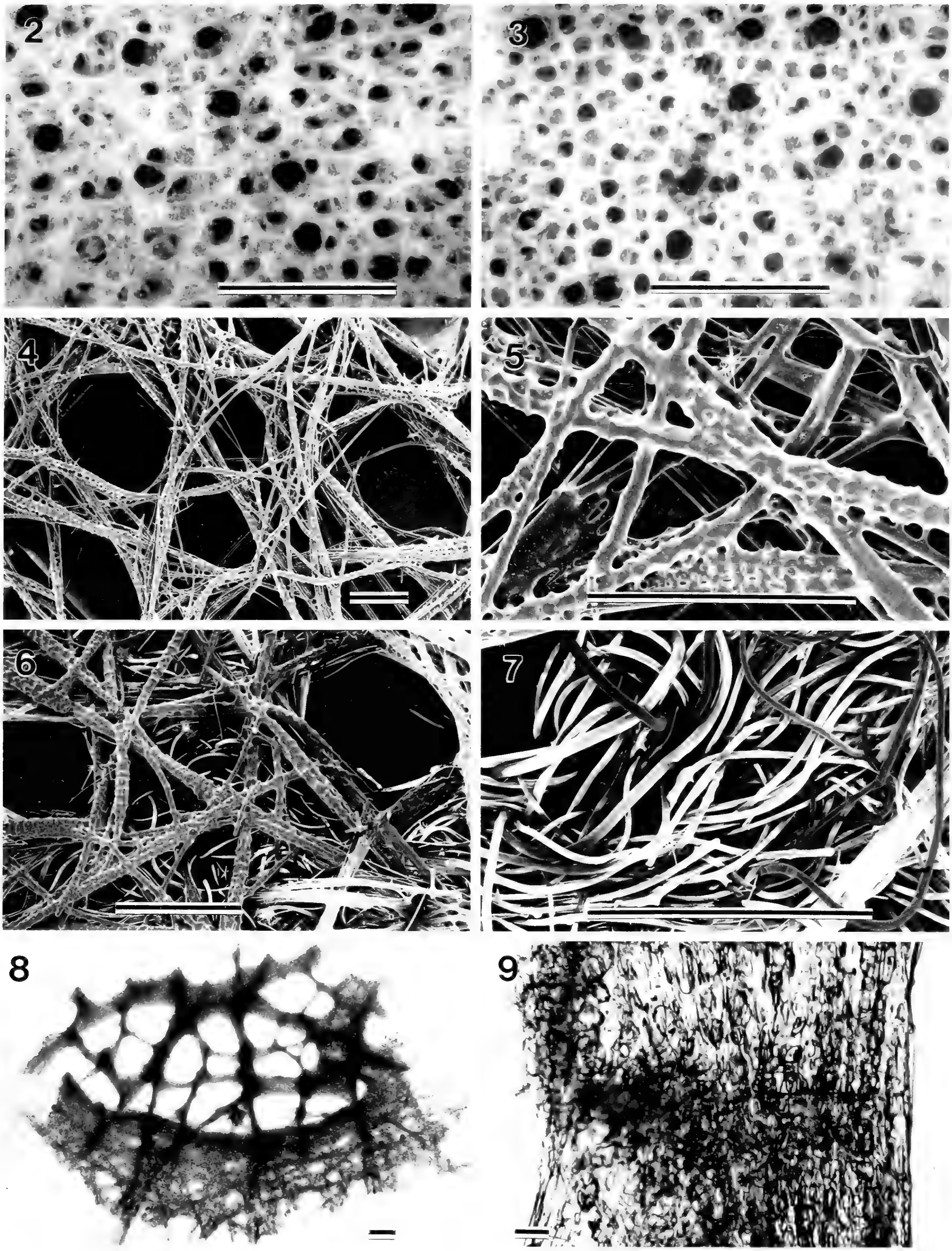
Color.—White in life and preserved in ethanol.

Skeleton.—The entire framework of the holotype (basal cup, lateral walls, sieve plate) has been solidified into a rigid structure by siliceous synapticulae so profuse as to obscure the nature of the primary framework-forming megascleres (Figs. 4–8). These are presumed to be diactins since hexactin nodes have not been found in this structure and diactins are known to be principalia of *H. corbicula.* Major siliceous elements of most of the framework appear randomly oriented (Fig. 4), but the outer layer contains major longitudinal bundles and the inner-most atrial bundles are transversely oriented. The outer-most strands of the framework are nodulated by secondary silicification (Fig. 5) while the middle and internal strands are smooth. Thickness of the framework is $1.6 \pm 0.2_{13}$ mm (1.2–1.9 mm). In the basal region of the body (Fig. 1), a dense matt of sinuous diactins joined by very short synapticulae or point cementation, is deposited on the internal surface of the framework (Fig. 6); this matt nearly fills the mesh spaces (Fig. 7), occludes some parietal oscula and strengthens the basal framework.

Elements of the sieve plate and marginal collar are rigidified and nearly filled to solid sheets by dense synapticulation (Figs. 8, 9). The marginal collar extends up from the body surface $1.9 \pm 0.4_{13}$ mm (1.4–2.4 mm), as a nearly solid sheet of fused, transversely-oriented, siliceous spicules. Major strands of the body framework extend up the inner side of the collar and project out into the oscular plane as sieve beams (Fig. 8). The sieve beams are unusual in their vertical sheet-like form, being taller than wide (septa-like), with beam height: $0.78 \pm 0.4_{25}$ mm (0.2–1.9 mm), width: $0.25 \pm 0.10_{25}$ mm (0.11–0.53 mm). Sieve pores are variable in shape and size (Fig. 9), but are mainly subtriangular with sides $1.5 \pm 0.4_{25}$ mm (0.6–2.3 mm).

Loose spicules.—Diagrams of spicule form and dimensions are summarized in Figure 10 and Table 1.

Megascleres: The major surface spicules of both dermal and gastral surfaces are smooth, sword-shaped hexactins with the short ray projecting from the tissue surface



Figs. 2–9. *Heterotella pomponae* n. sp. (holotype). 2–3. Photographs of dermal (2) and gastral (3) surfaces with tissues, showing differences in aperture distributions; scale equals 1 cm (LM). 4–5. External surface of acid-cleaned, fused framework of upper body wall; scale equals 1 mm (SEM). 6. External surface of basal region with meshes filled with sinuous diactins; scale equals 1 mm (SEM). 7. Internal surface of the cup base covered with dense pad of sinuous diactins; scale equals 1 mm (SEM). 8. Oblique vie of a fragment of the fused marginal collar and sieve plate showing continuity of sieve beams with wall bundles; scale equals 1 mm (LM). 9. Side view of a major sieve plate beam, top surface to left, showing complete fusion of constituent diactins; scale 0.1 mm (LM).

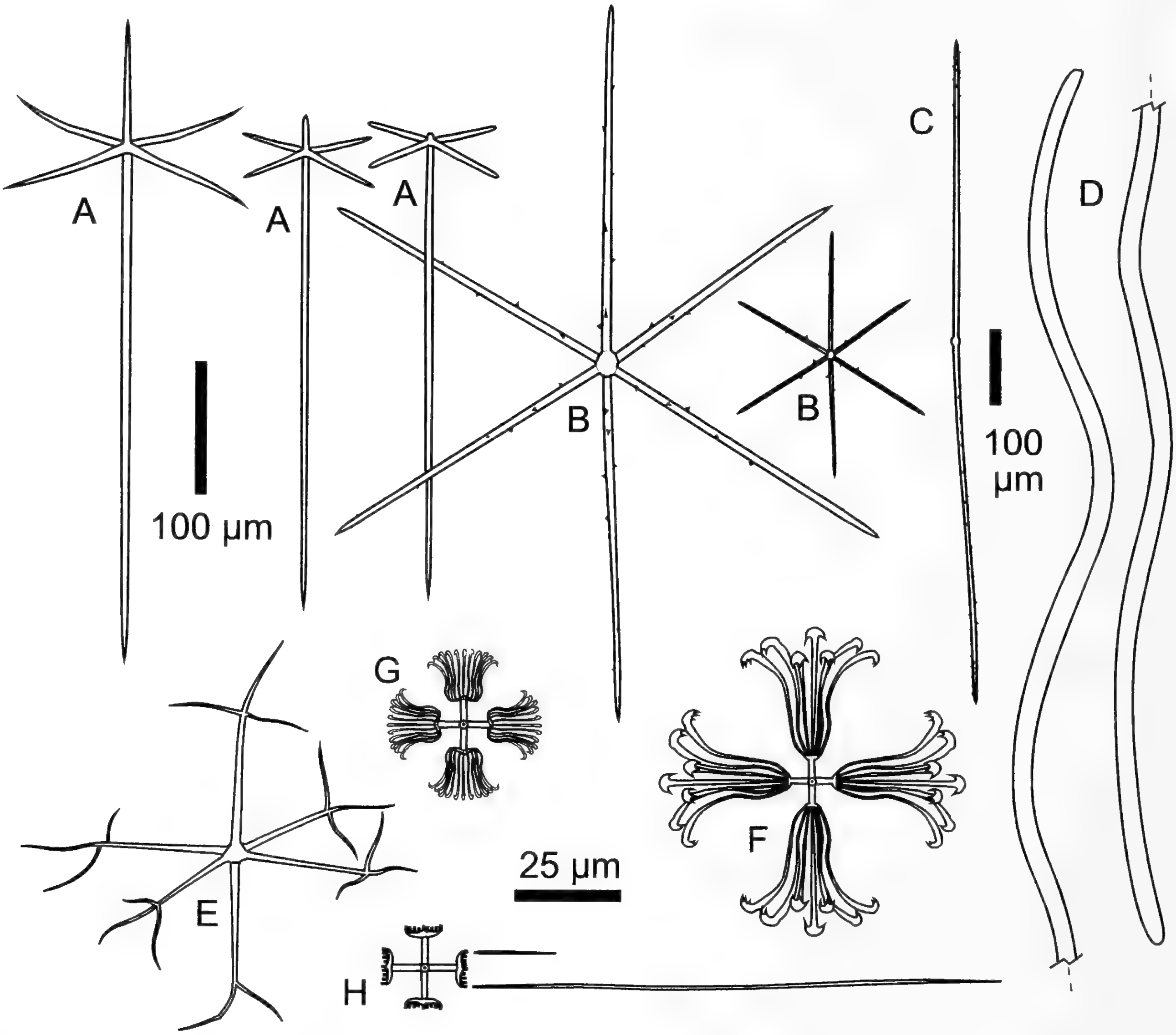


Fig. 10. Loose spicules of *Heterotella pomponae* n. sp. (holotype). A. Superficial dermal and gastral sword hexactins grading to pentactin. B. Choanosomal regular hexactins. C. Centrotylote diactin. D. Ends of sinuous diactins. E. Oxyhexaster. F. Floricome. G. Sigmatocome. H. Graphiocome centrum with long and short terminals (raphides). Scale bars: Left 100 µm bar applies to A, B; right 100 µm bar applies to C, D; 25 µm bar applies to E–H.

(Fig. 10A); a moderate number of pentactins (11%) may result by reduction of the distal ray. These occur in mixtures of thin and thick forms on both surfaces. True marginalia were not found—the marginal collar was devoid of tissues or loose spiculation. Nearly equal-rayed, sparsely-spined hexactins (Fig. 10B) occur throughout the choanosome in small numbers; they vary greatly in size and may consist of two classes, but frequency analysis was not performed. Sparsely-spined, centrotylote diactins with acute tips (Fig. 10C) are abundant throughout the choanosome. Smooth, sinuous diactins with rounded tips (Fig. 10D) pack the lower framework. They occur as fragments up to 6+ mm long in loose spicule preparations, presumably broken from their synapticular connections; loose complete spicules of this class have not been found.

Microscleres: All of the following microscleres, with exception of the short-rayed graphiocome noted below, are found in samples from both surfaces and the choanosome. The most common microsclere is a smooth, sharp-tipped form (Fig. 10E) which can be regarded either as an oxyhexaster with very irregular secondary

Table 1.—Spicule dimensions of *Heterotella pomponae* holotype in μm; SD = standard deviation; *n* = number of measurements.

Spicule type	Length[a] ± SD	Range	N	Width ± SD	Range	*n*
Hexactin, thick sword						
distal ray	43 ± 24	8–101	50	5.4 ± 0.8	4.2–6.7	25
tangential ray	88 ± 15	52–121	50	5.1 ± 0.7	3.9–6.4	25
proximal ray	507 ± 96	335–730	50	5.3 ± 0.7	4.3–6.7	25
Hexactin, thin sword						
distal ray	90 ± 17	35–118	50	3.5 ± 0.9	2.0–5.6	25
tangential ray	106 ± 18	67–141	50	3.3 ± 0.6	2.7–4.8	25
proximal ray	306 ± 77	171–541	50	3.5 ± 0.7	2.6–5.6	25
Hexactin, regular ray	151 ± 81	64–318	50	3.7 ± 0.9	2.0–5.9	50
Diactin, centrotylote	869 ± 257	320–1963	50	7.2 ± 2.1	3.8–12.3	50
Diactin, sinuous	—	—	—	23.1 ± 6.3	9.1–40.2	50
Oxyhexaster radius	50.5 ± 6.8	37.3–71.5	100	2.0 ± 0.4	1.1–2.7	25
oxyhexaster secondary ray	18.8 ± 4.5	5.8–28.7	100	1.2 ± 0.3	0.6–1.7	25
Floricome radius	35.1 ± 4.1	21.6–44.6	357	5.4 ± 1.0[b]	3.4–7.4	25
floricome centrum radius	7.2 ± 0.8	5.4–9.0	100	1.7 ± 0.3	1.1–2.5	25
Sigmatocome radius	17.1 ± 1.5	13.3–20.5	100	0.6 ± 0.2[b]	0.2–1.0	25
sigmatocome centrum radius	6.8 ± 0.8	5.1–9.5	100	1.1 ± 0.3	0.6–1.6	25
Graphiocome centrum radius	8.2 ± 0.9	6.3–11.1	100	1.3 ± 0.3	0.9–1.9	25
graphiocome long secondary ray	86 ± 9	63–151	100	0.9 ± 0.2	0.6–1.2	25
graphiocome short secondary ray	14.9 ± 1.8	11.6–21.9	100	0.6 ± 0.1	0.4–0.9	25

[a] Radius for microscleres, [b] Width of terminal flange.

rays (preferred here) or an oxyhexactin with long spines. The secondary rays (or spines) number 1–4, most commonly 3, and emanate from an elongate swelling at their junction. About 10% of these are without secondary rays but bear the swelling seen in the astrose form. A typical floricome (Fig. 10F) with usually 7 (6–9) terminal rays, bearing 3–5 claws on the terminal flange, is common. Although these occur in a wide size range, frequency analysis indicates these compose a single class. An uncommonly occurring sigmatocome (Fig. 10G) bears 25–35 sigmoid terminals, uniform in length, from a single marginal whorl on each recurved primary capitulum. Graphiocome centra, with stumps of 30–50 terminal attachments scattered across the face of each discoid capitulum, (Fig. 10H) are uncommon. The presumed raphide-like, long terminal rays are common on filters from all tissues, but the short versions are found only in gastral tissues. Intact graphiocomes have not been encountered.

Etymology.—This species is named to honour Dr. Shirley Pomponi in recognition of her many years of invaluable contributions to the knowledge of tropical marine biodiversity.

Remarks.—The vary large number of shared characters between the new species and *H. corbicula* leaves little doubt that the new the West Indian form belongs to *Heterotella.* Most of the differences between the two species can be attributed to their different stages of maturation. Only specimen B of *H. corbicula* exhibits incipient spicule fusion in its lower portion, while the *H. pomponae* specimen has completely fused its lyssacine net into a rigid framework. The absence of free large choanosomal diactins and marginalia in *H. pomponae* are attributable to this terminal growth stage, where further body extension (growth) has ceased. Surface megascleres and microscleres are almost identical in form and size in both species. The dermalia are thicker (to 30 μm) and the accessory diactins longer (to 5 mm) in *H. corbicula* than in *H. pomponae* (to 6.7 μm and 2 mm respectively). The distinctive oxyhexasters (oxyhexactins) are virtually identical in the two species. The most unambiguous difference between the two is the presence of sigmatocomes in *H. pomponae* and their absence in *H. corbicula,* confirmed by examination of new spicule preparations of Ijima's specimen A (the lectotype) and B (the nearly intact paralectotype) using filter techniques. Photographic records at HBOM suggest that *H. pomponae* is moderately common in the West Indian area. Younger specimens with incompletely fused skeletal networks are expected to be found in future collections.

Acknowledgments

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